THE SYNCHRONIZATION OF VENTILATION AND LOCOMOTION IN HORSES (*EQUUS CABALLUS*)

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Summary

Ciné film and synchronized records of respiratory flow were obtained from Thoroughbred racehorses cantering on a treadmill at speeds of 9 and $11\,\mathrm{m\,s^{-1}}$.

Horses and some other galloping and hopping mammals link their breathing and locomotion, taking exactly one breath per stride. Three theoretical mechanisms by which the movements of locomotion might drive ventilation are considered. (i) Flexion of the lumbosacral joint and the resulting forward sweep of the pelvis pushes the viscera against the diaphragm. However, back flexion lags behind ventilation at $11\,\mathrm{m\,s^{-1}}$ and could not exclusively drive ventilation at this speed. (ii) Loading of the thorax by the impact of the forelimbs with the ground might force air out of the lungs. If the respiratory system were damped sufficiently to perform as this mechanism requires, the work of driving ventilation would make up approximately 15% of the total work of running. In comparison with other estimates of the work of ventilation this seems improbably high. (iii) The observed phase relationship between displacements of the viscera, caused by the accelerations of the body during running, and respiratory airflow is not consistent with a tuned visceral piston mechanism driving breathing.

Thus, it would seem likely that back flexion is likely to contribute towards driving ventilation but loading of the thorax and the visceral piston mechanism do not.

Introduction

It has been observed that some running and hopping animals synchronize their ventilation and locomotion. Horses, dogs and hares all take exactly one breath per stride when they canter and gallop (Bramble and Carrier, 1983). Hopping

wallabies show a similar relationship (Baudinette *et al.* 1987). It has been suggested that this coupling could be due to a biomechanical linkage (Bramble and Carrier, 1983; Alexander, 1989; Baudinette *et al.* 1987): a ventilation mechanism, driven by the movements of running, might be responsible.

During periods of fast cursorial locomotion, many animals are observed to maintain an almost constant stride and respiratory frequency (Baudinette *et al.* 1987; Alexander, 1989; Bramble and Carrier, 1983; Attenburrow, 1983), increasing their speed and respiration by simply lengthening their stride and increasing their tidal volume. This would tend to suggest that a resonant mechanism may be operating.

This investigation considers three possible driving mechanisms that were proposed by Bramble and Carrier (1983) and later expounded by Alexander (1989) using mathematical models of the horse and wallaby. The three mechanisms are (i) flexion of the back, (ii) loading of the thorax by the forelimbs, and (iii) the visceral piston.

Bending of the back (i) occurs largely at the lumbosacral joint. Flexion of this region and the resulting forward sweep of the pelvis could displace the viscera forwards. The displaced volume of viscera would tend to push up against the diaphragm and, in turn, displace a volume of air from the lungs with each flexion of the back. Loading of the thorax by the forelimbs (ii) may compress it; if this occurs at the appropriate point in the respiratory cycle air would be forced out of the lungs. The viscera may be regarded as a mass suspended by elastic structures within the body wall rather like a piston within a cylinder (iii). Accelerations acting upon the body must cause displacements of this visceral piston relative to the body wall. The size and the phase of these displacements will be determined by the mass and viscoelastic properties of the viscera and their supporting structures. If this piston were to behave as a tuned oscillator, its displacements could drive ventilation. Alexander (1989) shows that this mechanism may operate to drive the breathing of hopping wallabies.

For his analysis of horses, Alexander (1989) had available ventilation and footfall patterns from only two short sequences of cantering and galloping (Bramble and Carrier, Fig. 3A) and had to infer accelerations as direct measurements were not available. We have now obtained more extensive data, including measured accelerations, which enable us to evaluate the proposed mechanisms more reliably. Our conclusions would tend to confirm those of Alexander (1989).

Materials and methods

The data analysed in this study were obtained from two Thoroughbred racehorses, of masses 460 kg and 480 kg and heights, measured at the withers, of 1.58 m (15 hands three inches) and 1.53 m (15 hands one inch), running upon a treadmill at speeds of $9\,\mathrm{m\,s^{-1}}$ and $11\,\mathrm{m\,s^{-1}}$.

