MECHANICS OF BREATHING IN HORSES AT REST AND DURING EXERCISE

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Summary

The respiratory mechanics together with the rate of work of breathing were studied in five healthy adult Standardbred horses at rest and during different levels of exercise on a treadmill (0.8–$2.3\,\mathrm{m\,s^{-1}}$, 7% slope). In three of the horses the stride frequency was also determined.

The ventilatory response to exercise increased linearly with treadmill speed up to 9.6 times the resting values and was sustained more by an increase in respiratory frequency than by an increase in tidal volume. At the most elevated work load, respiratory frequency and tidal volume averaged 5.2 and 1.4 times the resting values, respectively. Lung resistance decreased during the most intense level of exercise to about 30% of the average value observed at rest, while lung dynamic compliance remained unchanged. The rate of work of breathing ($\dot{W}_{\mathrm{resp}}$, in W) increased exponentially with ventilation ($\dot{V}_{\mathrm{E}}$, in $\mathrm{l\,min^{-1}}$) according to the equation: $\dot{W}_{\mathrm{resp}}=5.263\dot{V}_{\mathrm{E}}^{1.5897}\times10^{-4}$. In the three animals investigated a definite locomotor–respiratory coupling was observed at a trot and in two animals also during walking. This observation, together with other considerations based on available data on the energetics of respiration, suggests that the efficiency of the equine respiratory system is relatively high. In addition, when compared with other smaller mammals (man and dog), horses are, in mechanical terms, more economical breathers.

Introduction

Equine exercise physiology is gaining a progressive consideration among physiologists, mainly because of the remarkable aerobic potentialities displayed by horses. These permit the study of a great number of metabolically significant homeostatic responses to the perturbing action of exercise in a large, although easily available, terrestrial mammal. Indeed, horses have aerobic capacities much greater than those of other mammals of similar body mass (bovines). In fact several studies (Kayar *et al.* 1989; Jones *et al.* 1989) have shown that horses attain a maximal oxygen uptake per unit of body mass 2.5-fold greater than steers. Such a

remarkable aerobic metabolism sustained by horses appears to be achieved by the proportionally augmented capabilities of the machinery for the delivery of O_2 throughout the entire path from the alveolar gas to mitochondria (Gehr and Erni, 1980; Constantinopol et al. 1989; Jones et al. 1989; Kayar et al. 1989). Nonetheless, the mechanical features of the equine respiratory system during exercise are less well understood than at rest. So the degree of constraint and limitation imposed by the respiratory mechanics during extreme exercise is still speculative (Bayly and Grant, 1986; Rose and Evans, 1987a). In the present study the equine respiratory mechanics and the rate of mechanical work of breathing were analyzed at rest and at different levels of work intensity at low speed on an inclined treadmill and were compared with those of other mammals of different body mass. It was thus possible to demonstrate that the respiratory function in horses is, from a mechanical standpoint, less expensive than in the other species considered (man and dog) and it is proportional to the high aerobic metabolism attained by horses, thus conforming to the criteria of regulated morphogenesis (Taylor and Weibel, 1981).

Materials and methods

The experiments were carried out on five untrained adult Standardbred horses *Equus caballus* (body mass: 525.0±41.8 kg, age: 10.3±5.7 years; mean±s.D.), clinically free of any symptoms referable to acute or chronic respiratory disease. No tranquillizer was given at any stage of the experiments.

Respiratory airflow and oesophageal pressure were recorded at rest and during exercise on a treadmill. Airflow was assessed by a differential pressure transducer (model 270, Hewlett Packard, USA) measuring the pressure drop across a pneumotachograph (cross-section 90 cm^2, mesh size no. 300 and mean resistance 0.0127 kPa s l^{-1}). This was mounted on a modified plastic face mask for aerosol delivery (Medel Italiana, Italy), fitting the muzzle of the horse by means of a rubber foam seal. The shape of the mask was roughly comparable to the frustum of a cone, the pneumotachograph lying on a frontal plane and aligned with the animal's nostrils. Face mask dead space was separately determined by water displacement on the head of a dead horse of comparable size and was found to be of 1.12 l. The pneumotachograph was calibrated up to 50 l s^{-1} by means of two vacuum cleaners in parallel with a rotameter. A function was thus obtained for subsequent digital linearization. Oesophageal pressure was measured by an oesophageal thin-walled latex balloon (length 10 cm) sealing the perforated end of a plastic catheter (i.d. 4 mm). A differential pressure transducer (model 270, Hewlett Packard, USA) recorded the pressure difference between the balloon and the mouth opening inside the face mask, thus permitting the determination of transpulmonary pressure (P_{TP}). Measurements were obtained with the balloon placed 140–150 cm from the nostrils and inflated with 1–2 ml of air.

