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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.

The close cooperation of the second author, a biologist and jockey, with a research-minded owner of racing Thoroughbreds gave an opportunity to measure respiration under circumstances approximating racing conditions. A telemetric technique was used to obtain pneumotachograms on a breath-by-breath basis. The pulmonary ventilation of Thoroughbreds at fast gallop was found to be far larger than the ventilation measured in other forms of exercise. Respiration was immediately and completely synchronized with locomotion. The adaptation of ventilation to the metabolic requirements occurred by fine adjustments of tidal volume.

Materials and Methods

Animals and rider. Four English Thoroughbreds (three geldings, one mare; age 5–9 years, weighing 380–410 kg) were studied. All animals had been in training for at least two years. Before, between and after the respiratory measurements they all ran races and all won prizes. Three horses were studied four times, one gelding was injured during a race and could be studied only once. All horses were ridden by the second author who weighed 65 kg. Additional loads were saddle, 5 kg; mask with respiratory tube, 1.95 kg at the horses head; and transmitter and batteries, 5 kg, carried by the rider. Thus, the total load was 77 kg, about 20% of the horse's body weight.

Procedure. Warming up consisted of a 5 min walk, 2 min trot and 500 m slow gallop, followed by a 5 min walk. The 1000-m course had either deep grass or sand. Environmental temperature was 16 ± 5°C (range 10–25). The gallop began 50 m before the starting line, thus allowing a flying start. Velocity was maintained as stable as possible. The course was marked at 500, 800, 900 and 1000 m and the speed for all sections was measured by a stopwatch.

Equipment. A fiberglass mask was fitted to the horse's head by means of a rubber mask holder with a bit (Hörnicke *et al.*, 1984). Respiratory airflow was measured by means of the respiratory tube and transducer system designed by Kimmich and Spaan (1980). The effective dead space of the mask system was about one liter. The flow system was calibrated against gas meters at flow rates up to 100 l/sec. Heart rate was obtained from the electrocardiogram, step frequency from an accelerometer (Philips PR 9367/01) at the right front leg. Signals were transmitted by PCM telemetry (Glonner Biomes 80), received and stored on magnetic tape.

Signal analysis. Heart rate (HR), respiratory frequency (RF) and step frequency (SF) were obtained manually from the recorded tracings. The flow signals were analyzed by a special program written for the Apple II computer. The computer sampled the electrical flow signal at a rate of 100 times per second, transformed it to l/s, and calculated the duration, peak flow and volume for every respiratory half cycle. For a given number of breaths, tidal volume (VT), pulmonary ventilation (V), the ratio of the duration of expiration and inspiration (TE/TI) and their standard deviations were calculated. An averaged curve of the pneumotachogram with its standard deviation was then plotted on a printer.

Results

Table 1 gives the average values of body weight, velocity, RF, VT and pulmonary ventilation for the individual horses.

Velocity. The horses ran the 1000 m with a velocity between 736 and 881 m/min

TABLE 1. Pulmonary ventilation parameters of four horses over a 1000 meter course.

Horse	No. of experiments		Body weight kg	Velocity m/min	Respiratory frequency min^{-1}	Tidal volume l	Tidal volume ml/kg	Pulmonary ventilation l/min	Pulmonary ventilation l/kg/min
FP	4		380	825	133	10.6	28.0	1408	3.71
Na	4		420	797	128	13.1	31.2	1670	3.98
Nu	4		400	775	130	11.9	29.7	1539	3.84
Pa	1		410	881	138	11.3	27.5	1560	3.81
Mean	13	$\bar{x}$	403	805	131	11.8	29.5	1540	3.84
		s	17	42	6	1.1	1.7	129	.21
		C.V.	4.2	5.2	4.4	9.3	5.6	8.4	5.4

All volumes are corrected to body temperature and pressure, saturated (BTPS).
$\bar{x}$ = mean; s = standard deviation; C.V. = coefficient of variation (%)

depending on the soil conditions. They finished the course in 75 ± 4 s. The average speed was 797 ± 48 m/min for the first and 815 ± 60 m/min for the second 500 m, the difference not being significant.

Heart rate. Heart rate was 206 ± 8 beats/min for the first half of the course and 213 ± 5 for the second half. The heart rate increment was 1–16 beats/min. It took the horses 242–272 heartbeats to run 1000 m.

Respiration and step frequencies. During the gallop, respiration was immediately synchronized with step frequency. There was no period of breath-holding. Neither SF nor RF differed between the first and the second 500 m-section. The horses took 161–172 steps and 154–170 breaths during the 1000-m gallop. In spite of complete synchronization, the number of respirations was less than the number of strides because the animals swallowed a few times. This produced a characteristic pattern of the pneumotachogram with breath-holding during inspiration and loss of one respiratory cycle (Attenburrow, 1978).

