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The Oxygen Cost of Weight Loading and Inclined Treadmill Exercise in the Horse

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Summary

This study was carried out to determine the metabolic response to load carrying and inclined trotting during treadmill exercise in the horse. Five Standardbred trotters, trained for treadmill exercise, were initially subjected to an incremental exercise test, without and then with a load of approximately 10% body weight in the position of a riding saddle. Each horse was then run on the flat and subsequently at a 6.25% slope at speeds known to be of an aerobic intensity. Oxygen consumption ($\dot{V}O_2$), stride frequency, heart and respiratory rates were recorded while each horse ran for 5 min without the load, and later, 5 min with the load. The additional load did not increase the oxygen cost per kgm of the exercise and the ratio of increase in $\dot{V}O_2$ to increase in total mass was 1.04 ± 0.07 and 1.08 ± 0.11, respectively for horizontal and inclined exercise. Inclined trotting without the load was metabolically more expensive than load carrying horizontally or uphill due to an oxygen cost of ascent of 1.379 ml O_2/kgm. The increased oxygen requirements were met largely by an increase in ventilation until a maximal tidal volume was approached. We conclude that oxygen uptake during load carrying increases proportionally to the load during horizontal and inclined exercise, and that inclined exercise requires a greater increase in $\dot{V}O_2$ than does the addition of a load during either horizontal or inclined exercise.

Index terms: Oxygen uptake; exercise tests; ventilation.

Introduction

The ability to carry out a particular athletic exercise is largely dependent on the utilization of energy by the skeletal muscles. The amount of energy required and the rate at which it is consumed varies with the type of exercise performed. During locomotion, energy is required to both support the mass of an animal and to provide the forward movement. In animals varying widely in body mass this energy requirement, measured as oxygen consumption, increases in direct proportion to the mass supported by the muscles (Taylor *et al.*, 1980) and, over an interval of time, with running speed. For uphill running the increase in oxygen consumption normalised to body mass is greater in large than small animals (Taylor *et al.*, 1972).

Performance horses are reqularly required to carry an additional load, exercise over uphill grades and also sustain changes in body weight. They may be submitted to exercise tests on a horizontal or inclined treadmill. The present study was carried out to determine the effects of an added load, during horizontal and inclined treadmill exercise, on oxygen uptake in the horse.

Materials and Methods

Five Standardbred trotters (1 mare and 4 geldings), aged 7 to 19 years and trained for treadmill exercise, were acclimatized to carrying a load of approximately 10% body weight in the position of a riding saddle. Each horse was initially submitted to an incremental exercise test at speeds of 5, 6, 7 and 8 m/sec for 2 min each sequentially at a 6.25% slope without a load. During each test, heart rate (HR) was monitored continuously with a bipolar ECG lead and recorded during the last 20 sec at each speed, as was the respiratory rate (RR). Expiratory minute volume ($\dot{V}_E$), measured by a flow meter (GD-100, Fluid Inventor AB, Stockholm) and expired oxygen concentrations, determined by mass spectrometry, (Centronic 200 MGA), were monitored continuously and recorded during the last 30 sec at each speed for the derivation of oxygen uptake ($\dot{V}O_2$) (Essen *et al.*, 1978). Venous blood was collected through a jugular catheter before each test and during the last 15 sec at each speed for determination of blood lactate (LA) concentration. An aliquot (0.1 ml) of blood was added to 1 ml ice cold perchloric acid, mixed and stored at 4°C until analyzed. The LA concentrations were determined enzymatically (Boehringer Test Combination No. 124842). Stride frequency (SF) and stride length (SL) were determined at each speed from the time interval required for 50 strides. Two days later the horses repeated the initial test while carrying the load and the same observations were made. The V_{200} (the speed producing a HR of 200 beats/min) and V_{LA4} (the speed producing a plasma lactate concentration of 4 mmol/l) were derived by regression analysis of HR and LA, respectively on speed for each horse during the incremental tests (Fig. 1).