A low-resistance method for measuring high gas flow rates was employed to measure the respiratory airflow of the exercising horses (Woakes *et al.* 1987).

Airflow transducers are positioned by means of a fibreglass facemask such that an ultrasonic signal passes obliquely across the path of the expired and inspired air from each of the horse's nostrils. Two ultrasonic elements in each transducer alternate between transmitting and receiving the signal to or from each other. The phase shift in the received signal is detected and produces a voltage proportional to the rate of flow. The signal corresponding to zero flow rate is confirmed every time the horse swallows and does not alter within an experiment.

A ciné film was taken from the side of the treadmill to show the movements of the horse during locomotion. This was synchronized with the trace of respiratory airflow by flashing a light from behind a camera shutter into the camera. A light-dependent transistor in front of the shutter registered a small voltage when illuminated, and this was recorded on one channel of a pen recorder. The trace of respiratory airflow was recorded upon the second channel of the same pen recorder. A flash of light on the film corresponds to a 'blip' on the pen recorder, allowing synchronization of film and recordings to an accuracy determined by the period of a film frame (1/64th of a second). A video camera placed in front of the horse was used to record the relative phases of each footfall during the locomotory cycle, throughout the experiment.

Bony landmarks, palpated through the horse's skin, were marked with adhesive plasters so that they could be easily located on the ciné film. A point on the ilium, lateral to the lumbosacral joint (*a*), another on the sacrum (*b*), and a third upon the abdomen, lateral to the anterior lumbar vertebrae (*c*), were marked (Fig. 1).
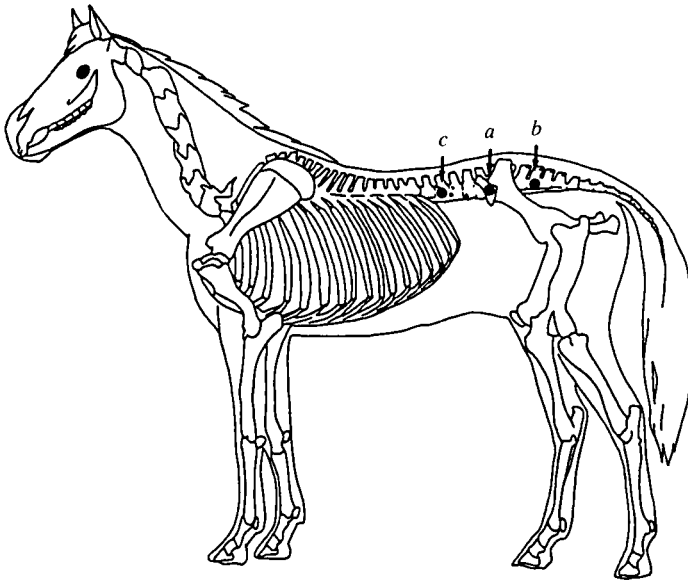

Fig. 1. Bony landmarks, palpated through the skin, were marked with adhesive plasters. One point was on the ilium in line with the lumbosacral joint (*a*), another upon the sacrum (*b*) and a third upon the abdomen (*c*).

The angle between lines ab and ac was taken to be the angle of flexion of the lumbosacral joint. Points a, b and c were recorded manually from a film analyser (PCD analyser and Visual Instruments analysis projector) onto transparent film and the angles were measured using a protractor.

The ciné film provides a synchronized record of hind footfall for the test period and the video provides a record of both the fore and hind footfalls. Together, the ciné film and video can be used to show the relative phases of limb action and respiratory airflow.