Tidal volume. All horses began the gallop with tidal volumes of 7–8 l. In the following 10–15 sec tidal volume increased rapidly, thereafter more slowly. Steady-state values were attained after 60–70 breaths, i.e. about 30 s after the begin of gallop. Figure 1 gives an example taken from horse FP. Conspicuous periodicities with an oscillation between shallow and deep breaths every 2–8 respiratory cycles were present in all records. Tidal volume changed from one breath to the other by up to 3.5 l in some horses. The mean tidal volume from all experiments with the four horses was 10.0 ± 0.8 l for the first 500 m, 10.8 ± 0.9 l for the second 500 m and 10.96 ± 0.84 l (27.3 ± 1.3 l/kg) for the last 100 m only.

Pulmonary ventilation. In the individual experiments the horses respired 1178–1504 l/min. The mean values are given in Table 1. While the respiratory frequencies of the horses were not much different, tidal volumes and pulmonary ventilation ranged according to body weight. The heaviest horse had the largest tidal volume and the largest pulmonary ventilation. Calculating weight-specific ventilation reduced the coefficient of variation. Since the run lasted 68–82 sec, the total ventilation during the 1000 m course was 1378–1958 l, average 1698 ± 162 l or 4.23 ± 0.29 l/kg

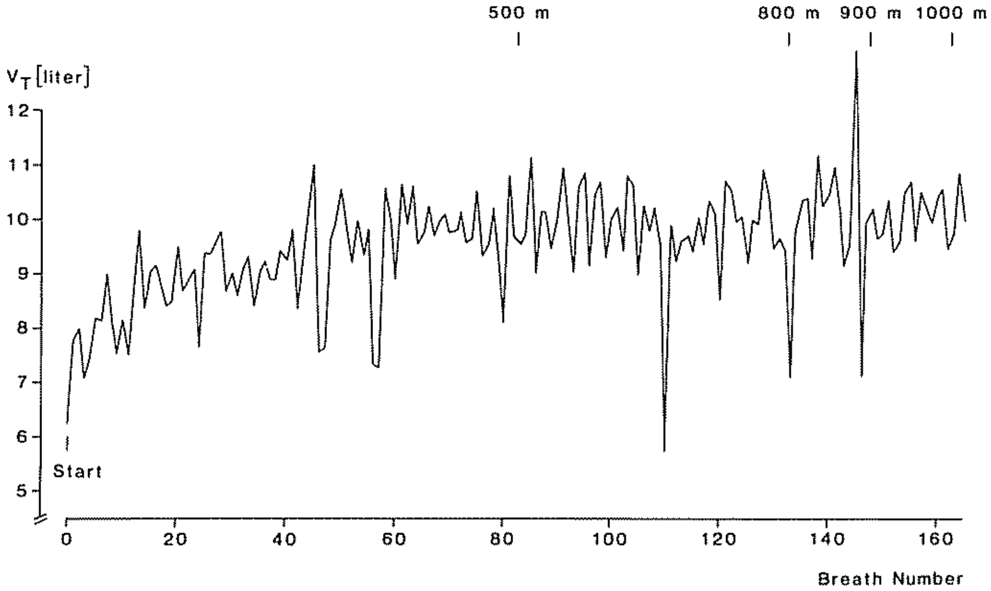

FIGURE 1 Tidal volume during the 1000 m gallop. Results from horse FP. Inspiratory tidal volume (V_T) is plotted against the number of breaths. Duration of the run 74.5 sec. Note the cyclic variations in tidal volume.

Time relationships of the respiratory cycle. Inspiration lasted 170–217 msec which was 48.5 ± 2.2% of the total respiratory cycle duration (355–474 msec). Expiratory time was 185–240 msec (Table 2). The respiratory time quotient (expiratory time/inspiratory time, TE/TI) did not change with time. It was 1.02–1.24 in horses, FP, Nu and Pa, but significantly lower in horse Na.

Respiratory air flow. The shape of the pneumotachogram was very regular. When

TABLE 2 Mean flow, peak flow and respiratory times.

Horse		Velocity m/min	Tidal volume Liter	Mean flow l/sec		Peak flow l/sec		Duration msec	
			I	I	E	I	E	I	E
F.P.		855	8.9	46.0	44.3	57.3	67.0	193	201
Na		841	11.5	50.2	50.2	61.1	73.2	229	229
Nu		746	10.1	50.9	44.1	61.0	67.3	197	229
Pa		881	10.0	57.8	53.2	65.7	74.5	173	188
Mean	x̄	831	10.1	51.2	48.0	61.3	70.5	198	212
	s	59	1.1	4.9	4.5	3.4	3.9	23	21