The alignment of airflow and oesophageal pressures was achieved by the use of

the same transducer model and catheter dimensions, and was checked with a sinusoidal pump up to 5 Hz.

At rest the animals breathed through the apparatus while standing on the treadmill, and the recording was started after a reasonably regular respiratory pattern appeared to be achieved. The horses exercised on the treadmill (7 % constant slope) at four successive speeds up to $2.3 \, \text{m s}^{-1}$, corresponding to a moderate trot. Measurements were started after the attainment of a steady state (2–3 min); after each exercise level the treadmill was stopped and the basal condition regained, while the pneumotachograph was cleaned to prevent droplet deposition. The calibration was checked and, when it changed, the results of that experiment were discarded. Sequences of 10–30 consecutive breaths were recorded for each condition in every experiment. In two horses the transitions at the onset and after the end of the exercise were also recorded for all work loads.

In three horses the stride frequency (fs) was determined by the pressure shift caused by the animal's foot contact with the ground during exercise on the treadmill and recorded by a rubber bulb fixed under a rear-leg hoof connected to a pressure transducer by appropriate tubing. Ambient temperature (15–23 °C) and relative humidity (50–75 %) were recorded during the experiments.

All traces were monitored on a strip-chart four-channel recorder (model 7754A, Hewlett Packard, USA), and simultaneously stored on a four-channel FM magnetic tape recorder (model 3960, Hewlett Packard, USA) for subsequent data acquisition and analysis by a computer (Minc 11/23, Digital Equipment, USA). This consisted of airflow digital linearization, conversion to BTPS (body temperature and pressure when saturated with water vapour) conditions and integration. Tidal volume (V_T), respiratory frequency (f_{resp}) and minute ventilation ($\dot{V}_E$) were then determined. Dynamic compliance of the lung ($C_{dyn}L$) and viscous resistance of the lung (R_L) were calculated on a single-breath basis. The former was obtained as V_T divided by the difference in P_{TP} at the two moments of zero airflow, before the beginning and after the end of inspiration. The latter was determined by selecting in both the inspiratory and expiratory phases two points when the lung volumes were identical and relating the P_{TP} differences at these points with the corresponding changes in airflow: this isovolume method gives the average pulmonary flow resistance for inspiration and expiration (Frank *et al.* 1957). R_L was calculated at three different lung volumes: 2.5, 5.0 and 7.5 l above the starting volume of inspiration. The dynamic work of breathing done on the lung (W_{resp}) was determined for each breath as the area of the P_{TP}–volume loop digitally calculated by an algorithm for the manipulation of geometric information (Freeman, 1961). The method, when compared with planimetric analysis at different levels of ventilation, did not give systematically different results. Finally, the rate of work of breathing per unit time, i.e. the respiratory power ($\dot{W}_{resp}$), was computed as the product of W_{resp} and f_{resp}.

Statistical multiple comparisons among variances were made by the Tukey q-test, while comparison among two means was made by Student's t-test for paired data, when appropriate. The criterion for statistical significance was $P < 0.05$.

Results

Tracings obtained in an individual horse, at rest and during exercise on the treadmill, showing respiratory airflow, transpulmonary pressure and foot contact, are depicted in Fig. 1. The average values of the respiratory parameters determined in five horses during nine separate experiments, each consisting of measurements at rest and during four successive levels of exercise, are summarized in Table 1; the results obtained on the same animal in different experiments were averaged before calculating a general grand mean. The ventilatory response to steady-state exercise was observed to rise to $1200 \, l \, min^{-1}$ in individual experiments and was correlated with treadmill speed (v). The linear regression equation relating the average values of $\dot{V}E$ ($l \, min^{-1}$) and v ($m \, s^{-1}$) was: $\dot{V}E = 59.92 + 351.87v$ ($r^2 = 0.972$). The increase in $\dot{V}E$ appeared to result more from a rise in f_{resp} (min^{-1}) than from a rise in V_T (l) throughout the entire range of exercise, since the changes in f_{resp} and V_T were, respectively, 3.7 and 1.4 times the resting value at the lowest exercise level, and 5.2 and 1.9 times the resting value at the most elevated level. In the three horses in which foot contact was determined, a marked correlation was found between fs (min^{-1}) and v, a linear regression yielding the equation: $fs = 11.67 + 27.79v$ ($r^2 = 0.971$, $N = 12$). A rather individual, although constant, locomotor–respiratory coupling was found in the three horses: in two horses it remained constant throughout the entire range of speed at
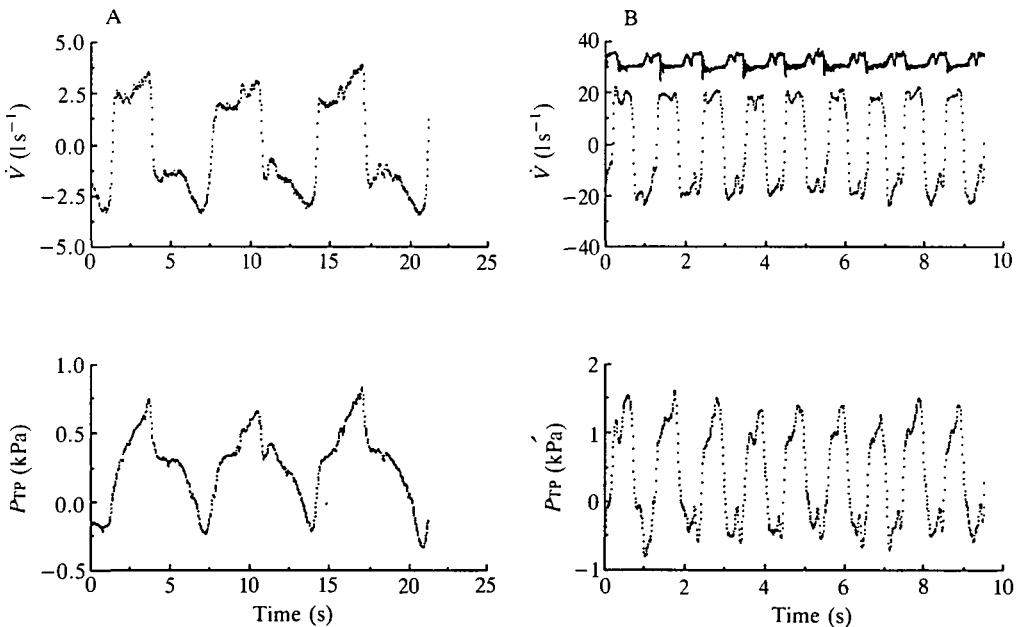

