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THE RELATIONSHIP BETWEEN MECHANICAL WORK AND ENERGY EXPENDITURE OF LOCOMOTION IN HORSES

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Summary

Three-dimensional motion capture and metabolic assessment were performed on four standardbred horses while walking, trotting and galloping on a motorized treadmill at different speeds. The mechanical work was partitioned into the internal work (W_{INT}), due to the speed changes of body segments with respect to the body centre of mass, and the external work (W_{EXT}), due to the position and speed changes of the body centre of mass with respect to the environment. The estimated total mechanical work ($W_{TOT}=W_{INT}+W_{EXT}$) increased with speed, while metabolic work (C) remained rather constant. As a consequence, the 'apparent efficiency' ($eff_{APP}=W_{TOT}/C$) increased from 10 % (walking) to over 100 % (galloping), setting the highest value to date for terrestrial locomotion. The contribution of elastic structures in the horse's limbs was evaluated by calculating the elastic energy stored and released during a single bounce ($W_{EL,BOUNCE}$), which was approximately 1.23 J kg^{-1} for trotting and up to 6 J kg^{-1} for galloping. When taking into account the elastic energy stored by the spine bending and released as W_{INT}, as suggested in the literature for galloping, $W_{EL,BOUNCE}$ was reduced by 0.88 J kg^{-1}. Indirect evidence indicates that force, in addition to mechanical work, is also a determinant of the metabolic energy expenditure in horse locomotion.

Key words: biomechanics, energetics, locomotion, efficiency, horse.

Introduction

The horse (*Equus caballus*) is a very interesting species for historical and athletic reasons. From ancient times to the industrial revolution it was utilised by man as a work generator in roles in public transportation, from the times of Alexander the Great (fourth century BC) to the Pony Express. The highly specialised evolution, with lengthening of the distal limbs and progressive reduction in the number of toes from five to one (Hildebrand, 1994), and thousands of years of selective breeding for speed and endurance have also made the horse an outstanding power generator. In fact, its maximum aerobic power output is 3.5 times higher than the value predicted by general mammalian allometric equations (Taylor et al., 1981). At speeds of approximately 10.5 and 16 m s^{-1}, for long-duration and sprinting bouts, respectively, the horse is one of the fastest quadrupeds on Earth. Since the movement actuator, the muscle, is considered to be structurally similar across different species and sizes (Schmidt-Nielsen, 1984), there is a great interest in the mechanisms underlying such an impressive performance.

A few metabolic measurements have been made during locomotion on full-sized horses (e.g. Eaton et al., 1995), but no data on the corresponding mechanical work is available. As a consequence, the locomotory efficiency has never been calculated. For bouncing gaits, such as running, trotting and galloping, a great deal of mechanical work is apparently generated, despite the rather low energy consumption required. A major challenge in the physiology of locomotion today is the precise measurement of the mechanical work actually generated by the muscles. These measurements are complicated by two factors: (1) the ability to store and release elastic strain energy in tendons and ligaments, and (2) the occurrence of isometric muscle contractions. The former affects the measured mechanical work, but not the metabolic expenditure (as in a bouncing rubber ball). The latter, conversely, increases the energy consumption and leaves the mechanical work unaffected (as in a standing man with a moderate degree of knee flexion). To complicate this scenario further, we need to consider that a muscle with in-series elastic structures can force oscillations (in periodic movements) that simultaneously involve both these factors, as has recently been observed in running turkeys (Roberts et al., 1997).

In this study, we concurrently assessed, at different gaits and speeds, the metabolic energy expenditure and the mechanical work of horse locomotion using three-dimensional motion analysis. In addition, we attempted to separate the work produced by muscles from that derived from passive elastic structures and to evaluate the cost of force generation.

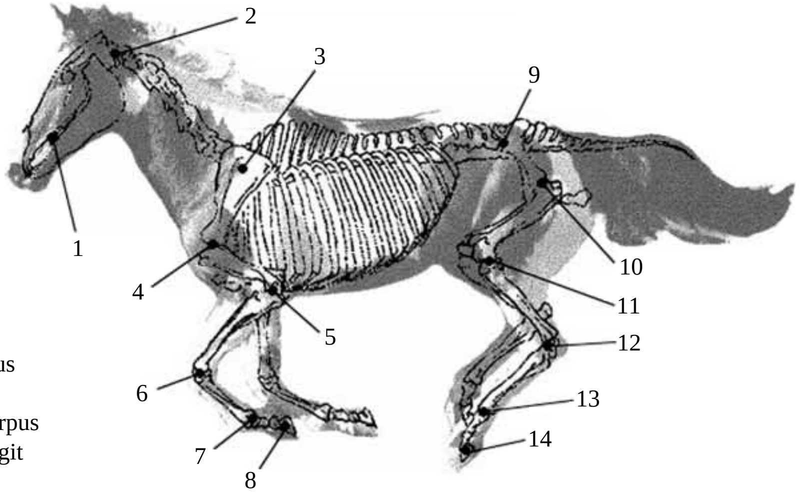

Fig. 1. Diagram showing the positions of reflective markers on each side of the horse's body. The list describes the 11 segments of each side that were used in the calculation of mechanical work.

Links	
1–2	Head
2–3	Neck
3–4	
4–5	Humerus
5–6	Radius
6–7	Metacarpus
7–8	Fore-digit
3–9	Trunk
9–10	
10–11	Femur
11–12	Tibia
12–13	Metatarsus
13–14	Hind-digit

Materials and methods

Four standardbred horses (mass 515.0±29.1 kg, mean ± S.D.; range 498–538 kg) walked (W), trotted (T) and galloped (G) on a motor-driven treadmill (Kagra 2000, Switzerland) at speeds ranging from 1 to 12 m s^{-1}. For each condition, simultaneous mechanical and metabolic measurements were made.

Biomechanical measurements

Each trial was recorded by means of an opto-electronic motion-analysis system (ELITE System, B.T.S., Italy) consisting of four cameras, each sampling at a rate of 100 Hz. Fourteen reflective hemispherical markers (diameter 4 cm) were placed on each side of the horse to identify the segments of interest: head, neck, trunk, humerus, radius, metacarpus, fore-digit, femur, tibia, metatarsus and hind-digit (Fig. 1). The three-dimensional positions of segment extremities were calculated stereometrically by the system. Each data acquisition lasted for 5 s, and the stride frequency was calculated by analysing the periodicity of the vertical coordinates and by counting the number of frames for a stride. One representative stride was extracted, according to the regularity of the vertical coordinates of the markers with respect to time, from the 5 s acquisition period and was successively fed into an algorithm for the determination of the mechanical work (see below).