Effect of load during horizontal exercise. To provide a relatively high level of aerobic exercise without LA accumulation the V_{LA4} from the loaded incremental test was chosen as the exercise speed. Each horse was trotted horizontally, at the V_{LA4} from its loaded exercise test, for 5 min unloaded and then for a further 5 min carrying the load. At 2, 3, 4 and 5 min of each exercise period $\dot{V}_E$, $\dot{V}O_2$, HR, RR, and SF were recorded and the mean values determined. The oxygen cost of exercise was defined as the amount of oxygen required to move 1 kg one meter and is expressed as ml $O_2 \cdot kg^{-1} \cdot m^{-1}$.

Effect of inclined exercise (unloaded) and that of a load during inclined exercise. To determine the effect on oxygen consumption of inclined versus horizontal exercise and a load during inclined exercise, each horse was trotted for 5 min horizontally, at a speed of 2 m/sec below its loaded V_{LA4}. While continuing to trot, the treadmill was inclined to a slope of 6.25% and the trotting continued for a further 5 min. The next day each horse repeated the 5 min inclined exercise, at a similar speed while carrying the load. A speed of 2 m/sec below the loaded V_{LA4} was used to avoid the possibility of inducing fatigue, as was observed with the first horse during this exercise (at her loaded V_{LA4}). The same observations were made as during horizontal exercise. Two

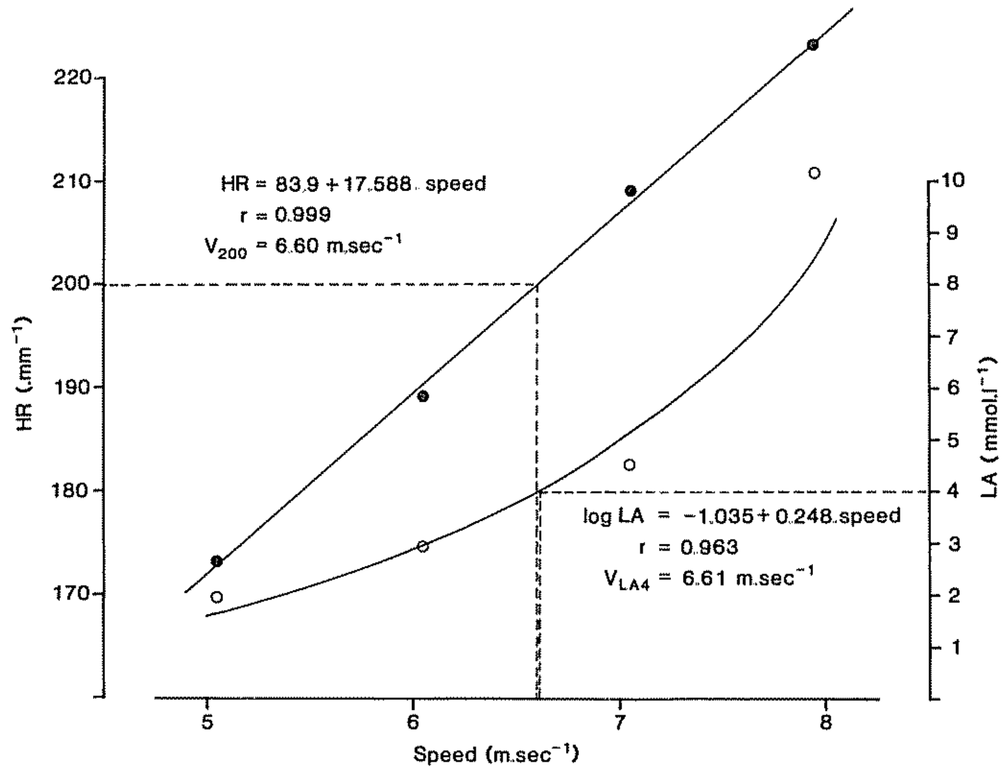

FIGURE 1. Derivation of V_{200} and V_{LA4} by regression analysis of heart rate and lactate on speed during incremental tests (Horse 1, loaded).

horses (4 and 5) did not provide adequate recordings during inclined loaded exercise and were retested (inclined unloaded and loaded only) 1 month later.

Statistical analyses. Data from loaded and unloaded exercise and from horizontal and inclined exercise were compared by means of Student's t test for paired observations. Results from the two incremental exercise tests were compared by regression analysis and covariance analysis. Results are expressed as means ± SD unless otherwise stated.