Fig. 1. Respiratory airflow ($\dot{V}$, in $l \, s^{-1}$), upper panels, and transpulmonary pressure (P_{TP}, in kPa), lower panels, recorded (A) at rest and (B) during exercise (velocity: $1.7 \, m \, s^{-1}$; incline: 7%) in an individual horse as a function of time. Inspiration is represented as a positive deflection of airflow. In B rear right limb contact with the ground is also shown, the downward deflection corresponding to the stance.

Table 1. *Mean values±S.D. of respiratory parameters observed at rest and during exercise at different treadmill speeds (7% incline) in five horses*

	N	v (m s^{-1})	V_T (1)	f_{resp} (min^{-1})	$\dot{V}_E$ (l min^{-1})	$\dot{W}_{resp}$ (W)
Rest	5	0	8.449±1.407	10.26±4.28	89.12±30.20	0.862±0.545
Level 1	5	1.106±0.077	11.568±2.216	38.09±9.89	425.72±92.22	8.020±2.869
Level 2	5	1.496±0.087	12.150±2.829	43.82±13.38	508.05±126.80	12.996±3.747
Level 3	5	1.816±0.089	15.445±3.602	48.86±17.25	740.77±284.54	18.989±9.731
Level 4	5	2.189±0.146	16.288±2.647	53.71±14.90	860.71±250.26	26.313±10.957

v, velocity, V_T, tidal volume; f_{resp}, respiratory frequency; $\dot{V}_E$, minute ventilation; $\dot{W}_{resp}$, rate of work of breathing.

a value of 2:1 (strides per breath) for one horse and 1:1 for the other one; in the third horse it shifted from an incomplete coupling averaging 1.5:1 while walking to a full coupling of 2:1 at a trot. In all animals, when the respiratory rhythm was locked to stride frequency, the beginning of inspiration always coincided with a rear-limb stance, as can be also appreciated from Fig. 1B.

$\dot{W}_{resp}$ (W) increased as a function of $\dot{V}_E$, being well described by the equation: $\dot{W}_{resp}=5.263\dot{V}_E^{1.5897}\times10^{-4}$, as shown in Fig. 2, in which 488 single breaths from five horses were analyzed from rest to the highest velocity attained.

C_{dynL} calculated from the same data gave a mean value of 19.78±5.20 l kPa^{-1} (±S.D.) at rest and did not change significantly during exercise (22.64±4.69 l kPa^{-1}).
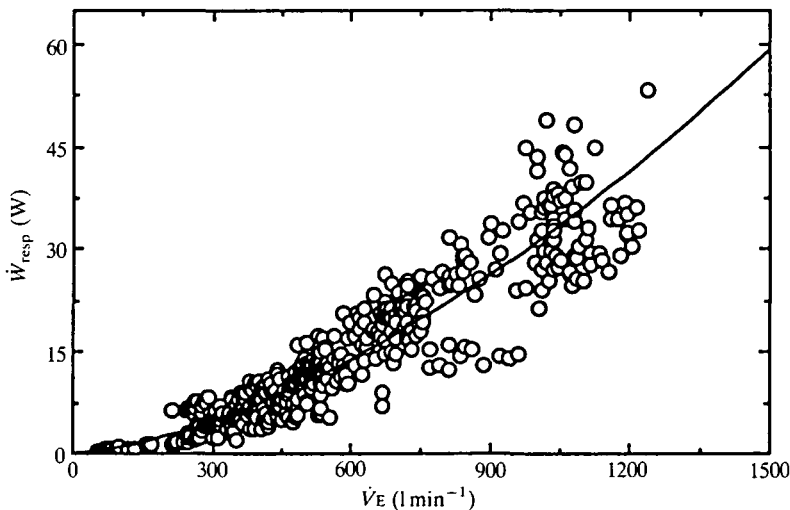

