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# High-speed gallop locomotion in the Thoroughbred racehorse. II. The effect of incline on centre of mass movement and mechanical energy fluctuation

K. J. Parsons*, T. Pfau, M. Ferrari and A. M. Wilson

Structure and Motion Laboratory, The Royal Veterinary College, University of London, North Mymms, Hatfield, Hertfordshire AL9 7TA, UK

*Author for correspondence (e-mail: kparsons@rvc.ac.uk)

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## SUMMARY

**During locomotion on an incline, mechanical work is performed to move an animal up the slope and increase the potential energy (PE) of the trunk and hence the centre of mass (CoM). Thus, at a given speed the total net mechanical work increases with the PE of the animal. In this study we investigate the mechanical energy (*ME*) fluctuations and the mechanical cost of transport (MCT) in six horses galloping up a range of gradients. We captured trunk movement with a six degrees-of-freedom inertial sensor mounted over the dorsal spinous process of the fourth to sixth thoracic vertebrae of the horse. Footfall timings were measured using a previously validated system of limb-mounted accelerometers. Speed was measured using a Global Positioning System (GPS) data logger. A track survey provided detailed incline information for the track. Linear (craniocaudal, mediolateral and dorsoventral) and rotational (roll, pitch and heading) kinematic parameters (displacement, velocity and acceleration) were calculated at speeds ranging from 9.0 to 12.0 m s$^{-1}$ during routine training over a range of inclines. Estimates of *ME* fluctuations and the MCT were made. Results showed the effect of incline on trunk motion during galloping was small. Increases in linear mechanical work and MCT were primarily explained by an increase in the work required to move the animal up the slope (and increase the *PE* of the CoM). Within the stride the majority of the work was performed during hindlimb stance. Our results have provided new insights into how horses power uphill locomotion.**

Key words: horse, incline, centre of mass movement, mechanical energy, high speed locomotion, biomechanics.

## INTRODUCTION

Locomotion of quadrupeds, such as horses, is rarely steady state or on level terrain. They have the ability to perform tasks such as accelerating from stationary, running uphill and jumping over obstacles. The production of mechanical power is of paramount importance for all modes of non-steady locomotion (Hedrick et al., 2003; McMahon, 1984) and raises the question of how animals power such locomotor tasks. There are two broad mechanisms by which muscle power output can be increased over a given time period in a cyclical activity: (1) by increasing the frequency of cyclic contractions or (2) by increasing the work per cycle. The contribution of each mechanism to overall power output varies in different situations. In trotting horses it has been shown that the increased power required on an incline is provided by increasing the work per step, i.e. they increase the work per cycle. This has been supported by EMG studies, which show an increase in muscle activation (Wickler et al., 2005). The frequency of cyclic contractions (i.e. the stride frequency) decreases slightly at a given speed on the incline (Wickler et al., 2005). Stride parameters measured during inclined galloping are the focus of the companion paper (Parsons et al., 2008) where it is shown that, in contrast to trotting on the treadmill, horses increase their stride frequency as climbing power requirement increases. It is likely that whilst galloping, there may also be an increase in the mechanical power per cycle to help meet the demands for elevating the centre of mass (CoM) up a slope. Here we aim to investigate the effect of incline on trunk movement, mechanical energy fluctuations and the modulation of power per cycle during galloping.