The displacement of the abdomen was assumed to be the same as the displacement of the point c which was placed as far anterior as possible, lateral to the anterior lumbar vertebrae, to avoid extraneous displacements due to flexion of the back at the lumbosacral joint and movements of the abdominal wall. Three complete locomotory cycles were analysed from each sequence of film and three or four of these sequences were acquired for each horse at each speed. Cartesian coordinates of point c were obtained by digitising the position of a corner of the adhesive plaster. Accelerations of this point can be calculated using software specially developed (by C. I. Smith, J. Oughton and I. S. Young) for this purpose. The problem of noise that arises in the calculation of second-order differentials of empirical functions was overcome by seven-point smoothing (Lanczos, 1957). We have tested the resolution of the seven-point smoothing formula by applying it to sine waves of various frequencies. We find that, when data are sampled at $1/64$ s intervals, calculated accelerations are 0.97–1.00 of the true values for frequencies up to 2 Hz and 0.90–1.00 for frequencies up to 4 Hz. When applied to the movements of galloping at about 2 Hz, the formula should give satisfactory estimates of acceleration at the fundamental frequency and the first harmonic, but will attenuate higher harmonics.

Smoothed x and y components of acceleration were calculated and were, in turn, used to calculate a component of acceleration directed towards the diaphragm. Measurements from an anatomical drawing (Getty, 1975) show that the diaphragm subtends an angle of approximately 45° to the horizontal. The acceleration perpendicular to this ($\ddot{s}$) may be calculated:

$$\ddot{s} = \ddot{x}\cos\theta + \ddot{y}\sin\theta \qquad (1)$$

where θ is the angle between the vector of the displacement s and the abdominal axis, $\ddot{x}$ is the horizontal and $\ddot{y}$ is the vertical component of acceleration. The sensitivity of the model to different choices of diaphragm angle was tested by calculation of the component of acceleration at 30° and 60° to the horizontal for several sequences. This acceleration was then used to calculate the displacements of the visceral piston. The amplitude of movement of the piston was decreased for diaphragm angles of 30° and increased for angles of 60°, but phase difference was altered by less than 5° in each case. Neither of these effects is large enough to alter our conclusions. A Fourier series of this component of acceleration was then derived and used to predict the displacement of the visceral piston (Thomson, 1981; Alexander, 1989).

If input accelerations are periodic with frequency ω, they can be represented by a Fourier series:

$$\ddot{s} = \sum_n (a_n \sin n\omega t + b_n \cos n\omega t) . \tag{2}$$

The response of the piston (shown in Fig. 2) can be represented by the Fourier series:

$$z = \sum_n \{Z_n[\sin(n\omega t - \delta_n) + (b_n/a_n)\cos(n\omega t - \delta_n)]\} , \tag{3}$$

where

$$Z_n = a_n/\{\omega_0^2[1 - (n\omega/\omega_0)^2]^2 + (2\zeta n\omega/\omega_0)^2\} \tag{4}$$

and

$$\tan(\delta_n - \pi) = (2\zeta n\omega/\omega_0)/[1 - (n\omega/\omega_0)^2] . \tag{5}$$

ω is the circular frequency ($2\pi f$, where f is the stride frequency) and ω_0 is the natural circular frequency. If the piston is tuned to the stride frequency, $\omega/\omega_0 = 1$. z is the displacement of the viscera, Z_n is the amplitude of the nth harmonic, t is time and δ is the phase given by equation 5 (Alexander, 1989, equations 6–9). The damping factor, ζ, is assigned a value of 0.5 as in Alexander (1989). This value was chosen because it produces predicted respiratory flow rate amplitudes close to those observed. Consequently, we cannot use predicted flow rate amplitudes to test the visceral piston hypothesis but only the phase relationship between flow rate and the acceleration of the abdomen.
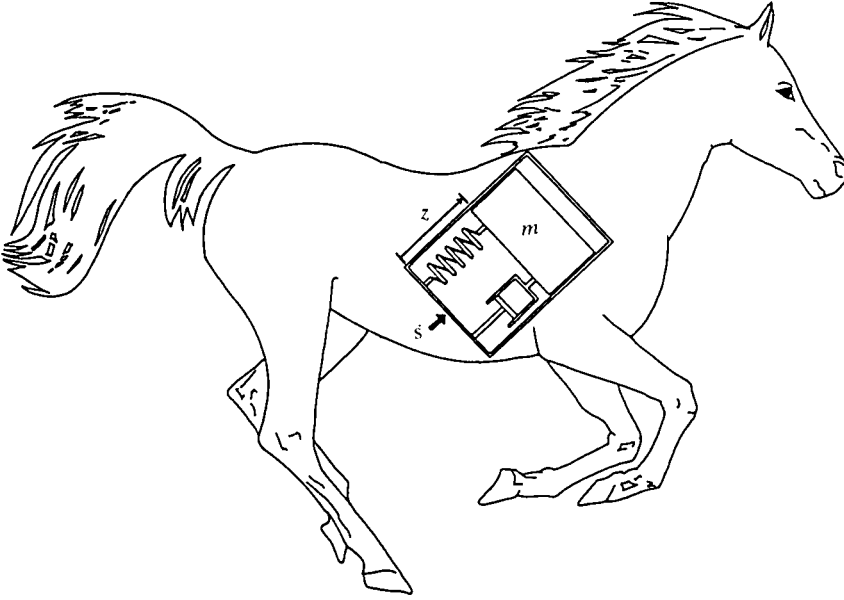

