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Energy Profile and the Locomotor Pattern of Trotting on an Inclined Treadmill

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ABSTRACT. A total of 152 healthy Standardbred trotters were exercised on a treadmill. Heart rate (HR), oxygen uptake ($\dot{V}O_2$) and blood lactate (LA) responses to exercise were expressed as treadmill velocity (V_{200}) and oxygen uptake ($\dot{V}O_2$-200) at HR=200 bpm and velocity at LA=4 mmol l^{-1} (V_{LA4}). Locomotion pattern was studied as stride length (SL_{200}) and stride frequency (SF_{200}) at V_{200}. Total red cell volume (CV) was measured immediately after exercise. Muscle biopsies from gluteus medius were used for analysis of fibre types and activities of the enzymes citrate synthase (CS), lactate dehydrogenase (LDH) and 3-hydroxy-acyl-CoA dehydrogenase (HAD). Stride length and stride frequency were both closely related to treadmill velocity, but, V_{200} was more dependent on SL_{200} (r=0.89) than on SF_{200} (r=0.48). V_{200} correlated with CV/BW (r=0.87), $\dot{V}O_2$–200/BW (r=0.68) and V_{LA4} (r=0.63) due mainly to significant dependencies of SL_{200} on the same markers for aerobic potential (r=0.79, 0.69 and 0.64, respectively) whereas SF_{200} correlated only with CV/BW (r=0.38). Similarly, SL_{200} was related with percentages of types I (r=0.43) and IIA fibres (r=0.64) and inversely with type IIB (r=−0.78), whereas SF_{200} was correlated only with type IIA (r=0.43). LDH correlated with V_{200} (r=−0.73), SL_{200} (r=−0.73) and SF_{200} (r=−0.38) whereas CS and HAD showed no relationships. It was concluded that during treadmill trotting at the anaerobic threshold, stride length seemed to be the primary determinant of both velocity and aerobic energy expenditure. Therefore, locomotion pattern may depend in part on both cardiorespiratory capacity and muscle metabolic profile in the Standardbred horse.

Key words Horses; oxygen uptake; heart rate; blood lactate; stride length; stride frequency

INTRODUCTION

The running speed of the horse and all other animals is a product of stride length (SL) and stride frequency (SF). Both these gait characteristics are dependent on a number of factors which effectively limit the performance potential of the race horse. Speed at the gallop is largely independent of SF which increases about 10% when speed is doubled.[11] Thus, SL is the primary determinant for acceleration. Elite pacers appear to have a greater range of limb motion and longer stride than less successful performers[24] and at near maximal speed a further increase in speed is achieved by an increase in SL.[25]

Many markers for aerobic potential, oxygen transport capacity and muscle metabolic properties have been used to assess racing potential, but information on the relationships between these and the locomotion pattern is limited. It is known that the efficiency of energy utilization is involved with the choice of gait,[13] but whether the co-ordination of SL and SF, regardless of gait, is important for the energetics of locomotion in the horse is unknown. The energy expended per kg bodyweight to sustain a constant speed is directly proportional to the SF.[11] However, the propulsive forces of the muscles act when the feet are in contact with the ground so the ability of the horse to propel itself forwards should be dependent on the

stance phase duration, and, therefore, proportional to the SL.

The aim of this project was to investigate the energy cost of locomotion and relationship between gait pattern and energy expenditure during trotting exercise on an inclined treadmill. In order to make energy expenditure comparable and measurable the horses were studied at a work load approximately equivalent to the lactate threshold (i.e. the work performed was a steady state, near maximal, predominantly aerobic one). The specific objectives of this study were to assess the relative importances of SL versus SF in keeping pace with treadmill speed at a slope and in utilizing energy at a work load approximating the lactate threshold, i.e. the work load at the onset of blood lactate accumulation which occurs, as an average, at a heart rate (HR) of 200 bpm in the horse.[18]

MATERIALS AND METHODS

Horses. The study was carried out retrospectively using material presented previously.[19] A total of 152 Standardbred trotters considered to be normal with respect to exercise tolerance were used. They showed no signs of disease likely to affect work capacity and were performing satisfactorily on the track as judged by their trainers. The state of training varied, but most horses were training and racing regularly. Some were former racehorses that had been out of regular training for several years.