Total mechanical energy ($ME_{tot}$) is equal to the sum of potential and kinetic energies (*PE* and *KE* respectively) of the CoM. $ME_{tot}$ fluctuates during the stride (Minetti et al., 1999; Pfau et al., 2006). Mechanical cost of transport (MCT, J kg$^{-1}$ m$^{-1}$), i.e. mechanical work performed per metre travelled and per kilogram (kg) body mass, is calculated from the sum of all positive increments in $ME_{tot}$ during the stride. MCT is therefore dependent on changes in $ME_{tot}$. During locomotion there is cyclical interchange between different forms of mechanical energy that enhances economy (Minetti et al., 1999). Elastic elements within the limbs of animals help to moderate the mechanical cost of locomotion by storing and releasing elastic energy, so enhancing mechanical economy (Minetti, 2000). If all the changes in *KE* were compensated for by changes in potential (*PE*) or elastic energy (*EES*) there would be no net change in $ME_{tot}$. However, energy is inevitably lost from the system by tendons [which have an energy return of 90–95% (Ker, 1981; Riemersma and Schamhardt, 1985)], incomplete interchange between energy types, and energy absorption by muscle and loss to the environment. Thus energy has to be added to the system to replace this 'lost energy'. The mechanical work required to replace energy lost to the environment or to power tasks such as acceleration or inclined locomotion may only be provided during stance periods. In the horse this work is most likely done by the hindlimbs due to the large proportion of total musculature found there (Payne et al., 2005; Payne et al., 2004). Hindlimb powering of locomotion has been described as a characteristic of quadrupeds (Usherwood and Wilson, 2005).

### External *vs* internal work

Mechanical work ($W$) is traditionally divided into two subcategories, namely (i) external mechanical work ($W_{ext}$), and (ii) internal mechanical work ($W_{int}$). $W_{ext}$ and $W_{int}$ are defined as energy changes of the CoM of the whole body relative to the ground and as energy changes of the body segments relative to the CoM, respectively (Minetti et al., 1999). In horses the limbs represent only a small portion of the total mass (Buchner et al., 1997) and most of the limb mass is proximal (Payne et al., 2005; Payne et al., 2004). $W_{int}$ increases with increasing speed (Fedak et al., 1982; Minetti et al., 1999). However, the proportion of internal to external work during galloping decreases with increasing speed, with internal work only making up approximately 28% at a gallop speed of 6 m s$^{-1}$, 18% at 10 m s$^{-1}$ and 16% at 12 m s$^{-1}$ (Minetti et al., 1999). This is because external work, principally due to the fluctuation in horizontal *KE*, increases with speed. $W_{int}$ therefore appears to be a minor component of the total mechanical work, particularly at high speeds (Minetti et al., 1999). Combining $W_{int}$ and $W_{ext}$ to give $W_{tot}$ may be an overestimate as the exact relationship between the two still remains controversial.

### Positive and negative mechanical work

$W_{ext}$ can be further partitioned into positive ($W^{+}_{ext}$) and negative increments ($W^{-}_{ext}$). During constant speed level running the amount of positive work is balanced by an equal amount of negative work (i.e. $W^{+}_{ext}$=$W^{-}_{ext}$). This contrasts with inclined locomotion where net work is required with each step to move the horse up the slope and increase its potential energy (*PE*). At a given speed, we would therefore expect the ratio of positive to negative work performed to increase. Muscle efficiency (work/metabolic energy spent) for negative work is estimated to be 3–5 times higher than for positive work (Abbott et al., 1952). It is for this reason the mechanical cost of negative work is usually omitted from estimates of efficiency. Ratios between positive and negative work and different efficiencies have, however, been used previously to predict the metabolic cost of walking from mechanical measurements (Minetti et al., 1993).

### Level *vs* incline

During level running the time of contact between the feet and the ground correlates with the metabolic cost (Kram and Taylor, 1990). It has been proposed that in human gradient walking and running the mechanical work is the major determinant of the actual metabolic cost (Minetti, 2000; Minetti et al., 1993; Minetti et al., 1994). Both the cost of generating work and the cost of exerting force must therefore be considered. In the horse, metabolic measurements have demonstrated that at speeds of 1–13 m s$^{-1}$ the metabolic cost of exercising on a 10% incline is more than twice that of exercising on the flat whilst walking, trotting and cantering (Eaton et al., 1995). Determination of mechanical cost of transport (MCT) from horses on an incline may provide an insight into the relationship between incline and the increased metabolic cost.