Fig. 2. The visceral piston. The viscera are represented as a mass, m, suspended by a spring and dashpot which represent the viscoelastic properties of the surrounding tissues. The component of acceleration directed towards the diaphragm, $\ddot{s}$, causes a displacement, z, of the viscera.

In Fig. 2 an acceleration ($\ddot{s}$) causes a corresponding displacement (z) of the viscera (mass, m) relative to the body wall. The viscoelastic properties of the supporting structures are represented by the spring (stiffness) and the dashpot (damping).

Back flexion and extension, footfall, predicted displacements of the viscera and respiratory airflow were plotted upon the same time axes. Their phase relationships and frequencies were determined from these plots. Phase comparisons are made using the following references. (1) 0° on the ventilation trace as the instant of zero flow rate at the onset of expiration (see Fig. 3). (2) 90° on the back flexion trace as maximum flexion. (3) 0° on the footfall trace as initial foot contact of the first forefoot. (4) 0° at the instant of zero displacement during the forward movement of the visceral piston. Mean frequencies and phase differences were calculated and 95 % confidence limits attached by using Student's t distribution.

A measurement of the height of the horse, taken at the withers, was used to scale a transverse section through a horse's trunk from an anatomical drawing (Getty, 1975). This was used to estimate the first moment of area (Warnock and Benham, 1965) of a transverse section through the abdominal cavity about an axis through the centrum of the vertebra at the lumbosacral joint (Alexander, 1989). The first moment of area, when multiplied by the range of flexion of the back, gives the volume swept forwards by lumbosacral flexion.

Results
Back flexion

Table 1 shows the phase difference between back angle and respiratory air flow at $9\,\mathrm{m\,s^{-1}}$ and at $11\,\mathrm{m\,s^{-1}}$. The phase relationships for animal 2 galloping at $11\,\mathrm{m\,s^{-1}}$ are shown in Fig. 3. The mean phase difference (calculated as the mean for different runs of the mean phase difference for the cycles within a run) for the combined data at $9\,\mathrm{m\,s^{-1}}$ is not significantly different from 90° (Table 1). At $11\,\mathrm{m\,s^{-1}}$ the mean phase difference of the combined data is slightly less than 90° (72 ± 16) (mean ± 95 % confidence limits).

The frequencies of back flexion and of ventilation in each cycle do not differ significantly (within 95 % confidence limits, Table 2).

The volume of viscera swept forward by the pelvis is calculated as the first moment of area of a transverse section through the horse's abdomen, $0.037\,\mathrm{m^3}$, multiplied by the angle through which the back moves in radians (for animal 1 at $9\,\mathrm{m\,s^{-1}}$, 27° or 0.47 rad), giving the volume swept forwards by lumbosacral flexion as about 17 l. This, in turn, might displace up to 17 l of air from the lungs compared to about 14 l calculated by integration of the flow trace. We would expect a larger volume than this to be displaced by this mechanism at higher running speeds as the angle through which the back moves increases with increasing speed. For animal 1, $27\pm1°$ to $30\pm1°$ and for animal 2, $24\pm1°$ to $29\pm22°$, at 9 and $11\,\mathrm{m\,s^{-1}}$, respectively.