Values for the segment mass (as a fraction of body mass), the position of the centre of mass and the radius of gyration were taken from Buchner et al. (1997). Positive internal and external work (W_{INT} and W_{EXT}, respectively) were computed using the method of Cavagna and Kaneko (1977), who used König's theorem to account for the changes in the kinetic energy of segments whose movements do not affect the position of the overall centre of mass (e.g. symmetrical limbs displacements). This theorem states that the total kinetic energy of a multi-link system can be divided into two parts: (a) the kinetic energy of the segments arising from their change of speed with respect to the overall centre of mass, and (b) the kinetic energy of the overall centre of mass with respect to the environment. The first term constitutes W_{INT}, while the second is included in the external work, W_{EXT}, defined as the work necessary to raise and accelerate the centre of mass of the body with respect to the environment. Other details of the experimental design were reported by Minetti et al. (1993).

The three-dimensional displacement of the centre of mass of the body was calculated for each frame from the positions of the 22 body segments (the head, neck and trunk segment were split into left and right parts). External work (W_{EXT}) was obtained by summing the increments of the total energy (E_{T}) with respect to time: $E_{\mathrm{T}}=E_{\mathrm{P}}+E_{\mathrm{Kx}}+E_{\mathrm{Ky}}$ (where E_{P} is the potential energy of the centre of mass of the body and E_{Kx} and E_{Ky} are the horizontal and vertical components, respectively, of the kinetic energy of the body's centre of mass). The total mechanical work (W_{TOT}) was computed as the sum of W_{EXT} and W_{INT}. Mechanical was expressed per kilogram of body mass and per unit distance (i.e. J kg^{-1} m^{-1}).

The 'energy recovery', an index of the ability of a system to recover mechanical energy through the interchange between E_{P} and E_{K} (equal to 100 % in an ideal pendulum), was obtained according to Cavagna et al. (1976).

All the data-processing and statistics were performed on an Athena 486/66 DX2 computer and an Apple Macintosh Duo 2300 computer. Low-pass filtering of the spatial coordinates was performed using the procedure of D'Amico and Ferrigno (1990), in which optimal filter cut-off frequencies are selected automatically. The range of cut-off frequencies was 5.0–9.0 Hz using this procedure. A custom-built program, created using LabView2/MacOS (National Instruments, USA), was used to analyse the three-dimensional data and to calculate the biomechanical variables for 209 strides.

Metabolic measurements

Standard open-circuit respirometry was used to determine the metabolic power requirements. The expired gas, flowing through a mask firmly positioned around the nostrils (BRDL, Birmingham, UK), was collected in Douglas bags, and ventilation rate was assessed by using a chronometer and a dry gas meter (Collins, USA). O_2 and CO_2 partial pressures were measured using gas analysers (Binos 1, Leybold-Heraeus and Oxynos 100, Rosemount, Germany). After converting values to STPD (laboratory air temperature was always within the range 14–16 °C), the rate of O_2 uptake was calculated. Values for the standing horse were subtracted from the steady-state values, reached after approximately 4 min of exercise, to obtain the net metabolic work rate during each trial. To express the metabolic work (*C*) in the same units as mechanical work ($\mathrm{J\,kg^{-1}\,m^{-1}}$), we divided the net metabolic work rate by the speed ($\mathrm{m\,s^{-1}}$) and assumed that 1 ml of O_2 is equivalent to 20.1 J (for a mean respiratory quotient of approximately 0.95) to convert metabolic into mechanical units.

The efficiency of locomotion, the ratio of mechanical to metabolic work, was calculated by dividing W_{TOT} by *C*.

Results

The rate of energy consumption of standing horses was $1.94\pm0.48\,\mathrm{ml\,O_2\,kg^{-1}\,min^{-1}}$ (mean ± S.D., *N*=4). Fig. 2 shows, for each gait, the metabolic cost at different speeds. Because of technical problems related to air leakage through the mask, only a subset of all the measurements was considered. The main criteria for rejecting some measurements were the lack of an increase in ventilation with increasing speed (within each gait) and a respiratory quotient exceeding 1.0.

Typical changes in mechanical energy for walking, trotting and galloping are shown in Fig. 3. By summing all the energy increases in E_{T} over the stride period and expressing the result per unit mass and distance, we obtained W_{EXT}. Fig. 4 shows these values (upper curve) and W_{INT} (lower curve).

Table 1 reports the regression coefficients for parabolic regressions for the main variables discussed in the paper. Second-order regression was used for descriptive purposes, since it can fit most linear and non-linear data without further increasing the complexity of the analysis.

Discussion

The energetics of horses locomotion shows some optimisation phenomena (Alexander, 1989). At each gait, a speed exists at which *C* is minimal, as originally discovered in a study on small horses (Hoyt and Taylor, 1981). In addition, minima in *C* are comparable at the different gaits, showing an overall constancy of the metabolic energy spent per unit distance travelled, despite the difference in speed, although the value of *C* during walking is lower than that reported by Hoyt and Taylor (1981). This is because the subtraction of basal (standing) metabolic rate from the metabolic measurements, as applied here, has a greater effect at low speeds than at higher speeds (for a review of different techniques for calculating *C*, see Full, 1991). While exceeding (by approximately 30 %) the allometric equation obtained for mammalian and bird species with masses ranging from 0.01 to 254 kg (Taylor et al., 1982), the present values of *C* are comparable with previous measurements on horses (Farley and Taylor, 1991; Eaton et al., 1995; Potard et al., 1998; Langsetmo et al., 1997; Butler et al., 1993; Wagner et al., 1989).