One experiment was analyzed for each horse. The figures represent the mean values of all single breaths during the 1000 m course. Volumes and flows are expressed at ATPS (ambient temperature and pressure, saturated). I = inspired; E = expired; s = standard deviation.

averaged over several respiratory cycles (Fig. 2), the standard deviation was particularly small during inspiration. The inspiratory flow approached a square pattern. This is also indicated by the fact that inspiratory peak flow rates (56–68 l/sec) were only slightly (8–26%) higher than mean flow rates (45–61 l/sec) (Table 2). The slight flow reduction at mid-inspiration typical for the resting pneumotachogram of the horse (Gillespie *et al.*, 1966) was also present in most of the inspiratory half cycles during gallop. Expiratory airflow patterns were variable in form, flow oscillations being seen in most of the exercise pneumotachograms. An indentation was nevertheless seen at mid-expiration. Peak flow rates were 10–20% higher than inspiratory peak flow. Flow rates were generally greater during the first half of expiration. Because of this asymmetry there was a greater discrepancy between mean and peak flow during expiration, the latter being 41–52% higher.

Discussion

Respiration was measured continuously breath-by-breath in all experiments but it was not possible to calculate oxygen consumption during these experiments because the short respiratory half-cycle duration (below 200 msec) was beyond the response time of the oxygen electrodes available at present. Sparks (1968, cited by Gillespie and Pascoe, 1983) claims that sprint horses are apneic for periods of 30 sec or more. There was no indication that our Thoroughbreds were apneic for longer than one respiratory cycle due to swallowing or change of hand.

The velocity was near-maximal for our horses. It remained about 20% below the record speeds for Thoroughbreds, partly because of the soil conditions, partly because of the higher than usual weight load. The high and reproducible heart rates (209 ± 8 min^{-1}) and the heart rate increment are within the range recorded during Thoroughbred races (Krzywanek *et al.*, 1970) and thus document maximal effort.

Analogous to the situation in the human athlete (Astrand and Rodahl, 1970), it can be assumed that in horses about 50% of the energy required for a 75 sec sprint comes from anaerobic metabolism. The continuous increase in tidal volume during the first half of the course improves pulmonary ventilation. The contribution of increasing ven-

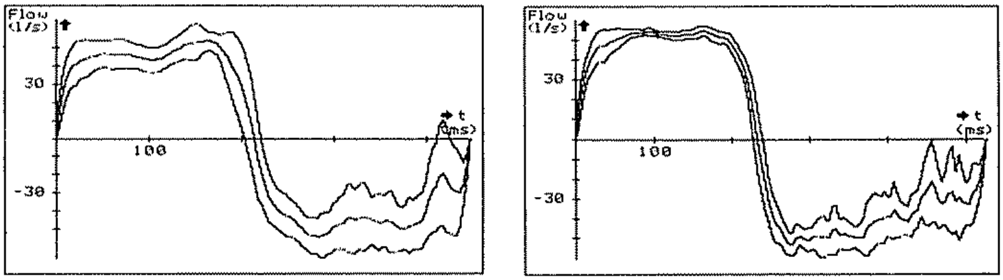

FIGURE 2. Averaged pneumotachograms of two galloping horses. The curves represent mean ± one standard deviation of the instantaneous flow rates. Because T_I and T_E varied slightly from breath-to-breath, the respiratory cycles were standardized to an average duration. Left: horse FP, average over all 85 breaths from 0–500 m (same experiment as in Fig. 1). Right: horse Nu, all 17 breaths between 800 and 900 m.

tilation to an adequate oxygen supply is completed after about 40 s when ventilation attains steady state.

Tidal volumes varied cyclically during the entire run. The correlation of tidal volume and inspiratory time suggests the operation of a short-term control system for pulmonary ventilation (Hörnicke and Meixner, 1977). It balances for mechanical disturbances of respiratory depth and duration. Mechanical factors such as slight phase differences between respiratory and locomotory cycle may induce particularly large or small breaths. This will be compensated for by appropriate changes in respiratory muscle force or in the respiratory phase-switching system during the subsequent 1–7 breaths.

In contrast to the situation during other forms of exercise, respiration during the gallop cannot be regulated by changes in respiratory frequency. Thus the fine control occurs entirely by variations in respiratory depth. This can be accompanied by shifts in the respiratory time quotient (RTQ = TE/TI). The RTQ was individually different. It may be of interest to investigate whether particularly successful horses have a particular phase-relationship between respiration and locomotion and thus a special flow-pattern or RTQ.

A comparison of pulmonary ventilation data from different studies is possible on the basis of body-weight- and BTPS-corrected figures (Table 3). The tidal volumes of our horses (30 ml/kg) are within the range of the volumes measured during other types of near-maximal exercise. Respiratory frequency was higher in our experiments because of the higher velocity. In Thoroughbreds at an average speed of 1006 m/min, Pratt (1983) measured step frequencies of 133–167 min^{-1}. Because of the respiration-locomotion-coupling we can expect these horses to have about the same RF (130–160 min^{-1}). Pulmonary ventilation in our fast galloping horses (3.8 l/kg/min) was higher than in all other forms of exercise performed with lower respiratory frequencies.