Fig. 2. Rate of respiratory work ($\dot{W}_{resp}$, in W) plotted against ventilation ($\dot{V}_E$, in l min^{-1}): data points refer to single breaths from all the experiments in five horses. The equation for the best-fitting line is: $\dot{W}_{resp}=5.263\dot{V}_E^{1.5897}\times10^{-4}$, $r^2=0.94$, $N=488$.

The relationship between P_{TP} (kPa) and airflow ($\dot{V}, \text{l s}^{-1}$) at rest and during exercise was investigated on a breath-by-breath basis, with the isovolume method, at three different levels of V_T. Values obtained at the three volumes did not differ significantly, as assessed by Student's t-test for paired data, and they were therefore pooled. A curvilinear relationship with upward concavity was observed in each steady-state condition, at all ventilatory levels and in all animals; this could be well fitted by an exponential function as described by Ainsworth and Eveleigh (1952): $P_{TP}=a\dot{V}^b$, where a and b are constants. Nonetheless, an overall decrease in the slope of the function was found when fitting data at successive velocity levels, so that a and b averaged at rest $6.77\times10^{-2}\pm4.69\times10^{-2}$ kPa s l^{-1} ($\pm$s.d.) and 1.274 ± 0.219, respectively (average $r^2=0.663\pm0.181$), while at the ventilation corresponding to the highest velocity the values decreased to $5.49\times10^{-3}\pm5.00\times10^{-3}$ kPa s l^{-1} ($\pm$s.d.) for a and rose to 1.673 ± 0.563 for b (average $r^2=0.559\pm0.014$). In Fig. 3 mean values ($\pm$s.d.) of P_{TP} determined at rest and at different level of exercise hyperpnoea in a single animal are plotted against the corresponding $\dot{V}$: continuous lines represent the function fitting breath-by-breath data at steady state by the above equation within any single level of exercise. Similar trends were observed in all horses.

The value of R_L calculated from these data was consequently found to decrease with the increase in ventilation as work level increased and the results obtained in five horses are summarized in Table 2. A multiple comparison between the different conditions was performed using Tukey's q-test and significant differences were found between the two higher levels and rest, as shown in Table 2.
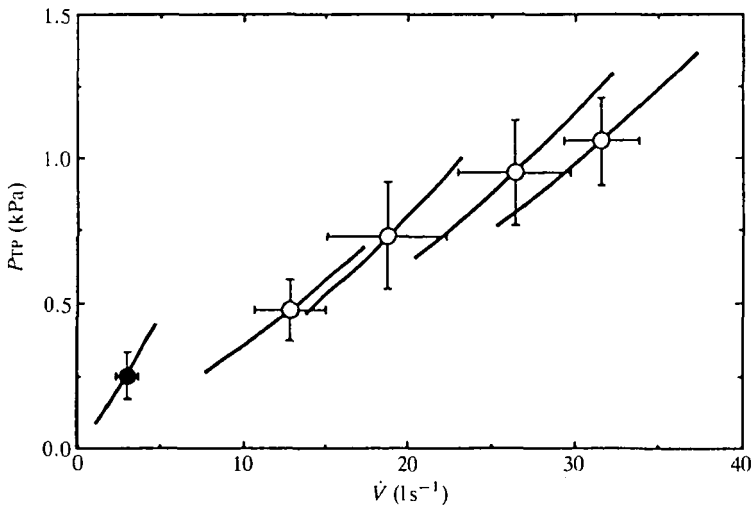

Fig. 3. Relationship between average values of transpulmonary pressure (P_{TP}, in kPa) and average values of respiratory airflow ($\dot{V}$, in l s^{-1}) observed in a single horse, at rest (closed circle) and during different levels of steady-state exercise (open circles; bars indicate s.d.). Continuous lines show the interpolation of single-breath values observed at each steady-state according to the function: $P_{TP}=a\dot{V}^b$.