In 110 horses trotting SL and SF were determined together with red cell volume (CV), HR and blood lactate (LA) responses to an incremental treadmill exercise. The sex and age of the horses are shown in Table 1. They ranged in age between 2 and 18 years (5.1 ± 3.1). Oxygen uptake ($\dot{V}O_2$) during exercise was measured in 50 of these horses (age = 5.3 ± 3.7 years) and muscle biopsies for histochemical and biochemical analyses were performed on 30 animals (age = 4.3 ± 2.4 years).

Treadmill exercise tests. Two methods of exercise testing on a high speed treadmill (Sikob, Stockholm) inclined at 6.25% (3.5°) were used. The first (SET) was a standardized incremental exercise test comprising 4 increments of treadmill velocity.[18] The second (MET) incorporated the use of a respiratory mask to determine $\dot{V}O_2$ and was performed within a week of SET. In the SET protocol HR was monitored continuously by a bipolar ECG lead (Mingograph 804, Siemens-Elema, Stockholm) and recorded during the last 15 s at each speed. HR response to exercise was expressed as the treadmill velocity (V) producing HR = 200 bpm (V_{200}, m s^{-1}) extrapolated from the linear HR/V relationship. This was considered to reflect the cardiac performance at the lactate threshold.[18] Stride frequency was determined by counting the number of steps of one forelimb over time towards the end of each speed and SL was calculated from treadmill velocity and SF. Being linear, the relationships between V and both SL and SF were expressed corresponding to V_{200} by extrapolation as SL_{200} and SF_{200}, respectively. SL and SF measured at 9 m s^{-1} (SL_9 and SF_9, respectively) either directly or by extrapolation in those few horses which were not able to follow that treadmill speed. Power output in Watts at V_{200} (W_{200}) was calculated as: body weight (BW, kg) × V_{200} × 60 × sin of treadmill angle × 6.12^{-1}.[6,14]

Venous blood was sampled from a jugular catheter during the last 15 s at each speed. In the majority of the heparinized blood samples blood lactate concentration (mmol l^{-1}) was determined enzymatically (Boehringer, Test combination No. 12482), but, in a number of horses the plasma lactate was determined using an Analox GM7 analyzer® (Analox Instruments Ltd, London, UK) and recalculated as blood lactate using the regression between plasma and blood lactate concentrations used in our laboratory (blood lactate = plasma lactate · 0.55 + 0.74). The treadmill velocity causing LA = 4 mmol l^{-1} (V_{LA4}, m s^{-1}), approximately corresponding to the lactate threshold in the horse,[18] was extrapolated from the exponential LA/V relationship. The test protocol also included

determination of CV. The total blood volume was calculated from the Evans blue dye space and the post-exercise hematocrit as previously described[17] and CV was derived from the difference between the total blood and plasma volumes.

In the MET protocol VO_2 was determined at each work level using an open circuit technique with collection of the expired air from a mask with one-way valves and covering the entire muzzle of the horse.[4] Respiratory minute volume, measured by a flow meter (GD-100, Fluid Inventor AB, Stockholm), and expired oxygen and carbon dioxide concentrations, determined by mass spectrometry (Centronic 200 MGA, Kjellbergs Successors AB, Stockholm), were recorded continuously. VO_2 was calculated from expired air flow and difference in oxygen concentration between inspired and expired air during the last 15 s of each work level of 2 min duration using standard equations.[1] Values were corrected to STPD (Standard temperature and pressure, dry).

Muscle biopsies. Muscle biopsies were taken from m. gluteus at a depth of 4 to 6 cm. One piece for biochemical analysis was immediately frozen in liquid N_2, while the other piece for histochemical analysis was rolled in talcum powder before being frozen in liquid N_2. Both pieces were stored at $-80°C$ until analysed.

Serial sections of 10 μm were cut for histochemical analysis in a cryostat at $-20°C$ and stained for myofibrillar ATPase after both acid (pH 4.3 and 4.6) and alkaline (pH 10.3) pre-incubations to identify type I, II A and II B fibres.[5]

Enzyme analyses were performed on muscle tissue freeze-dried and dissected free from fat, blood and connective tissue. The muscle tissue (1–2 mg) was homogenised in ice cold 0.1 M phosphate buffer (pH 7.3) with an ultrasound disintegrator. The activities of citrate synthase (CS) 3-OH-acyl CoA dehydrogenase (HAD) and lactate dehydrogenase (LDH) were analysed at 25°C using fluorimetric methods.[5]

Statistical analyses. Statistical calculations were carried out by standard methods. Correlation analysis and ANOVA were done with a computer and the SAS® program.[21] The results are presented as correlation coefficients and mean values and standard deviations (SD) unless otherwise indicated. $p<0.05$ was considered statistically significant.