Pulmonary function in heavy exercise performed at low velocities is characterized

TABLE 3 Pulmonary ventilation of horses during different types of heavy exercise

Breed	Body weight	Type of exercise	Oxygen consumption	Respiratory frequency	Tidal volume		Pulmonary ventilation		Reference
	kg		ml/kg/min	min^{-1}	l	ml/kg	l/min	l/kg/min	
Heavy crossbreed	550	Draft	103	69	15.8	28.8	1092	1.98	1
Orlov trotter	550*	Trot 710 m/min	117	68	21.2	37.3	1453	2.64	2
Orlov trotter	550*	Gallop 710 m/min	114	105	14.1	30.8	1646	3.00	2
Ponies	151	Treadmill 12–15% grade	—	95	4.6	30.5	435	2.90	3
	532	Tethered swimming	112	—	—	—	1000	1.88	4
Thoroughbred and Morgan	476	Treadmill 11.5% grade	80	—	—	—	1134	2.38	5
Thoroughbred	403	Gallop with rider	—	131	11.8	29.5	1540	3.84	Our data
	540	Predicted maximal ventilation		112	20.0	37.0	2250	4.17	6
				150	15.0	27.8	2250	4.17	6

Tidal volumes and pulmonary ventilation are corrected to BTPS, i.e. 38°C and saturated. The data in ref. 1 and 2 were expressed as STPD and thus multiplied by 1.2. * = estimated

References: 1 = Nadaljak (1960) 2 = Karlsen and Nadaljak (1964) 3 = Bisgard *et al.* (1978)
4 = Thomas *et al.* (1979) 5 = Thomas and Fregin (1981) 6 = Gillespie (1974)

by a high oxygen extraction as indicated by ventilatory equivalents (V_E/V_{O_2}) below 20. In the draft work experiments of Nadaljak (1960), respiratory equivalent decreased with increasing exertion from 34.7 at 20 kg load to 15.6 at 170 kg load. A higher velocity at heavy exercise causes a higher SF, a higher RF and also a higher ventilatory equivalent which in turn also favors the thermoregulatory efficiency of respiration. This is particularly the case at work intensities above $\dot{V}_{O_2}$ max. Thoroughbreds running at 1006 m/min with a tidal volume of 29.5 ml/kg and a RF of 130–160 min^{-1} would have a pulmonary ventilation of 3.8–4.7 l/kg/min, values in the range predicted by Gillespie (1974).

Respiratory flow maxima increase linearly with riding velocity. The body-weight-corrected values from the present study with an average velocity of 835 m/min (Table 2), i.e. inspiratory and expiratory peak flows of 152 and 175 ml/kg/sec, respectively, lie on the regression line extrapolated from the flow-values measured previously at lower velocities (Fig. 3 in Hörnicke *et al.*, 1983). The higher flow maxima during expiration may represent brief flow-peaks due to the characteristic expiratory flow oscillations present in most expirations during gallop.

The algorithm to convert the flow-signal into the pneumotachogram and tidal volumes is based on the assumption that both inspiratory and expiratory volume are equal. When inspiratory and expiratory mean flows are calculated on this basis, expiratory mean flow is slightly lower, because expiration lasts a few milliseconds longer. However, since the inspired volume expands in the airways due to warming and addition of water vapor, the expiratory mean flow may be actually larger. There is at present no way to make corrections for the dynamic and complex changes in physical properties of air, e.g. temperature, density, viscosity, during the inspiratory and expiratory passage through the flow-measuring system (Hardt and Zywietz, 1976).

The weight-specific maximum expiratory flows (ml/kg/sec) of horses found by Leith and Gillespie (1971) (133–200) and by us (167–187) correspond well with the values obtained in human beings by forced expiration (143 ml/kg/sec; Varène *et al.*, 1979). The values reported for exercising dogs (32–36; Morrow and Vosteen, 1953) and anesthetized rats (425; Diamond and O'Donnell, 1977) are more uncertain because of methodological limitations.

Inspiratory flow assumed a square pattern with near-maximal flow rates during most of the inspiratory time. Such an airflow shape optimizes power requirements during inspiration (Ruttimann and Yamamoto, 1972). Expiratory flow does not attain such a regular shape. In general, pulmonary ventilation during the gallop is not only achieved by the respiratory muscles, but also to an important extent by mechanical events related to locomotion (Bramble, 1984). The sequence of these events (load on the forelegs, piston action of the viscera, etc.) should have a large influence on the instantaneous flow particularly during expiration.

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