Table 2. *Mean values±s.D. of pulmonary viscous resistance (kPa s l⁻¹) at rest and during exercise at different intensities in five horses and significance compared with resting values resulting from multiple comparison with a Tukey's test*

	Rest	Level 1	Level 2	Level 3	Level 4
R_L	0.087±0.045	0.040±0.015	0.037±0.009	0.027±0.010	0.027±0.007
P				<0.05	<0.05

R_L, pulmonary viscous resistance.

In two horses the breath-by-breath values of R_L were also determined during the transition from rest to exercise and *vice versa* at all work loads. A rapid and progressive decrease of R_L was observed in both animals simultaneously with the onset of exercise until the attainment of a plateau. At the end of the exercise a change in the opposite direction was observed, albeit with much slower kinetics, so that a full restoration of the resting condition was not attained in the 2 min observation period of the present study. Fig. 4 shows changes of R_L as a function of time from rest to the attainment of the exercise steady state and after the end of exercise in an individual horse during a single experiment, which is representative of the changes observed in both horses at all velocities.

In Fig. 5 single-breath R_L values are plotted against the mean inspiratory flow, $\dot{V}_I$, calculated as V_T over the respective inspiratory duration, which is a good representation of the respiratory drive (Clark and von Euler, 1972). Data refer to
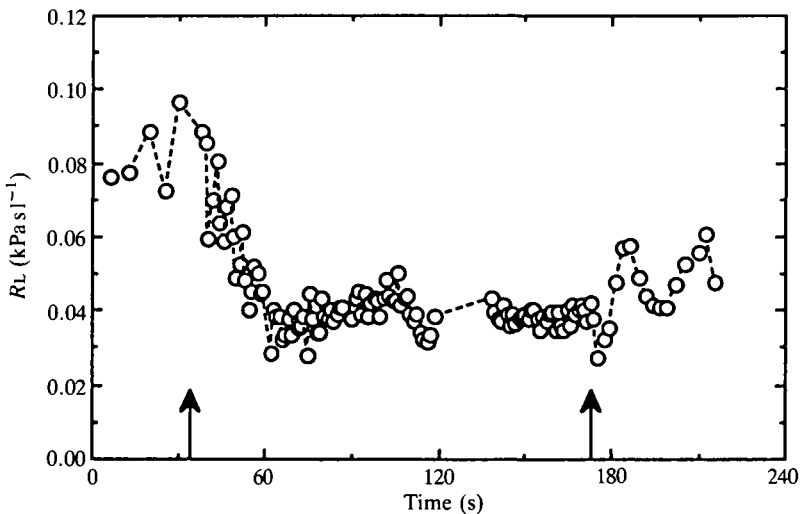

Fig. 4. The viscous resistance of the lung (R_L, kPa s l⁻¹) determined on a breath-by-breath basis in an individual horse is plotted as a function of time during the transition from rest to exercise and *vice versa*. The arrows denote the start and the end of the exercise.
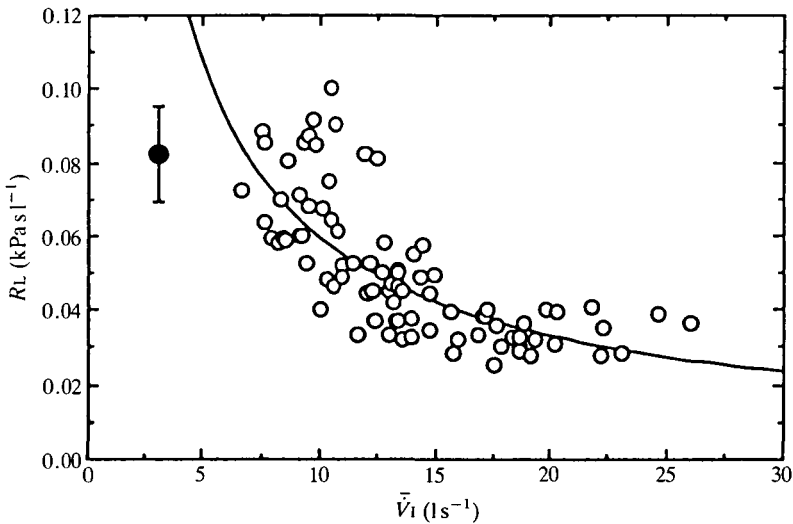
Fig. 5. Single-breath relationship between viscous resistance of the lung (R_L, kPa s l^{-1}) and mean inspiratory flow ($\bar{V}_I$, l s^{-1}) for the first 20–40 breaths after the onset of exercise in an individual horse at three different levels of exercise (open circles). The average value determined at rest ($N=16$) is also represented (closed circle; the bar indicates the s.d. of the mean).

the first 20–40 breaths after the onset of exercise and represent the change in R_L during the attainment of metabolic steady-state at three different levels of exercise in an individual horse. The average R_L value observed at rest is also presented in the figure. As the respiratory drive increased, R_L decreased to a minimum value which remained constant with further increases in drive and irrespective of the steady-state work level attained.