RESULTS

Both SL and SF were independent of gender at the same treadmill velocity (SL_9 and SF_9, respectively) in spite of differences in BW (Table 1). The velocity producing HR = 200 bpm (V_{200}) differed between mares and geldings. This was due to differences in SL_{200}, although marginally dependent on BW ($r=0.22$; $p<0.05$, Table 2). The work rate performed with HR = 200 bpm (W_{200}) was significantly higher both in stallions and geldings than in mares. Age had a significant influence on SL_{200} and SF_{200} (Table 2, Figs. 1 and 2) whereas SL_9 and SF_9 were independent of age. At a mean treadmill velocity of 8.45 m s^{-1} (V_{200}) SL ranged between 3.24 and 5.32 m and SF between 104 and 134 strides min^{-1}.

Mean values, interindividual variations and numbers of determinations of all variables reflecting the energy metabolic profile are exhibited in Table 3. Missed data accounted for the deviations from group numbers with respect to lactate and muscle biopsy data.

Both SL_{200} and SF_{200} correlated significantly with V_{200} (Figs. 3 and 4). The relationship was markedly more pronounced for SL_{200} ($r=0.89$), than for SF_{200} ($r=0.48$) (Table 2).

The calculated power output at V_{200} (W_{200}), which correlated significantly with CV ($r=0.92$) and V_{LA4} ($r=0.50$), was primarily associated with SL_{200} ($r=0.78$) as compared with SF_{200} ($r=0.28$). A significant dependency of V_{200} on CV/BW was also evident, apparently mainly due to a relationship between SL_{200} and CV/BW ($r=0.79$) as the correlation between SF_{200} and CV/BW

Table 1. *Sex and age distributions of body weight (BW, kg), treadmill velocity causing heart rate = 200 bpm (V_{200}, m s^{-1}), work rate at V_{200} (W_{200}, Watt), stride length at V_{200} (SL_{200}, m), stride frequency at V_{200} (SF_{200} min^{-1}), stride length at 9 m s^{-1} (SL_9, m), and stride frequency at 9 ms^{-1} (SF_9 min^{-1})*

	Age	BW	W_{200}	V_{200}	SL_{200}	SF_{200}	SL_9	SF_9
♀, $n=39$								
$\bar{X}$	3.9	417	2 031	8.13	4.14	117.7	4.49	120.9
SD	1.2	40	291	0.79	0.34	5.6	0.22	5.7
(♂), $n=30$								
$\bar{X}$	7.7[a]	445[a]	2 350[a]	8.84[a]	4.47[a]	118.9	4.55	119.2
SD	4.2	33	223	0.69	0.37	5.2	0.21	5.7
♂, $n=41$								
$\bar{X}$	4.4	444[a]	2 251[a]	8.48	4.33[a]	117.2	4.55	119.6
SD	2.2	28	323	1.05	0.47	6.6	0.20	5.5

[a] Significant difference from mares.

was weaker ($r=0.38$), although still significant. The relationship between V_{200} and V_{LA4} also appeared to be due to a correlation between SL_{200} and V_{LA4} ($r=0.64$) as SF_{200} was independent of V_{LA4} ($r=0.13$), whereas the blood lactate level at V_{200} (LA_{200}) appeared to be dependent on SF_{200}. Both SL_9 and SF_9 were correlated significantly with the markers for the blood lactate response to exercise. These relationships were weak with correlation coefficients ranging between 0.20 and 0.25. Although significant, the influence of BW on SL_{200} ($r=0.22$), SL_9 ($r=0.20$) and SF_9 ($r=0.20$) was slight. The extrapolated oxygen uptake at V_{200} ($\dot{V}O_2$-200) correlated significantly with V_{200} (Table 2). This relationship was due to relation with SL_{200} whereas no association with SF_{200} could be detected.