### Measurements during over-ground locomotion

Recent advances have made the study of truly high-speed locomotion (e.g. galloping) under field conditions more feasible (Pfau et al., 2005; Pfau et al., 2006; Witte et al., 2006; Witte et al., 2004; Witte and Wilson, 2005). A good estimate of CoM movement can be obtained from measuring overall trunk movement (Buchner et al., 2000). A six degree of freedom (d.f.) inertial sensor has been shown to provide accurate trunk movement data for horses during treadmill locomotion (Pfau et al., 2005) and has been used to calculate a fixed point estimate for CoM movement, which allows the calculation of $W_{ext}$ (Pfau et al., 2006). This estimate does not take into account the displacements of the CoM within the trunk but is the only practical method during over-ground high-speed locomotion. Due to low limb mass and large trunk inertia, changes in trunk rotational kinetic energy represent approximately 80% of $W_{int}$ in the horse [calculated using regression equation from Minetti et al. (Minetti et al., 1999) and data from Pfau et al. (Pfau et al., 2006) for a horse galloping at 10 m s$^{-1}$]. These velocities are measured by the sensor and, with estimates of body inertia, can be used to estimate internal work related to trunk movement ($W_{rot}$).

### Purpose of study and hypotheses

The purpose of the present study was to estimate the mechanical energy fluctuations and the MCT of galloping horses over a range of gradient slopes. Mechanical energy changes of a fixed-point estimate of the CoM were assessed under field conditions using an inertial sensor. Estimates of mechanical work per stride will allow us to approximate mechanical power per stride cycle and will provide new insights into mechanical demands made on the musculoskeletal system. We hypothesise that:

(i) *PE* is the only trunk energy that changes during inclined galloping, increasing as the animal moves up a slope. Motion of the trunk is otherwise unchanged on an inclined surface and the increase in mechanical energy cost is due to the increase in *PE*.

(ii) The majority of the mechanical work is performed during the period of hindlimb stance as most of the locomotor muscle is located in the hindlimbs (Payne et al., 2005).

## MATERIALS AND METHODS

### Horses

Six clinically sound Thoroughbred National Hunt racehorses of mean age 5 years, mean body mass 516 kg and mean height 1.66 m were used in the study. The animals were stabled and trained at the same national hunt training yard and were all undergoing similar exercise regimes. All horses were race fit. Body mass was measured prior to kinematic assessment using standard equine scales and the height of each horse was measured at the level of the fourth thoracic vertebra (the withers) using a standard height stick. Leg length of each horse was measured at the point of the mid scapula using the height stick. Mean leg length was 1.56 m. The mass of the jockey and riding equipment was 72 kg.

### Equipment

Each horse was equipped with a modified 6 d.f. inertial sensor (MT9 Xsens Technologies, B.V., Enschede, The Netherlands) and four foot-mounted accelerometers (ADXL 150, Analog Devices, Norwood, MA, USA). The jockey was equipped with a stand-alone GPS data logger (Trine II, Emtac, Byron, MN, USA). The sensor was mounted in a custom-made harness constructed of a resin casting material (Dynacast, Smith and Nephews, Wound Management, Hull, UK) and an elasticated band, mounted over the spinous processes of the fourth to sixth thoracic vertebrae of the horse, beneath the cranial edge of the saddle. The inertial sensor has previously been described (Pfau et al., 2005; Pfau et al., 2006). It consists of a tri-axial accelerometer (maximum ±10 g), a tri-axial gyroscope (maximum ±900 deg. s$^{-1}$), a tri-axial magnetometer and a thermometer. Inertial sensor data were low-pass filtered (3 dB analog low-pass filter, cut-off frequency 50 Hz for accelerometers and gyroscopes, 10 Hz for magnetometers; modified from standard manufacturer's specification) and subsequently AD-converted in the sensor into a binary serial RS232 data stream at 115.2 kbit $s^{-1}$. A cable ran from the sensor to a serial data logger (Antilog, Anticyclone systems Ltd, Morden, UK) mounted on the harness. Data were recorded at 250 samples $s^{-1}$ per each individual sensor. Thus, data files consisted of ten channels: the calibrated output from the three accelerometers, three gyroscopes and three magnetometers and the sensor temperature, each at 250 Hz.