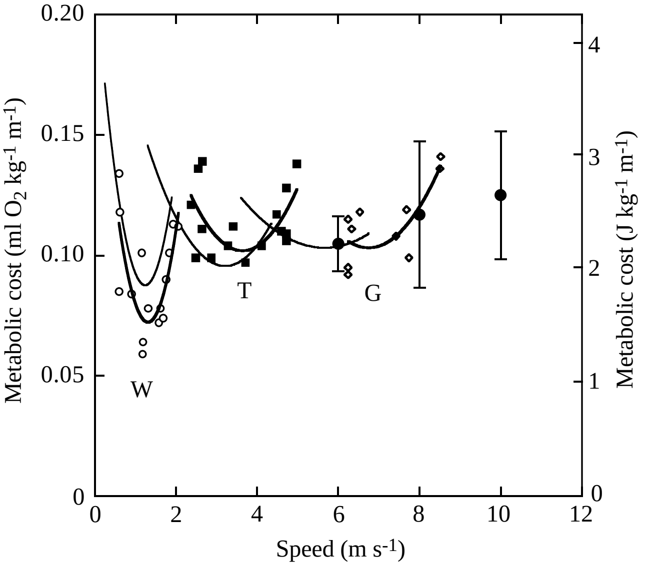

Fig. 2. Relationship between the metabolic energy cost (per unit mass and distance) and speed during walking (W), running (R) and galloping (G). The thick curves refer to parabolic fits of the experimental data (the regression coefficients are given in Table 1), while the thin curves represent the parabolic fits of the data of Hoyt and Taylor (1981) for a 140 kg horse. Filled circles shows mean galloping cost and bars refer to standard deviations (S.D.) of data taken from the literature (Eaton et al., 1995; Potard et al., 1998; Langsetmo et al., 1997; Butler et al., 1993; Wagner et al., 1989). Open circles represent data for walking, filled squares for trotting and open diamonds for galloping.

Mechanical work

The mechanical external work (Fig. 4, upper curves) during walking and trotting resemble the values for humans at corresponding gaits (Cavagna et al., 1976). Fig. 5 shows the three-dimensional range of movement of the centre of mass of the horse during single strides at the different gaits and speeds. It is surprising how the lateral displacement (d*z*) for a 500 kg horse drops from 50 mm (slow walking) to only a few millimetres during fast galloping and how the vertical displacement (d*y*) more than doubles when passing from trotting to galloping.

As it is calculated (Cavagna et al., 1976), W_{EXT} represents a good approximation of the mechanical work done by the muscles only for non-bouncing gaits such as walking. During

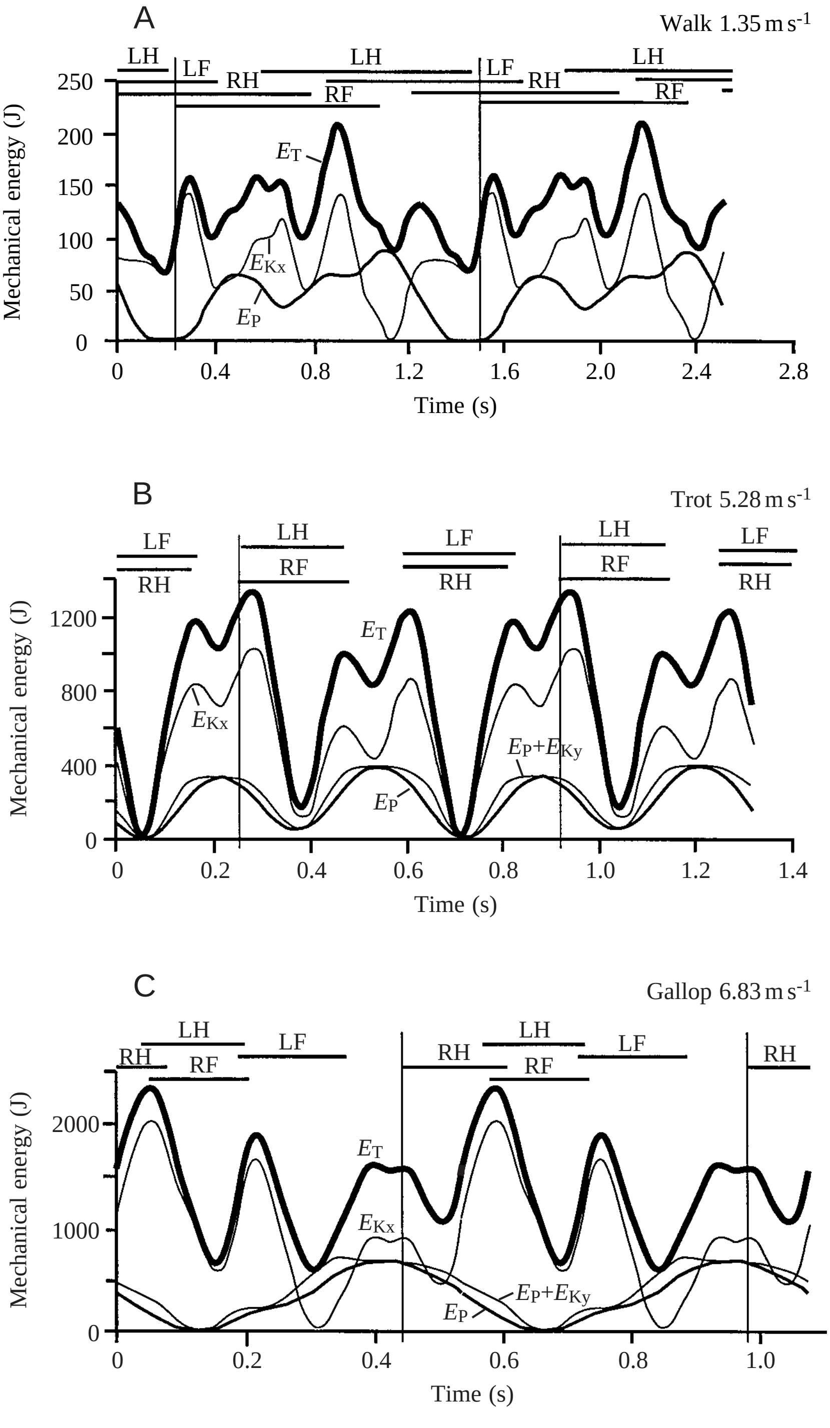

Fig. 3. Typical examples of changes in mechanical energy over time for each gait. The traces in each graph were obtained by duplicating a single experimental stride for illustrative purposes. Since the (positive) mechanical work is obtained by summing all the increases in the total energy (E_T) curve over the stride period (delimited by vertical bars), its main components (the potential energy E_P and the horizontal component of the kinetic energy, E_{Kx}) have been represented by removing an offset corresponding to their minimum value to accommodate all the curves in the same graph. Horizontal bars correspond to the contact time of the right-hind (RH), right-fore (RF), left-hind (LH) and left-fore (LF) hooves.