Discussion

The present investigation has revealed, in agreement with previous studies (Hörnicke et al. 1983; Thomas and Fregin, 1981; Woakes et al. 1987), a linear increase in $\dot{V}_E$ as a function of v. This progressive increase in $\dot{V}_E$ at successive levels of work load was achieved mainly by an increase of f_{resp} and, to a lesser extent, also of V_T. This trend in respiratory pattern is a common observation in horses (Rose and Evans, 1987b; Woakes et al. 1987; Pelletier et al. 1987) and ponies (Pan et al. 1983) and it has also been recently reported in exercising dogs (Ainsworth et al. 1989). However, it contrasts with findings on humans (Hey et al. 1966; Kay et al. 1975), possibly reflecting a feature of the quadrupedal gait. In fact, quadrupedal locomotion imposes mechanical constraints that require a certain degree of locomotor–respiratory integration (Bramble and Carrier, 1983), with respiration generally subordinate to locomotion, as also seems to be indicated by the strict correlation observed between f_S and v. It is known that f_S increases

linearly with v in the walk and trot and up to the trot–canter transition, beyond which stride length increments sustain further increases in v (Leach, 1987). It is possible that the rise in $\dot{V}$E above this transition speed is mainly due to increases in VT, but the mechanism controlling respiratory pattern at the transition needs further investigation. We found a constant coupling ratio in the three horses investigated for fs. At variance with previous studies (Hörnicke *et al.* 1983; Bramble and Carrier, 1983), which did not report any locomotor–respiratory coupling for gaits slower than a canter or slow gallop, our findings refer to a trot and also, in two horses, to a walk. It is possible that a different relationship between respiratory drive (and hence $\dot{V}$E) and velocity, due to the inclined treadmill exercising used in our experiments, may play a role in determining such a coupling for slower gaits, nevertheless entailing an intensified metabolic demand. Moreover, the untrained state of our animals may have further augmented $\dot{V}$E at a given work load, as is expected in this condition (Evans and Rose, 1988). The interplay of neurogenic and metabolic mechanisms controlling locomotor–respiratory coupling is not known in detail, but the observations of Bramble and Carrier (1983) support the importance of neurogenic control, although the relative influence of the central compared with the peripheral component is unknown. The observed synchronization between the beginning of the inspiratory phase and rear-limb stance and propulsion implies that the abdominal viscera should be subject to a sort of piston movement in phase with both locomotion and respiration (Bramble and Carrier, 1983); the importance of this in the respiratory strategy will be discussed later.

This study examined the relationship between pressure and flow observed at steady state. The findings indicate that in the respiratory system of the horse there is also some degree of turbulence at rest, as indicated by the value of b (approx. 1.3). The value of the constant b is considered to depend on the nature of the flow regimes, ranging between 1 (laminar flow) and 2 (fully developed turbulent flow) (Rodarte and Rehder, 1986). Nonetheless, when the respiratory drive increases during exercise hyperpnoea, a decrease in the slope ensues, although the increase of turbulence in airflow regimen can be inferred by the rise in the value of b (up to about 1.7). This trend, which is well depicted by the data presented in Fig. 3, is consistent with the decrease in RL we observed at higher levels of exercise hyperpnoea. Owing to the relatively large variability in RL at rest, the decrease in RL becomes statistically significant only at the upper levels of ventilation, but it is clear that a major drop ensues even at the ventilation rate corresponding to the lowest work load (see Table 2).

In the present study we failed to observe any effect of lung volume on RL for volumes corresponding to up to about 90 % of VT at rest and about 50 % at the highest ventilation attained, in spite of the fact that, in horses, the volume at the end of a spontaneous expiration (i.e. the functional residual capacity, FRC) is below the relaxation volume (Gillespie, 1983; Koterba *et al.* 1988) and hence they breathe in a region where a strong volume dependence is observed in humans (Bouhuys and Jonson, 1967). Since the absolute lung volume was not known and a

relatively small fraction of total lung capacity was studied, a definite conclusion concerning the relationship between R_L and lung volume in horses cannot be drawn.

The value of $C_{dyn}L$ we determined at rest is in good agreement with previously measured values in conscious horses (Gillespie et al. 1966; Willoughby and McDonnell, 1979; Koterba et al. 1988) and did not change significantly during exercise. This indicates that the elastic features of the lung are relatively linear (and unaffected by the respiratory frequency) in the range of volumes displayed during moderate exercise by healthy horses.