Results

Effect of load on response to the incremental exercise test. During the loaded exercise test, one of the horses failed to provide satisfactory recordings for $\dot{V}O_2$ and consequently the unloaded/loaded comparison is limited to 4 horses. The response of the horses to carrying the load during the exercise test was a significant ($P < 0.05$) reduction in both $\dot{V}_{200}$ and $\dot{V}_{LA4}$. There was no significant change in the slopes of the individual HR and $\dot{V}O_2$ responses as a result of carrying the load while mean HR and $\dot{V}O_2$, adjusted to average speed, increased significantly in 3 horses and 1 horse, respectively (Table 1A). The oxygen cost of the exercise test at any particular intensity did not change with the addition of the load. There was a considerable variation when the oxygen cost of exercise was related to treadmill speed and only horses 2 and 5 when unloaded, showed a significant relationship, $r = -0.999$, $P < 0.001$ and $r = 0.969$,

TABLE 1 (A) Regression analysis of heart rate and lactate on speed in five standardbred horses during incremental exercise tests to show effect of load on V_{200} and V_{LA4}

		Horse 1	2	3	4	5	Mean change with load (m/sec)
Heart rate							
U	Slope	15 351	15 754	10 999	18 090	12.233	
	Intercept	83 29	88 19	109.84	63 59	110 69	
	Adjusted mean†	182 5	185 5	181 1	185 6	188 2	
	V_{200}	7 60	7 10	8 20	7 54	7 30	
L	Slope	17 588	13 679	13.197	17 830	13 015	
	Intercept	83 87	102 60	100.05	69 54	108 35	
	Adjusted mean†	197 5**	187 4	185 6*	189 8	190 7*	
	V_{200}	6 60	6 82	7 57	7 32	7 04	−0 48* ± 0 34
$\dot{V}O_2$							
U	Slope	6 7937	5 5858	6.3683	5 9189	7 3680	
	Intercept	−3 3854	5 7416	−3 1485	3 4900	−7 6660	
	Adjusted mean	40.5	40 3	39 4	42 0	39 3	
L	Slope	6.1036	5 1753	4 5599	7 4576	Not Done	
	Intercept	2.5220	12 2212	13 5331	−3 0573	Not Done	
	Adjusted mean	41 9	44 2	43.8*	45 5	Not Done	
Lactate							
U	Slope	0.104	0 213	0 087	0 081	0 141	
	Intercept	−0 31	−0 83	−0 19	−0 28	−0 50	
	V_{LA4}	8 79	6 69	9 07	10 27	7 87	
L	Slope	0 248	0 244	0 159	0 186	0 150	
	Intercept	−1.04	−0 98	−0 54	−0.92	−0.53	
	V_{LA4}	6 61	6.50	7 19	8 18	7 51	−1 34* ± 0 98

†Mean HR or $\dot{V}O_2$ adjusted to average speed for covariance analysis.

(B) Regression analysis of the oxygen cost of exercise as a function of speed in five standardbred horses during incremental exercise tests

		1	2	3	4	5
U	Slope	0 0021	−0.0060	0 003	−0.0027	0 0079
	Intercept	0 2166	0 2679	0 1855	0 2376	0 1959
	r	0 263	−0 999†	0.720	−0 720	0 969**
L	Slope	−0.0025	−0 0090	−0.0093	0 0030	Not Done
	Intercept	0 2573	0 3100	0 2974	0 2173	Not Done
	r	−0.515	−0.547	−0 689	0 354	Not Done

U = no load, L = loaded, r = correlation coefficient, * = P < 0 05, ** = P < 0 01, † = P < 0 001

P < 0.01, respectively (Table 1B). The load had no effect on SF during the test.

Effect of load during horizontal exercise. The response of the horses to the load during horizontal trotting is shown in Table 2. There was a significant (P < 0.01) increase in mean oxygen consumption of 3 6 l/min (15%) with a mean load of 10.03% of body weight. Ventilation increased in 4 horses so that the mean $\dot{V}_E$ was 97 l/min

TABLE 2. Response of five standardbred horses to load bearing during horizontal treadmill trotting.