V_{200} was significantly correlated to the percentage of type IIA fibres and inversely on the percentage of IIB fibres (Table 4). These relationships corresponded to relations with SL_{200} which also showed an association with the percentage of type I fibres, whereas SF_{200} only correlated significantly with the percentage of the type IIA fibres. While the muscle enzyme activities of CS and HAD did not correlate with neither treadmill speed nor gait pattern at HR 200 there were significant inverse relationships between both V_{200} and the gait pattern variables and the LDH activity. The dependency of SL_{200} on LDH was more pronounced,

Table 2. *Speed and locomotion pattern interrelationships*

Abbreviations as in Table 3. Degrees of significances: * $p<0.05$, ** $p<0.01$, *** $p<0.001$

	Age	BW	V_{200}	W_{200}	CV/BW	V_{LA4}	LA_{200}	$\dot{V}O_2$-200
V_{200}	0.38***	0.13	–	0.82***	0.87***	0.63***	0.26**	0.68***
SL_{200}	0.30**	0.22*	0.89***	0.78***	0.79***	0.64***	0.13	0.69***
SF_{200}	0.23*	−0.13	0.48***	0.28**	0.38***	0.13	0.33***	0.10
N	110	110	110	110	110	108	109	50

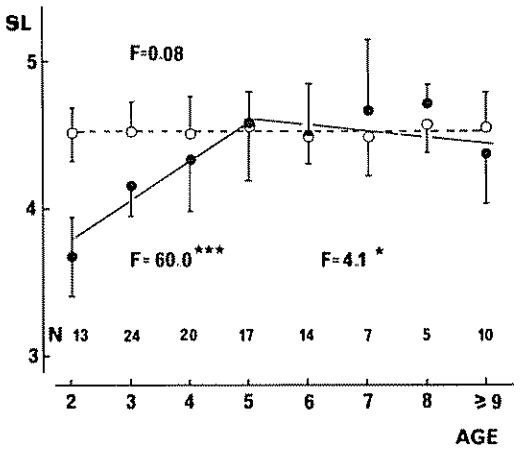

Fig. 1. Stride length (SL, m) dependency on age. Broken line and open symbols denote SL at 9 m s^{-1} (SL_9), means ± SD and continuous lines and closed symbols denote SL at the treadmill velocity causing heart rate = 200 bpm. Top F value refers to SL_9 dependency on age and low F values refer to SL_{200} dependency on age before and after 5 years of age. N = number of horses.

however, than that of SF_{200}. Neither SL_9 nor SF_9 was dependent on any of these muscle variables.

DISCUSSION

As the speed of locomotion is the product of SL and SF a change in one of these variables

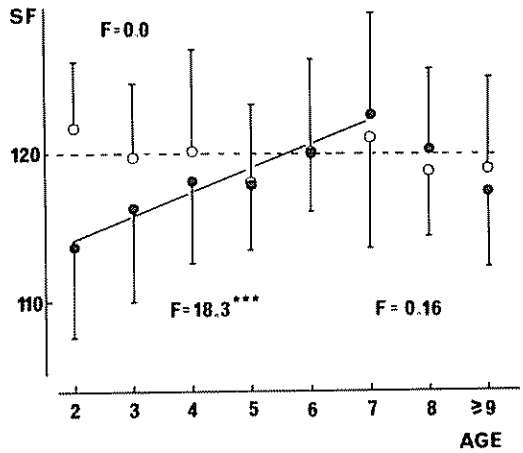

Fig. 2. Stride frequency (SF, strides min^{-1}) dependency on age. Lines and symbols as in Fig. 1.

Table 3. *Mean values ± SD and ranges for body weight (BW, kg), total red cell volume (CV/BW, ml kg^{-1}), treadmill velocity with heart rate = 200 bpm (V_{200}, m s^{-1}), oxygen uptake at V_{200} $\dot{V}O_2$-200, l min^{-1}), work rate at V_{200} (W_{200}, Watt), treadmill velocity causing a blood lactate of 4 mmol l^{-1} (V_{LA4}, m s^{-1}) blood lactate at V_{200} (LA_{200}, mmol l^{-1}), percentages of fibre types (I, IIA, IIB) and muscle enzyme activities μmol g^{-1} min^{-1} of citrate synthase (CS), 3-OH-acyl-CoA dehydrogenase (HAD), and lactate dehydrogenase (LDH). N = number of horses*

	N	Mean	SD	Min	Max
BW	110	435	36	337	520
CV/BW	110	69.7	10.8	43.0	92.0
V_{200}	110	8.45	0.91	5.84	10.52
$\dot{V}O_2$-200	50	47.7	7.8	29.4	66.6
W_{200}	110	2 200	314	1 239	2 783
V_{LA4}	108	8.74	1.20	5.66	12.12
LA_{200}	109	3.92	1.45	0.98	8.06
I	29	15.5	5.6	8	28
IIA	29	47.4	7.9	33	63
IIB	29	35.9	9.7	15	54
CS	30	47.4	13.9	14	78
HAD	30	24.4	5.2	16	34
LDH	30	1 170	352	573	1 675

at a given speed will inevitably result in a reciprocal change in the other. It has been demonstrated that both man and horse generally tend to adjust the gait pattern to optimize energy expenditure in unrestricted running at a given speed.[2,12,13] Consequently, the combination of SL and SF in adjustment to the treadmill velocity apears to be a compromise which is determined by the energy cost.