Footfall
Fig. 3 shows forefoot contact with the ground, denoted by the blocked regions.
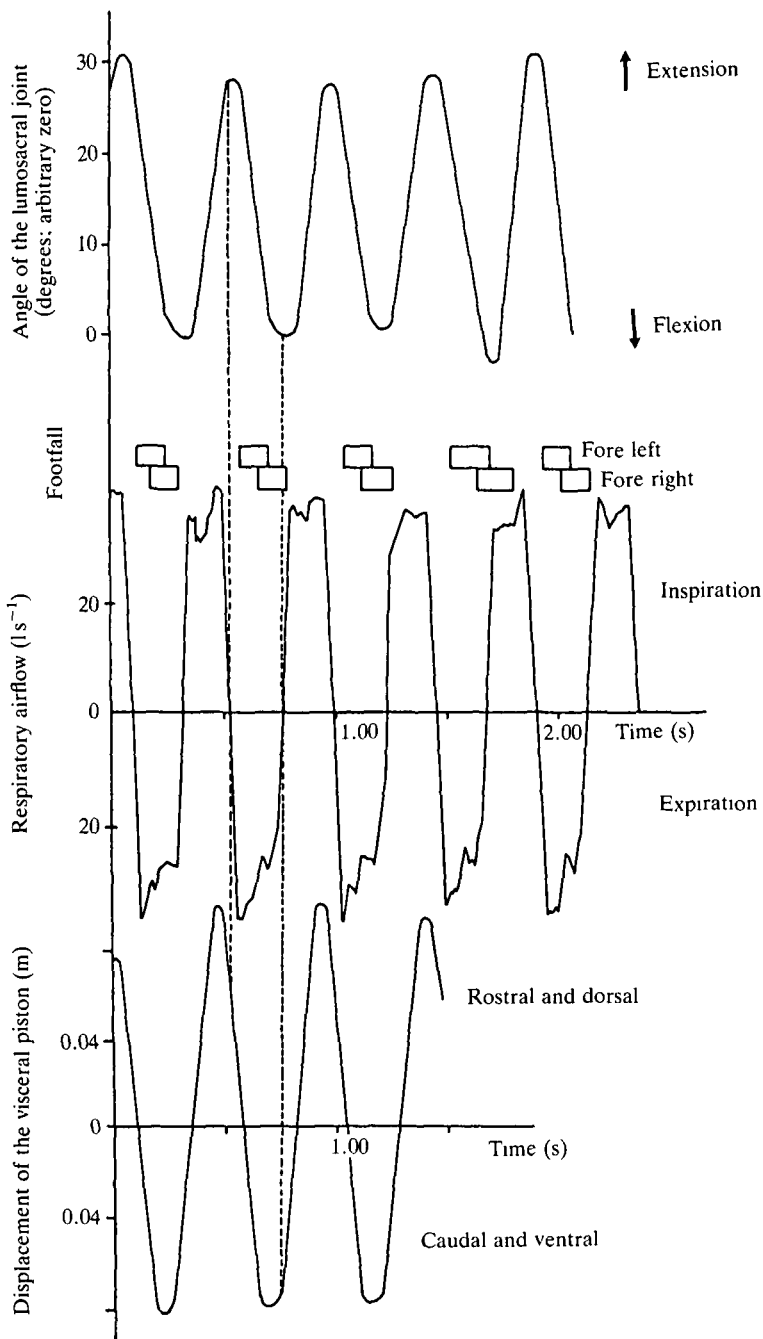
Fig. 3. A representative series of traces from animal 2 galloping at $11\,\mathrm{m\,s^{-1}}$. Flexion of the back, footfall, respiratory flow and the calculated displacement of the visceral mass are compared. The dotted lines indicate the beginning and end of one expiration.