		Horse 1	2	3	4	5	Mean change with load
Speed ($m \cdot sec^{-1}$)		6.62	6.50	7.23	8.14	7.50	
Weight (kg)		450	466	469	490	419	
Load (kg)		46	46	49	47	42	
$\dot{V}O_2 (l \cdot min^{-1})$	U	24.64	23.04	23.09	23.74	27.61	3.59**
	L	27.64	29.07	27.24	25.52	30.59	(1.60)**
$\frac{\dot{V}O_{2L}/\dot{V}O_2}{W + L/W}$		1.0178	1.1484	1.0681	0.9809	1.0070	1.0444 (0.0662)
$\dot{V}_E$ ($l \cdot min^{-1}$)	U	717	742	584	648	794	97
	L	790	941	560	788	891	(83)
F_{IO_2}-F_{EO_2} (%)	U	3.45	3.11	3.96	3.67	3.47	0.1
	L	3.51	3.09	4.88	3.24	3.43	(0.5)
HR ($\cdot min^{-1}$)	U	150	155	156	162	174	5.4
	L	153	162	169	164	176	(4.7)
RR ($\cdot min^{-1}$)	U	63	78	61	101	68	9.0
	L	86	90	57	104	79	(10.2)
SF ($\cdot min^{-1}$)	U	108.37	111.52	104.01	109.12	115.53	1.7*
	L	111.06	112.92	107.12	110.42	115.51	(1.2)
SL (m)	U	3.66	3.49	4.18	4.45	3.93	−0.08*
	L	3.57	3.46	4.05	4.41	3.83	(0.04)

U = no load, L = loaded, * = $P < 0.05$, ** = $P < 0.01$.

higher, when the load was carried, while the inspired-expired oxygen difference (F_{IO_2}-F_{EO_2}) did not effectively change.

For horizontal trotting the increment in $\dot{V}O_2$ per increment in total mass, expressed as the ratio

$$\frac{\dot{V}O_2 \text{ loaded}/\dot{V}O_2 \text{ unloaded}}{\text{wt. horse} + \text{load/wt. horse}}$$

was 1.0444 ± 0.0662, which did not differ significantly from 1.0000. There was no difference in oxygen cost $kg^{-1} \cdot m^{-1}$ of horizontal trotting between the horses when loaded and unloaded (0.124 ± 0.019 and 0.130 ± 0.022 ml $O_2 \cdot kg^{-1} \cdot m^{-1}$, respectively). The additional load resulted in a significant increase ($P < 0.05$) in SF and therefore a decrease in SL.

Effect of the inclined exercise. The response of the horse to unloaded exercise at an incline of 6.25% compared to that on the flat was a significant mean increase in $\dot{V}O_2$ of 13.4 l/min (76%, $P < 0.001$), $\dot{V}_E$ of 288 l/min (52%, $P < 0.001$), F_{IO_2}-F_{EO_2} of 0.57% (18%, $P < 0.01$) and HR of 21 beats/min (16%, $P < 0.01$). The SF frequency and SL length did not change (Table 3).

Effect of load during inclined exercise. The mean load during inclined exercise was 9.5% body weight and this resulted in a significant ($P < 0.05$) increase in $\dot{V}O_2$ of 5.5

TABLE 3. Response to five standardbred horses to trotting on an inclination of 6.25%.

		Horse 1	2	3	4	5	Mean change with slope
Speed ($m \cdot sec^{-1}$)		4.64	4.54	5.36	6.25	5.41	
Weight (kg)		453	464	472	491	419	
$\dot{V}O_2 (l \cdot min^{-1})$	F	13.54	16.03	16.84	24.90	17.34	13.41†
	S	26.39	27.15	30.74	39.30	32.13	(± 1.47)
VE ($l \cdot min^{-1}$)	F	467	551	532	673	551	287.6†
	S	806	787	739	1028	852	(± 64.3)
F_{IO_2}-F_{EO_2} (%)	F	2.90	2.91	3.17	3.54	3.14	0.57**
	S	3.28	3.46	4.16	3.84	3.77	(± 0.27)
HR ($\cdot min^{-1}$)	F	116	144	139	136	—	21†
	S	137	158	161	163	—	(± 5)
RR ($\cdot min^{-1}$)	F	74	63	69	69	100	9.6
	S	100	70	60	97	96	(± 16.9)
SF ($\cdot min^{-1}$)	F	100.1	102.4	99.1	103.6	106.2	0.73
	S	101.9	103.8	98.0	98.4	105.7	(± 2.82)
SL (m)	F	2.77	2.66	3.22	3.58	3.09	0.046
	S	2.74	2.63	3.27	3.78	3.13	(± 0.094)