walking, a pendulum-like mechanism flattens the E_T curve by the sequential exchange of potential and kinetic energy of the centre of mass, resulting in a low W_{EXT}. However, during bouncing gaits (such as trotting and galloping), W_{EXT} overestimates the mechanical work actually performed by the muscles because the increases in energy in the E_T curve also include the work performed by previously stretched elastic structures such as tendons and ligaments. It has been suggested that, during galloping, both energy-saving mechanisms operate simultaneously (Cavagna et al., 1977; Minetti, 1998a). In fact, W_{EXT} increases with speed (Fig. 4), and the ‘energy recovery’ parameter (related to the capacity to use pendulum-like energy-saving mechanisms) (Cavagna et al., 1976) is higher during galloping than during trotting (Fig. 6). This high level of energy recovery, originally reported for rams and dogs in an earlier study (Cavagna et al., 1977), is not a completely unexpected feature of the galloping gait. In the investigated speed range (6–12 m s^{-1}) of the gait (usually termed a slow gallop or a canter), the footfall sequence is a ternary rhythm with the middle beat formed by two diagonal hooves (left-hind,

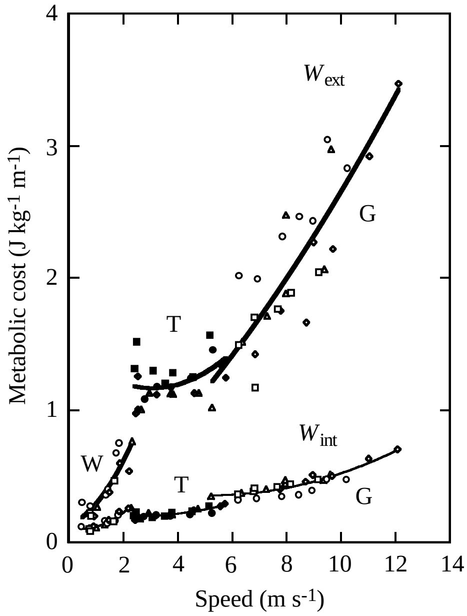

Fig. 4. Positive internal (W_{INT}) and external (W_{EXT}) mechanical work as a function of speed during walking (W), trotting (T) and galloping (G). Filled symbols refer to trotting. The superimposed curves represent the second-order regressions whose coefficients are listed in Table 1. The different symbols represent the individual horses.

LH, and right-fore, RF, for instance) hitting the ground simultaneously. This involves three downward peaks (braking) in the horizontal kinetic energy curve of the body's centre of mass (Fig. 3C). Since the potential energy curve is approximately sinusoidal, it is inevitable that E_P and E_{Kx} are out of phase in some parts of the stride, thus increasing energy recovery (Minetti, 1998a). The energy exchange is particularly evident at the first (RH) and third (LF) beats, whilst the middle beat (LH, RF) behaves similarly to the trot (Fig. 3B). Because of the dependence of E_{Kx} on speed and the independence of E_P from speed ($E_P = m\boldsymbol{g}dy$, where m is mass and $\boldsymbol{g}$ is the acceleration due to gravity; d*y* is shown in Fig. 5A), as also shown in other quadrupeds (Heglund et al., 1982), the energy recovery during galloping tends to decrease at high speeds (Fig. 6). A related similarity between walking and galloping is that the Lissajous contour of the centre of mass of the body (i.e. a plot of vertical *versus* horizontal coordinates), when seen from the left side of the animal, is a clockwise loop for both gaits, while it is a counterclockwise loop for trotting (as for running humans, see Cavagna et al., 1964).

The mechanical internal work has never been assessed in large (500 kg) horses. However, measurements in a 99 kg pony (Fedak et al., 1981) gave comparable results. The values for W_{INT} in Fig. 4 show that the dependency on speed may be different for each gait. This may be related to changes in limb positioning, e.g. folding of the limbs during the swing phase of bouncing gaits could reduce the moment arm and, consequently, W_{INT}. In fact, a recent W_{INT} model (Minetti, 1998b), when applied to the present data, is consistent with this

Table 1. *Coefficients for parabolic regressions between the indicated variables and speed*

		a	*b*	*c*	r^2
Total work, W_{TOT} (J kg^{-1} m^{-1})	W	0.128	0.045	0.240	0.858
	T	0.038	−0.222	1.689	0.301
	G	0.016	0.093	0.641	0.793
Metabolic work, *C* (ml O$_2$ kg^{-1} m^{-1})	W	0.081	−0.212	0.212	0.595
	T	0.014	−0.104	0.291	0.304
	G	0.011	−0.146	0.595	0.614
Stride frequency, *f* (Hz)	W	−0.032	0.407	0.318	0.911
	T	0.015	−0.015	1.249	0.880
	G	0.009	−0.109	2.114	0.659
Vertical displacement, d*y* (mm)	W	6.211	−11.924	23.895	0.293
	T	−3.341	28.488	4.243	0.452
	G	−3.429	58.610	−113.663	0.328
External work, W_{EXT} (J kg^{-1} m^{-1})	W	0.081	0.084	0.131	0.788
	T	0.031	−0.192	1.461	0.198
	G	0.009	0.168	0.088	0.728
Internal work, W_{INT} (J kg^{-1} m^{-1})	W	0.047	−0.038	0.109	0.923
	T	0.007	−0.030	0.228	0.720
	G	0.007	−0.076	0.552	0.838

Equations were of the form: $y = ax^2 + bx + c$, where x is speed (m s^{-1}). Sample size was 17 for walking, 24 for trotting and 27 for galloping for all variables except *C*, for which values of *N* were 15, 16 and 10 respectively.