Values of R_L in the range $0.06–0.12\,\mathrm{kPa\,s\,l^{-1}}$ are commonly observed in conscious horses breathing at rest (Gillespie et al. 1966; Purchase, 1966; Koterba et al. 1988), but measurements during exercise are scanty. In spite of the marked alinearity of the pressure/flow relationship displayed by the horse's respiratory system even at rest, we observed the value of R_L to decrease significantly during exercise. This implies that some mechanisms counteract not only the increase in airflow and turbulence which is observed in the airways of a horse when ventilation rises above the resting values, but also the tendency of the airways to collapse (the extrathoracic airways during inspiration, the intrathoracic ones during expiration) when transmural forces become important. Although a direct action of catecholamines released during exercise (Snow and Rose, 1981) on the nasal mucosa and/or on airway tone cannot be excluded, the very rapid time course of R_L change at the onset of exercise (Fig. 4) may indicate a possible contribution of upper airway muscle activation to the observed decrease of R_L. The breath-by-breath correlation between $\dot{V}_I$, which is a good indicator of the respiratory drive (Clark and von Euler, 1972), and R_L during the transition from rest to exercise, as shown in Fig. 5, also suggests that a mechanical direct effector rather than a humoral one might be at least partly involved. In fact, the coordination between motor neurones of the laryngeal muscles (intrinsic and extrinsic) and premotor neurones connected to respiratory motor neurones is well known in different species (Sant'Ambrogio and Mathew, 1988), and the direct action on upper airway patency by these muscles during the respiratory cycle is well documented (Bartlett, 1989). This action is strongly modulated by reflex activity of upper airway receptors (Sant'Ambrogio et al. 1985). Moreover, Cook (1982) concluded, on the basis of endoscopy and biomechanical data, that the laryngeal cross-sectional area of horses after galloping increased by about 350 % above resting control values.

These findings contrast with the results of Art et al. (1988), who found a 75 % increase of R_L in fast-trotting ponies compared with the resting condition. However, in another study, the same authors did not report any significant change in R_L in the same breed of pony under very similar experimental conditions (Art and Lekeux, 1988). Moreover, Derksen et al. (1986) found that upper airway resistance remained substantially unchanged in horses exercising on a treadmill. However, in both studies the animals underwent surgical preparation and received widespread cannulation, so the effect of previous general anaesthesia and/or of

local anaesthetics, which are known to suppress or greatly reduce laryngeal activity (Bartlett, 1989), cannot be excluded.

Our experiments showed that $\dot{W}_{resp}$ increased during exercise as an exponential function of $\dot{V}_E$, the exponent being approximately 1.6. This figure reflects the decrease in resistance observed during exercise.

At the maximal oxygen uptake ($\dot{V}_{O_2max}$; i.e. $135\,ml\,min^{-1}\,kg^{-1}$, according to Jones *et al.* 1989) and using the ventilatory equivalent determined by Hörnicke *et al.* (1983) and by Thomas and Fregin (1981), $\dot{V}_E$ should be in the range $1600-1700\,l\,min^{-1}$. If the value of $\dot{W}_{resp}$ is extrapolated to this $\dot{V}_E$ a value of $65-75\,W$ is obtained, provided that the relationship found in the experimental range up to $1200\,l\,min^{-1}$ also holds for higher values of $\dot{V}_E$. With a respiratory quotient around unity, this figure corresponds in energetic terms to an oxygen uptake of $0.19-0.21\,l\,min^{-1}$. Indeed, the value of $\dot{W}_{resp}$ obtained from oesophageal pressure changes and the volume at the mouth do not account for all the work of breathing, because the work performed on the elastic and non-elastic forces of the chest wall, and on the elastic forces of the lung, is not measured. So, a more realistic estimate should include a further 25 % increase during exercise hyperpnoea (Roussos and Campbell, 1986). Should the average efficiency of the respiratory muscle (approx. 4.5 %) found by Dodd *et al.* (1989), who studied inspiratory and expiratory muscles separately during resistive breathing in man, also hold for horses, the oxygen uptake sustained by the respiratory muscles ($\dot{V}_{O_2resp}$) at $\dot{V}_{O_2max}$ in our conditions would be $5.2-5.7\,l\,min^{-1}$. Kayar *et al.* (1989) and Manohar *et al.* (1988) found, using different methods, that the diaphragmatic maximal oxygen uptake in horses is about $50\,ml\,min^{-1}\,100\,g^{-1}$ tissue. If this figure is applied to our horses, whose diaphragm, inferred from the results of these authors, could average $3.7\,kg$, the diaphragmatic maximal oxygen uptake should be about $1.85\,l\,min^{-1}$. Unfortunately, a quantitative partitioning of contributions of the different respiratory muscles to the development of V_T has not yet been determined, mainly because of the uncertainties concerning the biomechanical interpretation of their coordinated action. Hence, the energetic partitioning between diaphragm and extradiaphragmatic respiratory muscles is even more complex. However, the total respiratory energetic requirements calculated from our data on the basis of the respiratory efficiency determined in humans (Dodd *et al.* 1989) seem to contrast with the results derived from direct measurements of the diaphragmatic maximal oxygen uptake, since the contribution of the extradiaphragmatic muscles, which can be evaluated by difference, would account for 65–70 % of the total respiratory energetic expenditure. Although the contribution of the expiratory muscles is not known, this estimate seems unlikely to be realistic, since several studies measuring respiratory muscle blood flow in different animals, including horses (Roussos and Campbell, 1986; Manohar, 1987, 1988), indicate a dominant role of the diaphragm in exercise hyperpnoea. Thus, the efficiency of the respiratory muscles in the horse during exercise may be higher than that determined in man. Several biological differences may put the respiratory pump at an advantage in the horse. First, the quadrupedal posture during locomotion implies a horizontal acceleration and