The principal findings in this study were that the adjustment to the treadmill speed, which approximately corresponded to the individual lactate threshold (cf. V_{200}), was mainly dependent on SL and that this gait variable at the trot primarily was associated with the markers for cardiovascular fitness and energy metabolism. Comparisons of the

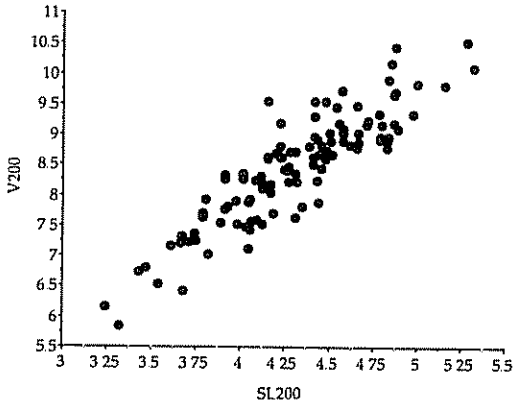

Fig 3 Stride length (SL_{200}, m) vs treadmill velocity (V_{200}, m s^{-1}) at heart rate 200 bpm

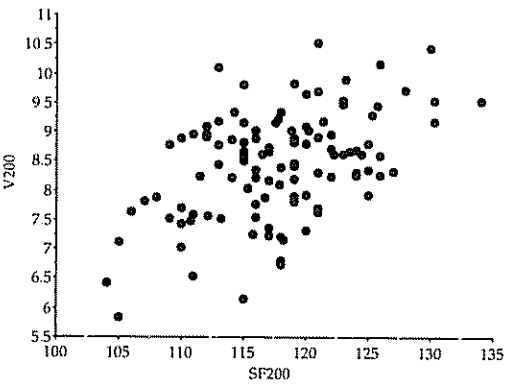

Fig 4 Stride frequency (SF_{200}, strides min^{-1}) vs treadmill velocity (V_{200}, m s^{-1}) at heart rate 200 bpm

horses when they performed at the same speed (9 m s^{-1}) revealed only low grade or lack of relationships with the markers for the energy metabolic potential used in this study. This could be expected as, although varying greatly in fitness and performance potential, the horses showed a remarkably small range of variation in SL_9 (4.07–5.05 m) in comparison with SL_{200} (3.24–5.32 m), the SD of the latter being twice that of SL_9. The SL was only marginally associated with body size expressed as BW which is in agreement with the opinion of Wilson et al.[25] that, although to some extent related to the size of the animal, the variation of SL and SF for a given pacing speed is mainly associated with the pacing technique. Studied on a wide range of body sizes in various animal species, however, the SF at the trot/gallop transition point is a function of body mass.[10]

The observation that V_{200} depended primarily on SL_{200} is in accordance with previous reports stating that in pacers an increase in speed on the track is achieved by an increase in SL (i.e. at each speed the fast horses use long strides) and SL is correlated to the speed whereas SF is not.[24,25] In man, acceleration is also attained by increased SL on the treadmill.[12] While in a number of quadruped species, ranging in body size from 30 g mice to 200 kg horses, SF increased nearly linearly with increasing speed on a treadmill during a trot, the galloping frequency was nearly independent of speed.[11]

The mean treadmill speed causing HR = 200 bpm in this study (8.45 m s^{-1}) is approximately equivalent to 66% of the average normal racing speed performed by trotters on a track, whereas the SL_{200} averaged at

Table 4 *Speed and locomotion pattern relationships with muscle fibre types and enzyme activities*

Abbreviations as in Tables 2 and 3

	I	II*A*	II*B*	CS	HAD	LDH
V_{200}	0.29	0.69***	−0.75***	0.24	0.16	−0.73***
SL_{200}	0.43*	0.64***	−0.78***	0.27	0.17	−0.73***
SF_{200}	0.05	0.43*	−0.34	0.07	0.14	−0.38*