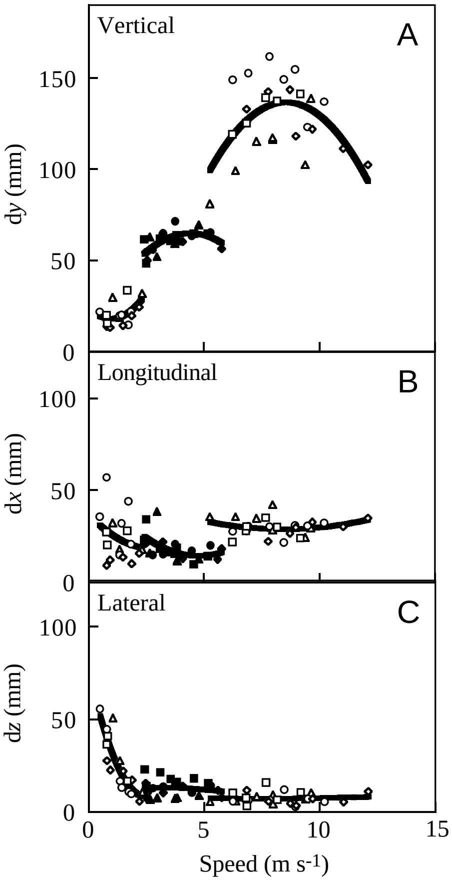

Fig. 5. Vertical (dy) (A), horizontal (dx) (B) and lateral (dz) (C) displacements of the centre of mass of the horse's body during a single stride at different gaits and speeds. Symbols as for Fig. 4.

hypothesis during trotting (W_{INT} is lower than during walking by 19 %) and, to an even greater extent (37 % lower) during galloping. Such a reduction in W_{INT}, mostly deriving from the change in limb geometry during the swing phase, could also be the consequence of the evolution of limb structures with the centre of mass located very proximally with respect to the pivoting point (as noted by D'Arcy Thompson, 1961). Furthermore, the model (Minetti, 1998b) shows that W_{INT} depends strongly on speed, stride frequency and duty factor (i.e. the fraction of the stride for which one foot is in contact with the ground). Since the relationship between the last two variables and speed is different for walking, trotting and galloping, the same applies to W_{INT}. While W_{INT} appears to be a minor contributor to the total mechanical work at high speed (see Fig. 4), the removal of the elastic component from the measured external work is expected to make it worthwhile to reduce W_{INT}. The contributions of single limbs to the estimated W_{INT} may change from one gait to another. In fact, in symmetrical gaits (walking and trotting), all limbs contribute equally to the overall W_{INT}, while during galloping the first-down hind limb (also called the leading rear) exhibits a greater W_{INT} (23–29 %) than the other limbs, giving it a predominant role in propulsion.

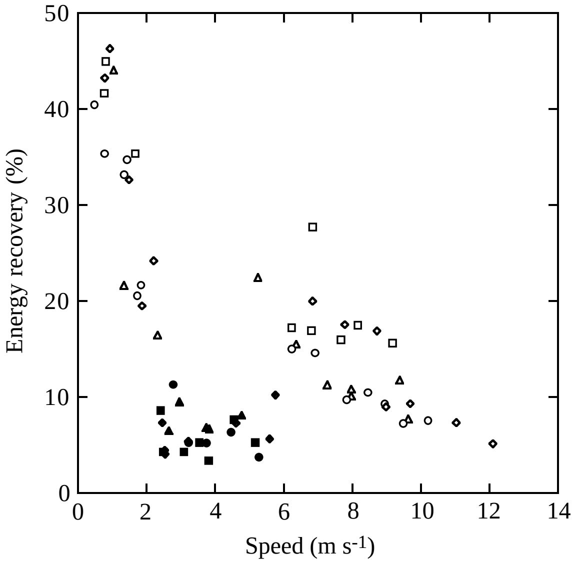

Fig. 6. Mechanical energy recovery representing the interchange between potential and kinetic energy of the centre of mass of the body, calculated according to Cavagna and Kaneko (1977), plotted against speed. Symbols as for Fig. 4.

Efficiency

The capacity to maintain a high mechanical energy of the body by periodic storage and release of elastic energy (during trotting and galloping), the additional ability to exchange potential and kinetic energy at faster gaits (galloping) and the very high aerobic power output (Taylor et al., 1981) are the keys to the athletic performance of horses. The structural design of the limbs and the actuator architecture, based on long tendons coupled with short, thick muscles (Dimery et al., 1986), reflects the development of fast gaits at reduced metabolic cost. The efficiency of locomotion can be calculated as:

$$eff_{APP} = \frac{W_{EXT} + W_{INT}}{C}\,. \tag{1}$$

The efficiency values shown in Fig. 7A range from approximately 10 % (for walking) to more than 100 % (galloping). [Note that these values, obtained by disregarding an amount of negative work equal to the positive work in level periodic movements, actually approximate the efficiency of positive work. It can be shown, by assuming that the efficiency of generating negative work is five times greater than that of generating positive work (Abbott et al., 1952), that the 'true' positive work efficiency values are underestimated by 17 %.] While Taylor (1994) suggested that this could be the case by extrapolating from mechanical data for different smaller animals, the present values for galloping are, to the authors' knowledge, the highest ever measured for animal locomotion. In contrast to walking, the efficiencies of trotting and galloping far exceed the value usually obtained from the thermodynamics of muscular contraction (25–35 %; Woledge et al., 1985). This is the reason why such efficiency is sometimes termed 'apparent efficiency' (eff_{APP}; Full, 1991). Among the terms

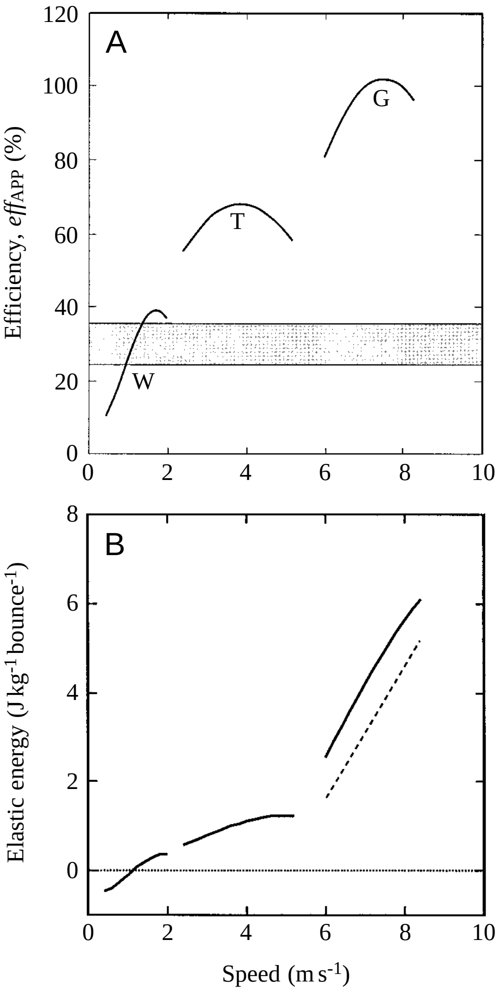

Fig. 7. (A) relationship between apparent efficiency (eff_{APP}) and speed obtained from the present measurements and equation 1; the shaded area represents the efficiency range of concentric muscle contraction as reported in the literature (Woledge et al., 1985). (B) The elastic energy stored and released during a single bounce (trotting, two bounces per stride; galloping, one bounce per stride) obtained using equation 3; the dashed line represents the elastic energy for galloping when the effect of spine bending on internal work (W_{INT}) is taken into account (see Discussion for details). G, galloping; T, trotting; W, walking.