The GPS device was configured to log speed (km $h^{-1}$), position (latitude and longitude, in decimal degrees) and time (h, min and s) data once per second. The GPS device (dimensions 50×89×21 mm, mass 78 g) was mounted securely on the rider's hat with a custom-made elastic strap and was powered on 10 min before the jockey mounted the horse. The unit was kept in a stationary position with a clear view of the sky for this period. Data were logged continuously from this time for the duration of exercise and were then downloaded *via* Bluetooth for analysis on a personal computer.

Foot-on and foot-off events of all four limbs were determined by measuring foot accelerations using solid-state capacitive accelerometers with a dynamic range of ±50 g (ADXL150, Analog Devices; sensitivity 38 mV $g^{-1}$). Accelerometers were encased with epoxy impregnated Kevlar fibres and attached to the dorsal midline of each hoof using hot glue (Bostick Findley Inc., Stafford, UK). A short, fatigue-resistant cable was constructed of multi-strand copper wire, helically coiled around a flexible 2 mm diameter core of climbing cord and surrounded with PVC braid. The cable ran along the lateral aspect of the digit and metacarpal/tarsal bone and linked the accelerometer to a battery supply and data recorder. Output signals were logged into a MP3 recorder (Cowon iAUDIO U2, Cowon, Seoul, Korea) at a bit rate of 128 kbps (44.1 kHz). The MP3 recorder and accelerometer battery were mounted within a standard exercise boot. The combined weight of the unit and exercise boot was 333 g (98 g and 235 g, respectively). See elsewhere for more detail (Parsons and Wilson, 2006).

Prior to attachment of the inertial sensor and the MP3/accelerometer data acquisition units to the horse, a 1.5 V pulse was applied to the line-in of all the MP3 recorders with a simultaneous electromagnetic pulse to the inertial sensor. The GPS time of the pulse application was recorded from a handheld GPS unit to allow for subsequent synchronisation.

### Exercise

The horses were ridden by their regular jockies during the study and all were exercised in groups of two. Data were collected from only one horse at a time. Each horse was warmed up for approximately 15 min by walking and trotting to the training track and subsequently galloped along the track. The track was a woodchip racetrack of length 1077 m and overall elevation from start to finish of 50 m. The horses were then walked back to the start of the track and the exercise repeated one more time. Exercise duration was kept within the limits of the horses usual exercise regime (typically less than 40 min total duration, with two gallop sessions lasting approximately 90 s each).

### Track survey

A complete survey of the outer edges of the track was made using two dual-frequency carrier wave, differential GPS systems (Novatel OEM-4, NovAtel Inc., Calgary, Canada), one as a rover and sampled at 20 Hz and one as a local base station sampling at 5 Hz. Pseudo range data were post-processed in Waypoint software (NovAtel Inc.). Processed track survey data contained latitude, longitude and altitude in m with a median error of 2 cm.

### Data analysis

GPS data were downloaded from the horse-mounted GPS data logger *via* a Bluetooth wireless link, and over-ground speed, position and time data were extracted for each position fix using custom software written in MATLAB.

The track survey was processed to provide information from position fixes along the edge of the track. This information was then used to calculate the slope of the track at each position along its length. The slope angle (θ) was calculated from the elevation between points at ±0.75 m distance. The slope angle was used to calculate slope percent. Position data from the jockey-mounted GPS position fixes were then compared to data from the track survey to determine the slope (in percent) at each position fix of the jockey.