76 and 66% in comparison with trotters and pacers, respectively.[3,24,25] Thus, the V_{200} on the inclined treadmill is well below the trot-/gallop transition point which corresponds to the maximum sustained SF.[10]

The mean power output at V_{200} in Watts ($W_{200}=2200\pm314$) amounts to only 50–57% of the maximal values found in untrained and trained Thoroughbreds galloping on a treadmill[7] or to 58% of treadmill exercise values measured on Standardbreds at $\dot{V}O_2max$.[9] This is somewhat unexpected as the oxygen cost at this work level was relatively higher (i.e. 75% of VO_2max). This discrepancy presumably mirrors the energy cost of breathing and heat production. This may partially explain the unexpectedly low W_{200} relative to the predicted maximum value.

The oxygen consumption at V_{200} in this study (110 ml kg^{-1} min^{-1}) compares favourably with that reported for Standardbred geldings (102 ml kg^{-1} min^{-1})[8] and for Thoroughbreds varying in age between 1 and 4 years (84–127 ml kg^{-1})[20] considering that the Thoroughbred has a higher aerobic potential than the Standardbred as reflected by a larger CV.[17] The $\dot{V}O_2$-200 amounts to approximately 75–80% of $\dot{V}O_2max$ reported for both Standardbreds and Thoroughbreds.[7,8,15,20] The energy cost of horizontal treadmill exercise depends mainly on the cost of supporting the BW during the stance phase and the force needed to move the limbs and is less than running along the ground which also includes the cost of transport.[16,18,22] Inclining the treadmill adds to the oxygen cost in proportion to the degree of elevation.[4] Consequently, direct comparisons between different studies of cost efficiency of treadmill and track running are usually not feasible.

Evidently SL is the main determinant of the aerobic energy consumption during trotting on the inclined treadmill with a work rate corresponding to the lactate threshold. This seems to be a valid presumption as all markers for oxygen transport capacity and utilization used in this study were exclusively or primarily correlated with SL_{200}. Thus, the variables CV, V_{200}, V_{LA4} and $\dot{V}O_2$-200 have been suggested to reflect the aerobic potential[17,18] and this concept has, with the exception of CV, been corroborated recently.[20] The muscle fibre distribution apparently being associated with long strides at V_{200} seems to suggest that longer strides are primarily achieved by recruitment of type II A fibres which are dependent on aerobic energy release.[23] The lack of correlation between SL_{200} and the enzyme markers for aerobic metabolism CS and HAD may seem to contradict this view, but, they were associated neither with V_{200} nor with SF_{200}. Furthermore, the muscle enzyme LDH which is generally used as a marker for the glycolytic capacity[23] was inversely correlated with both V_{200} and SL_{200} and less so with SF_{200} suggesting that the SL_{200} was not limited by the rate of glycolysis. Consequently, the lactate threshold (V_{LA4}) being positively correlated with SL_{200} would mean a lower lactate accumulation during this standardized submaximal exercise test. This again may indicate that the locomotion pattern preferred by the horse to follow the treadmill speed (i.e. increment of the SL) is primarily attained with recruitment of the aerobic type II A fibres. While training of horses eventually leads to increased aerobic capacity regardless of training regimen little is known of the effects of training on the locomotion pattern of the Standardbred trotter. The fact that one particular training effect is a conversion of II B fibres into II A[5] seems to indicate that longer strides may be facilitated which could imply an improvement in racing performance.[11,24] Although, there was a significant increase of SL_{200} with age this relationship was valid only up to 5 years of age (Fig. 1) and was present for SF_{200} as well (Fig. 2). It is also tempting to speculate whether adjustment to changes in speed made by increased SF is dependent more on recruitment of type II B fibres as SF_{200} was significantly correlated with LA_{200} which SL_{200} was not.

In conclusion, at inclined treadmill trotting approximately corresponding to the lac-

tate threshold Standardbred horses seem to rely preferentially on SL to keep pace with the treadmill. The work rate being predominantly aerobic at this threshold, only markers for aerobic potential were found to be positively related with the work output. It appeared that SL may be the primary determinant for the energy expenditure for trotting at or near the lactate threshold and, consequently, that locomotion pattern may be partly dependent both on the oxygen transport capacity and on the muscle metabolic profile in the Standardbred horse.