involved in equation 1, W_{EXT} is the most likely to be inaccurate (i.e. overestimated with respect to the positive work actually done by muscles, as already mentioned). We will attempt, in the following, to calculate the elastic energy (stored and) released during each bounce for the different gaits and speeds. The following equation:

$$eff_{\mathrm{MUS}} = \frac{(W_{\mathrm{EXT}} - W_{\mathrm{EL}}) + W_{\mathrm{INT}}}{C}\,, \qquad (2)$$

where W_{EL} is the elastic work (J kg^{-1} m^{-1}) released by the limb tendons, is similar to equation 1 and deals with the muscle efficiency (eff_{MUS}) of transforming metabolic work into ‘fresh’ (rather than ‘previously stored’) mechanical work. Equation 2 tells us that, by assuming eff_{MUS} to be constant (=0.30; Woledge et al., 1985), the elastic contribution to the total mechanical work, as measured, can be calculated. In addition, by considering that trotting and cantering (slow galloping) differ in the number of bounces per stride (n_{BOUNCE} is 2 for trotting and 1 for galloping), the elastic work per bounce ($W_{\mathrm{EL,BOUNCE}}$) can be obtained:

$$W_{\mathrm{EL,BOUNCE}} = W_{\mathrm{EL}}\,\frac{v}{f n_{\mathrm{BOUNCE}}}\,, \qquad (3)$$

where v is speed and f is the stride frquency. Alexander and his co-workers (Alexander, 1988b; Ker et al., 1987) estimated that the amount of elastic energy stored during a running step was 35 J for the Achilles tendon and 17 J for the arch of the foot (a total of 52 J for a mean body mass of 70 kg, or 0.75 J kg^{-1} bounce^{-1}). The values for horses, computed using equation 3 and the regression equations given in Table 1, have been plotted in relation to speed in Fig. 7B as continuous lines. $W_{\mathrm{EL,BOUNCE}}$ is negligible during walking, as expected, but is remarkably high during trotting and galloping. Values for trotting can be compared with human running, the corresponding gait for bipeds. The 64 % higher $W_{\mathrm{EL,BOUNCE}}$ during trotting (1.23 J kg^{-1} bounce^{-1}), however, turns out to be more similar (–18 %) to the values for human running when the elastic work per bounce and per limb is considered. The highest value of $W_{\mathrm{EL,BOUNCE}}$ is for galloping, 6 J kg^{-1} bounce^{-1}, and the curve suggests a further increase with speed.

It has been proposed that additional storage and release of elastic energy during galloping (but not during trotting) could occur in the musculo-ligamentous apparatus along the spine, which extends (storage) during the foot-contact time and recoils (release) during the flight period (Alexander, 1988a). It has been postulated that this elastic energy saving affects only W_{INT}. The energy stored in the spine during the contact phase would be available for regrouping the limbs under the body during the flight period. Alexander (1988a) estimated that the amount of energy released was 44 J stride^{-1} in a 50 kg deer (*Dama dama*) or 0.88 J kg^{-1} bounce^{-1}. In the lower graph of Fig. 7B, the $W_{\mathrm{EL,BOUNCE}}$ attributable to limb elastic structures for a galloping horse (dashed line) has been calculated according to this energy-saving strategy. To provide evidence for the bending of the spine at different speeds and gaits, we positioned seven markers on the skin corresponding to the spinous processes of vertebrae and analysed their three-dimensional motion in one horse walking at 1.41 m s^{-1}, trotting at 3.49 m s^{-1} and galloping at three speeds (6.36, 7.80 and 9.17 m s^{-1}). Fig. 8 shows the time course of the vertical coordinates at all these speeds. It is apparent that the spine translates vertically without changing its shape during trotting, whereas the out-of-phase waveforms suggest a bending–recoil sequence within each stride during galloping. Moreover, the relationships among waveforms seem not to be affected by galloping speed. It can be therefore be hypothesised that the energy saving per stride by this mechanism depends on stride frequency alone.

The values of $W_{\mathrm{EL,BOUNCE}}$ obtained in this study are expected to be quite realistic because the calculation has been derived from experimental measurements. However, the