F = flat, S = slope, ** = $P < 0.01$, † = $P < 0.001$.

l/min, or 18% over that when unloaded. Ventilation increased by 9% and F_{IO_2}-F_{EO_2} by 8%. Heartrate increased significantly ($P < 0.001$) and there was no change in SF or SL (Table 4).

For inclined trotting, at a slope of 6.25%, the increment in $\dot{V}O_2$ per increment in total mass was 1.0803 ± 0.081 which was not different from that during horizontal exercise. There was no difference in the oxygen cost $\cdot kg^{-1} \cdot m^{-1}$ of inclined trotting between the horses when unloaded or loaded (0.217 ± 0.007 and 0.227 ± 0.025 ml $O_2 \cdot kg^{-1} \cdot m^{-1}$, respectively).

The oxygen cost of exercise per kg total mass (ml $O_2 \cdot kg^{-1} \cdot m^{-1}$) was significantly ($P < 0.001$) greater at an incline of 6.25% (0.208 ml $O_2 \cdot kg^{-1} \cdot m^{-1}$) than on the flat (0.122 ml $O_2 \cdot kg^{-1} \cdot m^{-1}$). The addition of the load to horses exercising either on the flat or incline did not change the oxygen cost of exercise.

Discussion

The use of an incremental treadmill exercise test provides a convenient means of performance assessment by permitting the derivation of V_{200} and V_{LA4}. Both these variables have been used as indicators of fitness in the horse. V_{200} approximates the anaerobic threshold and is considered the best simple parameter of aerobic fitness (Persson, 1983) while V_{LA4} represents the point above which LA starts to accumulate in the blood (Wilson *et al.*, 1983) and thus a transition to greater anaerobic contribution to metabolism.

The reduction in both V_{200} and V_{LA4} when the load was carried reflects the increased demand for oxygen this imposed on the horses, thus lowering the speed of trotting at

TABLE 4. Response to five standardbred horses to load bearing during inclined treadmill trotting

		Horse 1	2	3	4	5	Mean change with load
Speed ($m \cdot sec^{-1}$)		4.64	4.56	5.36	6.25	5.41	
Weight (kg)		453	464	472	491	419	
Load (kg)		44	46	48	48	42	
$\dot{V}O_2 (l \cdot min^{-1})$	U	26.39	27.15	30.74	38.62	30.11	5.46*
	L	28.32	37.78	36.88	42.51	34.82	(3.27)
$\frac{VO_{2L}/VO_2}{W + L/W}$		0.9920	1.2611	1.0910	1.0083	1.0488	1.0803 (0.1081)
$\dot{V}E (l \cdot min^{-1})$	U	806	787	739	857	861	74.8
	L	844	983	797	882	918	(69.14)
F_{IO_2}-F_{EO_2} (%)	U	3.28	3.46	4.16	3.84	3.77	0.40**
	L	3.38	3.85	4.64	4.83	3.79	(0.14)
HR (min^{-1})	U	137	158	161	167	169	11.6**
	L	145	174	173	179	179	(3.0)
RR (min^{-1})	U	100	70	60	97	96	1.0
	L	103	67	60	66	84	(4.5)
SF (min^{-1})	U	101.98	103.97	97.97	101.81	104.52	0.35
	L	101.70	104.35	97.74	99.16	105.25	(1.36)
SL (m)	U	2.74	2.63	3.27	3.67	3.10	0.04
	L	2.73	2.64	3.32	3.80	3.10	(0.06)

U = no load, L = loaded, * = $P < 0.05$, ** = $P < 0.01$.