Table 1. *Phase difference between back flexion and breathing and displacement and breathing at $9\,m\,s^{-1}$ and $11\,m\,s^{-1}$*

	$9\,\mathrm{m\,s^{-1}}$	$11\,\mathrm{m\,s^{-1}}$
Flexion		
Animal 1	92 ($\pm$3) $N=9$	79 ($\pm$16) $N=9$
Animal 2	69 ($\pm$11) $N=12$	65 ($\pm$22) $N=9$
Combined	79 ($\pm$10) $N=21$	72 ($\pm$14) $N=18$
Displacement		
Animal 1	226 ($\pm$9) $N=9$	252 ($\pm$8) $N=9$
Animal 2	233 ($\pm$9) $N=12$	234 ($\pm$9) $N=9$
Combined	230 ($\pm$6) $N=21$	243 ($\pm$7) $N=18$

Values are mean run phase difference in degrees ($\pm$95 % confidence limits) and number of cycles averaged.

By comparison with the plot of ventilation, it can be seen that the period when the forefeet are on the ground corresponds to the period of maximal expiration. The stride frequency and respiratory frequency were not significantly different (Table 2).

The visceral piston

At $9\,\mathrm{m\,s^{-1}}$ the calculated displacements have a range of about 0.10 m. Such displacements, acting over the 0.13 m² area of the diaphragm (estimated from drawings in Getty, 1975) would displace about 13 l of air at each stride. The actual air movement obtained by integrating the flow trace is 14 l. The frequency of the displacement cycle and that of ventilation are not significantly different (Table 2). However, the period of rostral and dorsal displacement does not coincide with expiratory airflow as it must if this mechanism were driving ventilation (Fig. 3). Table 1 shows the phase difference between the start of rostral and dorsal displacement and the start of expiratory airflow. For $9\,\mathrm{m\,s^{-1}}$ and $11\,\mathrm{m\,s^{-1}}$ the phase differences are ($\pm$95 % confidence interval) 230° ($\pm$6°) and 243° ($\pm$7°) respectively.

Discussion

Flexion of the back

This model assumes that back flexion results in a forward movement of the

Table 2. *Mean frequencies of flexion, footfall, displacement and ventilation for animals 1 and 2 at 9 and 11 m s^{-1}*

	Run 1	Run 2	Run 3	Run 4
Animal 1 at 11 m s^{-1}				
Flexion	2.2 (±0.3)	2.2 (±0.1)	2.1 (±0.1)	
Footfall	2.2 (±0.1)	2.2 (±0.1)	2.1 (±0.1)	
Displacement	2.1 (±0.1)	2.2 (±0.1)	2.1 (±0.1)	
Ventilation	2.1 (±0.1)	2.2 (±0.1)	2.2 (±0)	
Animal 1 at 9 m s^{-1}				
Flexion	2.0 (±0.2)	2.0 (±0.1)	2.0 (±0)	
Footfall	2.1 (±0.1)	2.0 (±0.3)	2.0 (±0.1)	
Displacement	2.0 (±0.1)	2.0 (±0.3)	1.9 (±0.1)	
Ventilation	2.0 (±0.1)	2.0 (±0.1)	2.0 (±0.1)	
Animal 2 at 11 m s^{-1}				
Flexion	2.2 (±0.2)	2.2 (±0.1)	2.2 (±0)	
Footfall	2.2 (±0.2)	2.2 (±0.1)	2.2 (±0.2)	
Displacement	2.2 (±0.1)	2.1 (±0.2)	2.1 (±0.2)	
Ventilation	2.3 (±0.1)	2.2 (±0.1)	2.3 (±0.1)	
Animal 2 at 9 m s^{-1}				
Flexion	2.2 (±0.2)	2.1 (±0.1)	2.2 (±0.1)	2.2 (±0.2)
Footfall	2.2 (±0)	2.2 (±0.2)	2.1 (±0)	2.1 (±0)
Displacement	2.1 (±0.1)	2.1 (±0.1)	2.1 (±0.2)	2.1 (±0.1)
Ventilation	2.2 (±0.1)	2.1 (±0.1)	2.1 (±0.1)	2.2 (±0.1)