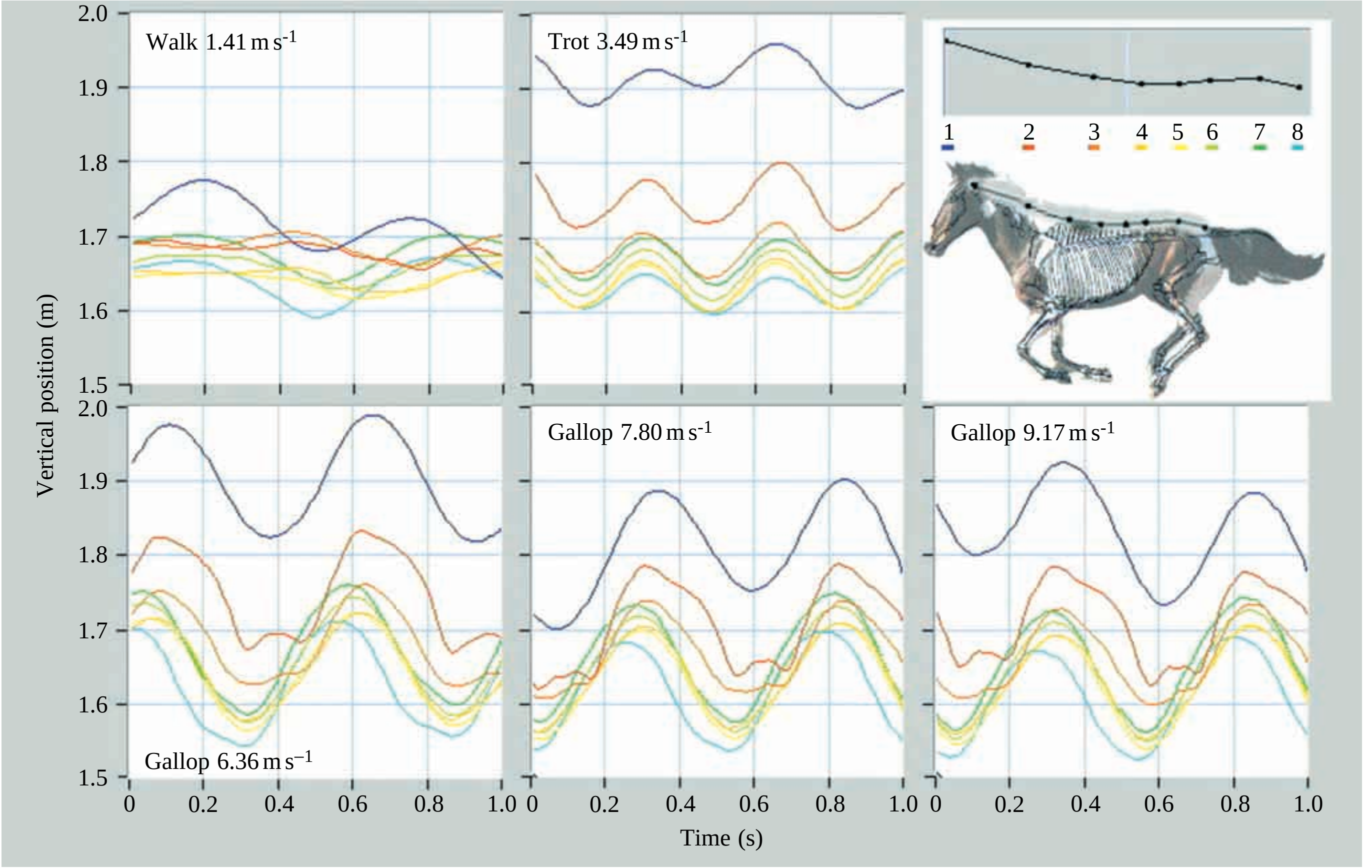

Fig. 8. Vertical positions of seven markers located along the spine with respect to time. The lowest two speeds refer to walking and trotting, while the other three pertain to galloping. The phase shift between the markers during galloping indicates bending of the spine.

assumption that eff_{MUS} is constant at the different speeds and gaits is questionable, although previous studies on human walking and running at different speeds and with different gradients (Minetti et al., 1993, 1994; Minetti, 1995) succeeded in matching mechanics to energetics using such a simplification. It should be noted that W_{EL} as obtained from equation 2 represents the lowest estimate of the elastic contribution to locomotion, since it would be higher if the muscles were to operate at a lower than optimal efficiency.

There is an unusual relationship between the apparent efficiency (eff_{AP}, Fig. 7A) and the vertical excursion of the centre of mass during the stride (dy; Fig. 5A). The eff_{AP} maxima for trotting and galloping correspond to the speeds at which dy is also maximal. This suggests that, at each gait, a ‘resonant’ frequency (and thus a ‘resonant’ speed) exists at which the greatest elastic contribution (dy; i.e. the compression of the spring) is obtained *via* the minimum forced-oscillation effort.

The force hypothesis

When comparing mechanical work and metabolic cost, another issue should be considered. Muscles utilise metabolic fuel both for generating work and for maintaining force (with no shortening, thus with no work). The roles of the force exerted in energy expenditure during running (Kram and Taylor, 1990) and in the gait choice (Farley and Taylor, 1991) have been recently pointed out. Experimental findings on running turkeys (Roberts et al., 1997) suggest that extensor muscles shorten very little during the stance phase of bouncing gaits, whilst the elastic structures (tendons) stretch and recoil. In this view, the muscles should contract almost isometrically and do little work during stance. If this were true, a remarkable proportion of the metabolic cost might be set by the cost associated with the generation of tension. According to this hypothesis, Kram and Taylor (1990) introduced the reciprocal of the stride length, defined as the distance travelled by the centre of mass during the support phase (their equation 4), as a predictor of the cost of transport (corresponding to C in the present paper). We calculated and plotted this predictor for trotting and galloping (Fig. 9). When comparing this graph with a plot of C versus speed (Fig. 2), it emerges that the shapes of the curves are different, with (stride length)$^{-1}$ decreasing monotonically with speed (Fig. 9) and C being approximately constant for all gaits (Fig. 2). Conversely, the ‘net’ mechanical work, calculated by removing from the measured mechanical work the estimated elastic energy released, increases with speed for each gait. It is possible, therefore, that a combination of the cost of generating force and the cost of producing mechanical work is necessary to explain the energy expenditure of locomotion in horses.

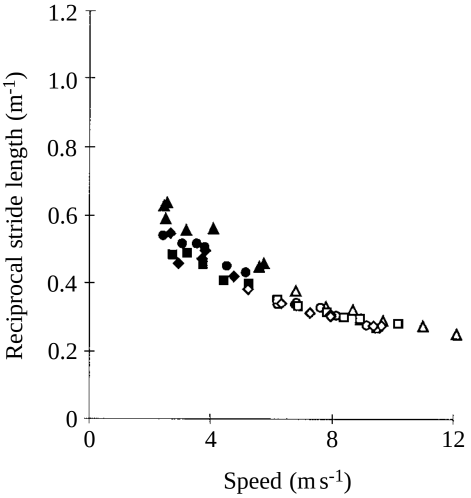

Fig. 9. A graph showing the reciprocal of the stride length, a predictor of the cost of locomotion (see Kram and Taylor, 1990), plotted against speed for trotting and galloping. Filled symbols represent trotting, open symbols represent galloping; the different symbol shapes indicate the individual horses.

In conclusion, horses probably represent the biggest quadrupeds for which metabolic and mechanical measurements of locomotion can be made in a controlled environment (constant-speed treadmill). The relationship between these variables, which are associated with athletic performance, sheds light on the role of the different gaits (walking and galloping are the most common gaits in quadrupeds, while trotting is optional in some cases; Pennycuick, 1975).