which LA will accumulate and fatigue develop. It is interesting to question the use of V_{LA4} derived from an incremental test, as an indication of a work level suitable for prolonged and intense aerobic exercise. The intensity of the inclined exercise in this study was originally intended to be that of the loaded V_{LA4} or just below. However, when the first horse ran at this speed for 5 min unloaded then for 5 min with the load, she was tiring perceptibly by the end of the period. Although LA was not measured her respiratory quotient had reached 1.05 and her HR 204 beats/min suggesting she was very close to, if not over, her "anaerobic" threshold. The reduction of the speed of inclined exercise by an arbitrary 2 m/sec avoided this development of fatigue in all 5 horses. The only report of the response to exercise at V_{LA4} in horses is that of Wilson *et al.* (1983) where horses were submitted to repeated (4 times) 1000 m runs 3 days after determination of their V_{LA4}. These were interval runs, with 3 min rests between, and when the speed was at just below V_{LA4} no LA accumulated. It is thus not known whether horses can exercise for prolonged periods at V_{LA4} or whether their level of fitness is an important factor in this regard.

The response of a horse to carrying additional weight at any particular speed is to increase its oxygen uptake (metabolic rate) in proportion to the total mass supported by its limbs. This relationship appears to be applicable to both horizontal and inclined treadmill exercise where the mean values for the ratio of increase in $\dot{V}O_2$ to increase in mass supported, during horizontal and inclined trotting (1.0444 ± 0.0662 and 1.0803

± 0.1081) were similar to that (1.01 ± 0.017) reported from a number of species including ponies during flat running (Taylor *et al.*, 1980). It follows that a decrease in body weight (i.e. body fat) of a horse would result in a proportionally lower energy requirement for exercise, a factor of potential importance in the preparation of a racehorse.

The oxygen cost per kg meter, although greater while trotting at an incline than horizontally, does not appear to be affected by speed. The mean values for horizontal exercise of 0.124 and 0.122 ml $O_2 \cdot kg^{-1} \cdot m^{-1}$ for speeds of 6.50 to 8.14 and 4.5 to 6.25 m/sec, respectively from the present study are similar to those derived from results for a 431 kg horse walking, 0.128 (Zuntz and Hagemann, 1898) or a 119 kg pony trotting, 0.133 (Taylor *et al.*, 1980). Somewhat higher mean values of 0.21 ± 0.07 and 0.19 ± 0.04, respectively for walking and trotting or galloping (Hornicke *et al.*, 1983) were averaged from a range of speeds at each gait thus including other than optimal speeds which are considered less energy efficient (Hoyt and Taylor, 1981). The mean values of 0.217 and 0.208 for similar speeds during inclined exercise in the present study agree with that 0.22 for similar speeds during inclined exercise in the present study agree with that 0.22 of Persson (1983) and support his view, at least for the range of trotting speeds (5–8 m/sec) used, that the oxygen cost of treadmill trotting (at an incline of 6.25%) is virtually unaffected by the state of training or treadmill speeds in adult horses. It may be that Standardbred trotters differ from other horses or ponies in that the wide range of speeds at which they trot does not constitute an extended gait, with its attendant loss of efficiency as described by Hoyt and Taylor (1981). The lack of a consistent relationship between oxygen cost of exercise and treadmill speed for the horses individually during the exercise tests suggests that this may well be the case.

The increase in $\dot{V}O_2$ brought about by the load during horizontal exercise and the transition from horizontal to inclined trotting resulted largely from an increase in ventilation. However, during uphill trotting the additional increase in $\dot{V}O_2$ required when the load was added was met by almost equal contributions from ventilation and oxygen extraction from the inspired air. As oxygen uptake is closely and linearly related to pulmonary ventilation (Hornicke *et al.*, 1983) it is to be expected that an increased demand for oxygen (occasioned by a load or inclined trotting) will largely be met by ventilation. That the additional oxygen demand of the load during inclined trotting was met in equal amounts by ventilation and pulmonary oxygen extraction suggests that, as there was no change is respiratory rate, tidal volume approached a maximum and an increase in oxygen extraction provided the only alternative means available to increase $\dot{V}O_2$. From the data in Table 4, calculated tidal volume during unloaded inclined trotting increased significantly ($P < 0.05$) by 2.61 ± 1.45 l to a mean of 10.22 ± 1.74. When compared to that in larger horses (9.1 ± 1.6 and 11.3 ± 1.41) at a fast trot or gallop (Hornicke *et al.*, 1983) these results support this view.