Values are mean cycle frequency (Hz) within each run (±95 % confidence limits).

pelvis driving a volume of viscera before it, which, in turn, pushes up against the diaphragm and cause a displacement of air from the lungs. If ventilation were to be driven by this process then certain relationships must be observed. If we assume that the abdominal contents are largely solid or liquid, and therefore relatively incompressible, and that airway resistance is not excessive, flexion of the back should occur approximately at the same time as expiration and extension of the back at the same time as inspiration. This would require both frequency and phase to be matched. The rate of flow of air must be proportional to the rate of change of angle. There must be a phase difference of 90° between flexion of the back (which displaces the viscera towards the diaphragm) and respiratory airflow (which is proportional to the rate of this displacement).

An initial requirement for linkage is satisfied in this study as the frequencies of ventilation and back flexion are essentially the same. For the combined data in Table 1, the phase difference at 9 m s^{-1} is not significantly different from 90°, as would be predicted if ventilation were driven by flexion of the back. However, at 11 m s^{-1} the phase difference is slightly less than ideal (by about 18±16°, mean ± 95 % confidence limits), the onset of expiration being slightly earlier than the beginning of the flexion of the back. The difference is small in both cases. If this difference is significant then flexion of the back could not exclusively be

driving ventilation and, for a very small proportion of the expiratory period, will hinder it. Another mechanism must be involved.

Calculation of the volume of viscera swept forward by the pelvis by each flexion gives an estimate of the possible volume that can be driven out of the lungs during each cycle. This was calculated as 17 l and is probably an over-estimate of air displaced from the lungs for at least two reasons. (1) Not all of the volume swept out by the pelvis will reach the diaphragm; some will be lost due to ventral bulging of the belly. However, ventral bulging of the belly might be reduced by an increased muscle tone in the abdominal muscles at the appropriate point in the respiratory–locomotory cycle. Abdominal muscle activity is observed to occur at appropriate times in the stride in dogs (Tokuriki, 1974), which are also known to link locomotion and ventilation (Bramble and Carrier, 1983). (2) Not all of the period of flexion may correspond to expiration and, therefore, would not help to increase the volume of air displaced. The results obtained in this study indicate that this correspondence would only apply to a very small proportion of the total period and that therefore this effect would be quite small.

The tidal volume of a 500 kg horse cantering at 9m s^{-1} is about 14 l. This suggests that flexion of the back could displace a sufficient volume of air to drive ventilation were the phase relationship correct. Even allowing for some departure from the ideal phase relationship, this mechanism may still contribute substantially to driving ventilation.

Footfall

The period when the forefeet are on the ground corresponds to the period of increasing and maximum expiratory flow (Fig. 3). Compressive forces will therefore be acting upon the thorax almost all of the time that the horse is exhaling. This is consistent with the suggestion that dorsoventral compression of the thorax drives respiration. However, for the reasons explained by Alexander (1989), this phase relationship between thoracic compression and breathing implies a heavily damped system. If the system were only lightly damped, it would be compressed as the load on the thorax increased and then recover while the force decreased, but continue to vibrate when the feet were off the ground. Damping implies that work would be done on the thorax as it was compressed, and that this work would be dissipated, not stored as strain energy. We will estimate the work required and consider whether it could be accounted for by the work of breathing. If not, it would have to be done by some other mechanism, of which the most likely seems to be negative work by muscles resisting thoracic compression.

An estimate of the volume of a horse's thorax may be made by calculating cross-sectional areas of 'slices' at known intervals using anatomical drawings (Getty, 1975). If the thoracic length and breadth remain the same, then the vertical compression of the thorax necessary to produce the measured tidal volume is about 0.056 m. This is the same fraction of the total thoracic height as the tidal volume is of the total thoracic volume.