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REFERENCES

1 Åstrand, P O and Rodahl, K (1986). *Textbook of Work Physiology*. 3rd ed., McGraw-Hill, New York
2 Cavanagh, P R and Williams, K R (1982) The effect of stride length variation on oxygen uptake during distance running Med Sci Sports Exerc 14, 30–35
3 Dalin, G and Jeffcott, L B (1985) Locomotion and gait analysis *In*: R J Rose (ed.): *Exercise Physiology*, Vet Clinic North Am, Equine Practice, W B Saunders, Philadelphia, pp 549–572
4 Essén, B, Lindholm, A, Persson, S G B and Thornton, J R (1978) Experimental procedures for the evaluation of exercise capability in the horse Proc Meeting Acad Soc Large Animal Med, Berne
5 Essén, B, Lindholm, A and Thornton, J R (1980). Histochemical properties of muscle fibre types and enzyme activities in skeletal muscle of Standardbred trotters of different ages Equine Vet J 12, 174–180
6 Evans, D L and Rose, R J (1988) Cardiovascular and respiratory responses in Thoroughbred horses during treadmill exercise. J Exp Biol 134, 397–408
7 Evans, D L and Rose, R J (1988) Cardiovascular and respiratory responses to submaximal exercise training in the Thoroughbred horse Pflügers Arch 411, 316–321
8 Evans, D L and Rose, R J (1988). Determination and repeatability of maximum oxygen uptake and other cardiorespiratory measurements in the exercising horse Equine Vet J, 20, 94–98
9 Evans, D L and Rose, R J (1988) Dynamics of cardiorespiratory function in Standardbred horses during different intensities of constant-load exercise J Comp Physiol B, 157, 791–799
10 Heglund, N C, Taylor, C R and McMahon, T A (1974) Scaling stride frequency and gait to animal size: mice to horses Science 186, 1112–1113
11 Heglund, N C and Taylor, C R (1988) Speed, stride frequency and energy cost per stride: How do they change with body size and gait? J Exp Biol 138, 301–318
12 Högberg, P (1952) Length of stride, stride frequency, "flight" period and maximum distance between the feet during running with different speeds Arbeitsphysiol 14, 431–436
13 Hoyt, D F and Taylor, C R (1981) Gait and the energetics of locomotion in horses Nature 292, 239–240
14 Jones, N L and Campbell, E J M (1982) *Clinical Exercise Testing*, W B Saunders, Philadelphia
15 Karlsen, G G and Nadaljak, E A (1964). Gas and energy exchange in breathing of trotters during exercise Konevdstvo Konnyj Sport 34, 27–31
16 Kram, R and Taylor, C R (1990) Energetics of running: a new perspective Nature 346, 265–266
17 Persson, S G B (1967) On blood volume and working capacity in horses Acta Vet Scand Suppl 19, 1–189
18 Persson, S G B (1983) Analysis of fitness and state of training *In*: Snow, D H, Persson, S G B and Rose, R J (eds): *Equine Exercise Physiology*, Granta Editions, Cambridge, pp 441–457
19 Persson, S G B and Forssberg, P (1987) Exercise tolerance in Standardbred trotters with T-wave abnormalities in the electrocardiogram *In*: Gillespie, J R and Robinson, N E (eds): *Equine Exercise Physiology 2*, ICEEP Publications, CA, pp 772–780
20 Rose, R J, Hendrickson, D K and Knight, P K (1990) Clinical exercise testing in the Thoroughbred racehorse: Evaluation of responses to exercise in the normal horse Aust Vet J 67, 345–348
21 SAS Institute (1985) SAS® User's Guide: Statistics, Version 5 Edition, SAS Institute Inc., Cary, N C
22 Taylor, C R, Heglund, N C, McMahon, T A and Looney, T R (1980) Energetic cost of generating muscular force during running J Exp Biol 86, 9–18
23 Valberg, S and Essén-Gustavsson, B (1987) Metabolic response to racing determined in pools of type I, II A and II B fibers *In*: Gillespie, J R and Robinson, N E (eds): *Equine Exercise Physiology 2*, ICEEP Publications, CA, pp 290–301
24 Wilson, B D, Neal, R J, Howard, A and Groenendyk, S (1988) The gait of pacers 1: kinematics of the racing stride Equine Vet J 20, 341–346
25 Wilson, B D, Neal, R J, Howard, A and Groenendyk, S (1988) The gait of pacers 2: factors influencing pacing speed Equine Vet J 20, 347–351