The use of an inclined treadmill has become an integral part of exercise testing as a means of increasing the workload to which the horse is subjected without the necessity for high speeds. From the present results it is apparent that the increase in metabolic rate of the horse trotting uphill is much greater than that induced by the carrying of additional weight during either horizontal or inclined exercise. As there was no change in stride frequency (or length) as the treadmill was inclined to the 6.25% slope it is likely that the increased oxygen uptake reflects the energy required for the horse to lift its body mass with each stride over that needed to maintain its forward speed. From the difference between the oxygen costs/per kilogram meter for unloaded horizontal and inclined trotting (0.086 ml $O_2 \cdot kg^{-1} \cdot m^{-1}$) in the present results it can be calculated that the energy cost of ascent was 1.379 ml O_2/kgm. This figure, while lower, is comparable to those of 1.420 for a walk and 1.526 for a slow trot on a steeper slope of 10.7% (Zuntz and Hagemann, 1898).

We conclude from this study that Standardbred trotters carrying a load during horizontal or inclined exercise increase their oxygen uptake at any particular speed in proportion to the total mass of horse and load (as previously shown in level trotting in ponies (Taylor *et al.*, 1980)). Further, that until such time as the tidal volume approaches a maximum this increase is achieved largely by an increase in ventilation. The oxygen cost of exercise per kilogram of total mass for each meter covered is not influenced by the load carried or apparently by the speed of trotting over the range of speeds (5 to 8 m/sec) used.

While the highest oxygen consumption at the slowest speed can be achieved with inclined trotting with a load, the single greatest contribution to the metabolic rate was the incline. The use of the inclined treadmill or uphill running will therefore provide convenient, and relatively low speed, assessment and training procedures for performance horses.

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Pulmonary Ventilation in Thoroughbred Horses at Maximum Performance

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Summary

Four trained English Thoroughbreds, weighing 380–420 kg, were studied four times during the racing season. The horses were ridden, with a flying start, over a 1000 m test course of either deep grass or sand at constant velocities (735–854 m/min). Electrocardiogram, footfall and respiratory airflow were transmitted by telemetry and stored on magnetic tape. Heart rates were 200–219 min^{-1} with little variation from test to test. Respiratory frequencies, 120–148 min^{-1}, were identical with step frequencies except for a few interruptions due to swallowing. Tidal volume increased within 20–30 sec from 7–8 l to a steady state of 10–12 l. Pulmonary ventilation was 1178–1504 l/min ATPS (3.10–3.58 l/kg/min). We recorded peak flow rates of 56–68 l/sec during inspiration and of 67–76 l/sec during expiration. The pneumotachogram approximated a regular square wave during inspiration. The ratios of expired to inspired time (TE/TI) were 0.94–1.25 and varied between horses.

Index terms: respiration; tidal volume; pneumotachogram; respiratory telemetry; respiratory time quotients; respiratory air flow.

Introduction

Pulmonary ventilation of horses at near-maximum exertion has been measured during draft work (Nadaljak, 1960), in trotters (Karlsen and Nadaljak 1964), during swimming (Thomas *et al.*, 1979) and on inclined treadmills at moderate speed (Bisgard *et al.*, 1978, Thomas and Fregin 1981). Horses under saddle have been studied only at submaximal riding velocities (Hörnicke *et al.*, 1983). Because of the close coupling of respiration and locomotion (Bramble and Carrier, 1983), riding velocity determines respiratory frequency. The characteristics of pulmonary ventilation can therefore be very different in various types of exercise.

The limits of diffusion in the equine lung have been determined morphometrically (Gehr and Erni, 1980). But the limits of pulmonary ventilation are not yet known. Leith and Gillespie (1971) found maximal expiratory air flow rates of 60–90 l/sec in anesthetized horses. On this basis Gillespie (1974) predicted a maximal pulmonary ventilation of 4.17 l/kg/min.