About 60 % of the body weight (60 % of 5000 N) is supported by the forelimbs

(Björck, 1958), so the mean value (over a complete stride) of the ground force upon the forelimbs will be 3000 N. The mean compressive force imposed by the forelegs while their feet are on the ground may be estimated as the mean ground force divided by the fraction of the stride for which one or both forefeet are on the ground (0.65 at 9 m s^{-1}), or about 4.5 kN. The work done in compressing the thorax can be calculated by multiplying this force by the distance that the thorax is compressed, 0.056 m, giving a value of 250 J. Heglund *et al.* (1982) calculate mechanical work per stride as about 3.5 J stride^{-1} kg^{-1} or 1.75 kJ for a 500 kg horse. Thus, if the proposed mechanism is driving ventilation, the work of breathing will make up almost 15 % of the total work of running. Lafortuna and Saibene (1991) have calculated the rate of respiratory work for horses exercising upon a treadmill for an experimental range of ventilation rates up to 1200 l min^{-1}, which are comparable with the lower ventilation rates measured in our study. They show that the mechanical power of breathing (W_{resp}, in watts) increases with the minute volume (ventilation rate, $\dot{V}$E, in l min^{-1}) according to the equation:

$$W_{resp} = 5.26\,\dot{V}\text{E}^{1.59} \times 10^{-4}.$$

They then add 25 % to this value to account for work done upon the elastic and non-elastic forces of the chest and the elastic forces of the lungs. It would seem reasonable to use the above equation to provide an estimate of the expected rate of work of breathing in our experiments.

For a ventilation rate of 1640 l min^{-1} (corresponding to the tidal volume of 14 l and a stride and ventilation frequency of 2 Hz), the estimated rate of work of breathing is about 88 W or 44 J per stride. We have shown that thoracic loading could not be driving ventilation unless the work for compressing the thorax were six times as high, 250 J per stride. This would imply substantial and apparently unnecessary energy losses, presumably due to damping by the thoracic muscles doing negative work. Thus, it seems unlikely that ventilation is driven principally by this mechanism.

The visceral piston

The visceral piston is essentially a tuned oscillator, a mass (the viscera) within a moving frame (the body of the horse) suspended by elastic structures having a certain degree of damping associated with them. A Fourier series of the component of acceleration directed towards the diaphragm was used to predict the response of the visceral mass.

If the visceral piston is driving ventilation, then the predicted displacement would have the same frequency and lead respiratory airflow by 90°. Fig. 3 shows traces of displacement upon the same time axes as respiratory airflow. With a phase shift of 90° between expiration and displacement, the onset of expiration would coincide exactly with the onset of rostral and dorsal displacement. However, this displacement lags behind expiration by between a quarter and half a cycle or, in terms of the values given in Table 1, it leads the next expiration by between half and three-quarters of a cycle (230±6° at 9 m s^{-1} and 243±7° at

$11 \mathrm{m\,s^{-1}}$). Fig. 3 shows that expiration occurs during caudal and ventral movement of the visceral piston. Given this phase relationship, the visceral piston mechanism could not be driving breathing.

In conclusion, we have shown that the forces imposed on the thorax cannot be driving ventilation unless the work directly or indirectly associated with breathing is much higher than has been previously estimated, approximately 15 % of the work of running.

At a running speed of $9 \mathrm{m\,s^{-1}}$, flexion of the back and the resulting compression of the viscera have an appropriate frequency and calculated magnitude to drive ventilation. The phase difference seems to be a little greater than 90° but this difference from 90° is only significant at $11 \mathrm{m\,s^{-1}}$. This indicates that back flexion does not have an appropriate phase relationship to respiratory airflow to be driving ventilation exclusively: that is, the flow begins slightly before the flexion that could be driving it. However, this discrepancy is only small and flexion of the back probably contributes considerably towards the driving of breathing.

The phase relationship of the displacements of the visceral piston with respect to respiratory airflow show that ventilation cannot be driven by a tuned visceral piston mechanism.

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