deceleration of the visceral mass which, loosely connected to the skeletal structure, has been shown to act in phase and synergistically with the respiratory muscles (Bramble and Carrier, 1983; Alexander, 1988). Moreover, in horses the last part of expiration is active, as shown by electromyographic studies (Koterba *et al.* 1988), and FRC is lower than the relaxation volume: this implies that the diaphragm is passively stretched during the last part of expiration and operates in a most advantageous region of its force/length curve. In mechanical terms this pattern implies: (a) that a reduced amount of work is actively performed on the elastic structures of the respiratory system, as can be seen from a simple geometric demonstration on a pressure–volume diagram; (b) that a greater fraction of the total respiratory work is contributed by the expiratory muscles, so reducing the burden impinging on the inspiratory muscles; and (c) that pressure to overcome respiratory inertia, which has been shown to be remarkable in exercising horses (Art *et al.* 1989), is partly recovered from the energy stored in the elastic structures at the beginning of both inspiration and expiration. Further investigation is necessary to quantify the importance of these factors in the equine respiratory strategy.

Finally, if the relationship between $\dot{W}_{resp}$ and $\dot{V}E$ is normalized for the resting value, one can appreciate that, for a given increase in $\dot{V}E$, $\dot{W}_{resp}$ increases much less in horses than in other species. In Fig. 6 this relationship determined on the horse is compared with the results obtained in our laboratory on man (Lafortuna *et al.* 1984) and on the dog (Saibene *et al.* 1981), the latter breathing normally or panting. It appears that a 10-fold increase in $\dot{V}E$ corresponds to an approximately
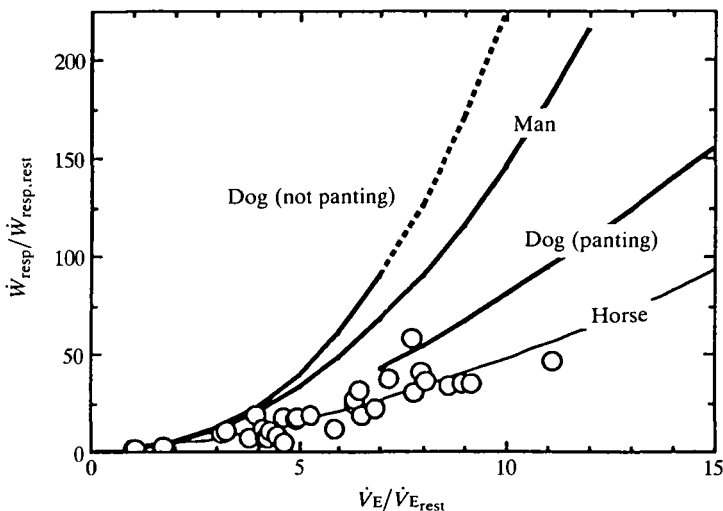

Fig. 6. Relationship between rate of respiratory work and ventilation normalized for the resting values ($\dot{W}_{resp}/\dot{W}_{resp, rest}$ and $\dot{V}E/\dot{V}E_{rest}$) observed in the horse: open circles are average values obtained in single experiments on five animals. The same relationship is presented as continuous lines for man and dog, either breathing normally or panting. The broken line shows a region of the function seldom observed in dogs, as in these conditions a panting pattern is adopted.

50-fold increase in $\dot{W}_{resp}$ for the horse, an approximately 150-fold increase for man and an approximately 225-fold or 75-fold increases for a dog breathing normally or panting, respectively; panting is the most common pattern of breathing during heavy exercise in this animal.

Although the data refer to the dynamic $\dot{W}_{resp}$, it is clear that the horse is the most economical breather among the species considered. This is achieved not only by the lower respiratory resistance, which results at rest from the scaling of airway calibre as a function of body mass (Leith, 1983), but also by active mechanisms that decrease the respiratory resistance during exercise.

The present study shows that the mechanical features of the respiratory system in horses appear commensurate with the functional needs of this species, seemingly conforming to the criteria of regulated morphogenesis (Taylor and Weibel, 1981). Whether this is the result of evolutionary (adaptive) or allometric (size-dependent) variation still remains to be evaluated by further investigation on other mammals of similar size.

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