An 'apparent' efficiency of locomotion exceeding 100 % at high speeds, the highest value reported to date, implies that a huge amount of elastic energy is continuously stored and released to maintain the body in motion. Additional elastic structures, such as the ligaments in the spine, a highly specialised limb design and the concurrent use of pendulum-like mechanics at high speeds, are responsible of the athletic performance of horses. The combined energy-saving strategy adopted during the gallop can potentially explain the evolutionary advantage of introducing such a gait and deserves further investigation.

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References

Abbott, B. C., Bigland, B. and Ritchie, J. M. (1952). The physiological cost of negative work. *J. Physiol., Lond.* **117**, 380–390.

Alexander, R. McN. (1988a). Why mammals gallop. *Am. Zool.* **28**, 237–245.

Alexander, R. McN. (1988b). *Elastic Mechanisms in Animal Movement*. Cambridge: Cambridge University Press.

Alexander, R. McN. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.

Buchner, H. H. F., Savelberg, H. H. C. M., Schamhardt, H. C. and Barneveld, A. (1997). Inertial properties of Dutch Warmblood horses. *J. Biomech.* **30**, 653–658.

Butler, P. J., Woakes, A. J., Smale, K., Roberts, C. A., Hillidge, C. J., Snow, D. H. and Marlin, D. J. (1993). Respiratory and cardiovascular adjustments during exercise of increasing intensity and during recovery in Thoroughbred racehorses. *J. Exp. Biol.* **179**, 159–180.

Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.

Cavagna, G. A. and Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol., Lond.* **268**, 467–481.

Cavagna, G. A., Saibene, F. P. and Margaria, R. (1964). Mechanical work in running. *J. Appl. Physiol.* **19**, 249–256.

Cavagna, G. A., Thys, H. and Zamboni, A. (1976). The sources of external work in level walking and running. *J. Physiol., Lond.* **262**, 639–657.

D'Amico, M. and Ferrigno, G. (1990). Technique for the evaluation of derivatives from noisy biomechanical displacement data using a model based bandwidth-selection procedure. *Med. Biol. Eng. Comp.* **28**, 407–415.

D'Arcy Thompson, W. (1961). *On Growth and Form*. Cambridge: Cambridge University Press.

Dimery, N. J., Alexander, R.McN. and Ker, R. F. (1986). Elastic extension of the leg tendons in the locomotion of horses (*Equus caballus*). *J. Zool., Lond.*, **205**, 415–425.

Eaton, M. D., Evans, D. L., Hodgson, D. R. and Reuben, J. R. (1995). Effect of treadmill incline and speed on metabolic rate during exercise in Thoroughbred horses. *J. Appl. Physiol.* **79**, 951–957.

Farley, C. T. and Taylor, C. R. (1991). A mechanical trigger for the trot–gallop transition in horses. *Science* **253**, 306–308.

Fedak, M. A., Heglund, N. C. and Taylor, C. R. (1981). Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 23–40.

Full, R. J. (1991). The concepts of efficiency and economy in land locomotion. In *Efficiency and Economy in Animal Physiology* (ed. E. W. Blake), pp. 97–131, Cambridge: Cambridge University Press.

Heglund, N. C., Cavagna, G. A. and Taylor, C. R. (1982). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 41–56.

Hildebrand, M. (1994). *Analysis of Vertebrate Structure*, 4th edn. New York: Wiley.

Hoyt, D. F. and Taylor, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.

Ker, R. F., Bennet, M. B., Bibby, S. R., Kester, R. C. and Alexander, R. McN. (1987). The spring in the arch of the human foot. *Nature* **325**, 147–149.

Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265–266.

Langsetmo, I., Weigle, G. E., Fedde, M. R., Erickson, H. H., Bartsow, T. J. and Poole, D. C. (1997). $\dot{V}_{O_2}$ kinetics in the horse during moderate and heavy exercise. *J. Appl. Physiol.* **83**, 1235–1241.

Minetti, A. E. (1995). Optimum gradient of mountain paths. *J. Appl. Physiol.* **79**, 1698–1703.

Minetti, A. E. (1998a). The biomechanics of skipping gaits: a third locomotion paradigm? *Proc. R. Soc. Lond. B* **265**, 1227–1235.

Minetti, A. E. (1998b). A model equation for the prediction of mechanical internal work of terrestrial locomotion. *J. Biomech.* **31**, 463–468.

Minetti, A. E., Ardigò, L. P. and Saibene, F. (1993). Mechanical determinants of gradient walking energetics in man. *J. Physiol., Lond.* **472**, 725–736.

Minetti, A. E., Ardigò, L. P. and Saibene, F. (1994). Mechanical determinants of the minimum energy cost of gradient running. *J. Exp. Biol.* **195**, 211–225.

Pennycuick, C. J. (1975). On the running of the gnu (*Connochaetes taurinus*) and other animals. *J. Exp. Biol.* **63**, 775–799.

Potard, U. S., Leith, D. E. and Fedde, M. R. (1998). Force, speed and oxygen consumption in Thoroughbred and draft horses. *J. Appl. Physiol.* **84**, 2052–2059.

Roberts, T. J., Marsh, E. L., Weyand, P. G. and Taylor, C. R. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113–1115.

Schmidt-Nielsen, K. (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.

Taylor, C. R. (1994). Relating mechanics and energetics during exercise. *Adv. Vet. Sci. Comp. Med.* **38**A, 181–215.

Taylor, C. R., Heglund, N. C. and Maloiy, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1–21.

Taylor, C. R., Maloiy, G. M. O., Weibel, E. R., Langman, V. A., Kamau, J. M. Z., Seeherman, H. J. and Heglund, N. C. (1981). Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir. Physiol.* **44**, 25–37.

Wagner, P. D., Gillespie, J. R., Landgren, G. L., Fedde, M. R., Jones, B. W., Debowes, R. M., Pieschl, R. L. and Erikson, H. H. (1989). Mechanism of exercise-induced hypoxemia in horses. *J. Appl. Physiol.* **66**, 1227–1233.

Woledge, R. C., Curtin, N. A. and Homsher, E. (1985). *Energetic Aspects of Muscle Contraction*. London: Academic Press.