Inertial sensor and foot-mounted accelerometer data were synchronised with GPS time from the synchronisation pulse applied at the start of the experiment. Analysis of trunk movement data from the inertial sensor mainly followed the process described previously (Pfau et al., 2005; Pfau et al., 2006). The main difference in the analysis here consisted of the pitch angle being used to calculate the 'sensor to horse' reference system rotation matrix. Instead of using the sensor pitch calculated by the sensor fusion algorithm (MTsoftware, Xsens BV, Enschede, The Netherlands), sensor pitch was corrected using the slope angle for each stride. Thus the horse-based reference frame (craniocaudal, mediolateral and dorsoventral) followed the slope of the track, i.e. craniocaudal was parallel and dorsoventral was perpendicular to the track. Accelerations in the horse reference system were then double integrated and projected to the CoM following the procedures described (Pfau et al., 2006). Integration was performed over three strides (<1.5 s) and based on the assumption of cyclical movement to determine integration constants (Pfau et al., 2005). Integration errors can therefore be considered small (Pfau et al., 2005). In addition, vertical displacement (using the original pitch value during processing) was used for the calculation of potential energy.

Trunk movement features were used to segment the inertial sensor data for each individual stride. The maximum sensor craniocaudal velocity was chosen as a consistent feature and was identified within each stride. Linear accelerations were projected from the sensor coordinate system into a horse-referenced coordinate system based on the rotation matrix data. Accelerations were then double integrated to displacements based on stride segmentations described above. Angular velocities and accelerations were derived from orientation data using numerical differentiation of a regression line fitted to 11 data points (current with 5 neighbouring data points on each side). A fixed-point estimate of the CoM relative to the sensor position was used (Pfau et al., 2006). Estimates of the CoM movement were derived from the combination of sensor linear movement and sensor orientation to calculate the movement of a fixed point estimate of 200 mm behind and 250 mm below the sensor position were used. Velocity and acceleration were calculated by numerical differentiation.

Linear mechanical energies ($ME_{\mathrm{lin(CoM)}}$) [i.e. the sum of *KE* (craniocaudal, mediolateral and dorsoventral) and *PE*] were calculated routinely. *KE* values were calculated within the horse-based coordinate system ($KE=\frac{1}{2}M_bV^2$ where $M_b$=mass of horse, and $V$=velocity) to give $KE_{cc}$ (craniocaudal kinetic energy), $KE_{ml}$ (mediolateral kinetic energy) and $KE_{dv}$ (dorsoventral kinetic energy). Craniocaudal velocity was calculated from the sum of the average speed for the stride (from the GPS data) and the mean subtracted velocity output of the inertial sensor. *PE* was calculated using the expression $PE=M_b\mathbf{g}\Delta h$ (where $\Delta h$=change in vertical position). For calculation of *PE*, average speed of the horse plus the mean subtracted velocity output of the inertial sensor was rotated into the global (i.e. $x$, $y$, $z$) coordinate system using knowledge of the slope incline at the given position. This allowed the calculation of *PE* from the vertical elevation of the CoM of the horse within a stride and the vertical elevation of the CoM up a slope at a given time. Strides that contained more than 10% of the samples outside ±2 s.d. of the mean stride values at the equivalent time-point were excluded from the analysis. Rotational mechanical energies ($ME_{rot}$) associated with trunk movements around the CoM were calculated from rotational moment of inertia of the animal. The horse trunk movement of inertia was estimated by modelling the trunk as a cylinder of radius 0.3 m and length 2.9 m (total volume 0.57 m$^3$). Roll, pitch and heading moments of inertia were then calculated ($I$). It was then possible to calculate the kinetic energy of roll, pitch and heading ($KE_{rot}=\frac{1}{2}I\omega^2$).

For each stride we calculated [as in Minetti et al. (Minetti et al., 1999) and Ruina et al. (Ruina et al., 2005)] the following: $W_{lin(CoM)}$, total of the increases in $ME_{lin(CoM)}$; $W_{rot}$, total of the increases in $ME_{rot}$; $W_{lin(CoM)+rot}$, total of the increases in the sum of $ME_{rot}$ and $ME_{lin(CoM)}$; $W_{KE(CoM)}$, total increase in linear kinetic energy; $W_{PE(CoM)}$, total increase in potential energy per stride.

These mechanical works were normalised with respect to body mass and speed to calculate the MCT: $W_{rot}$, $W_{lin(CoM)}$ and $W_{lin(CoM)+rot}$ were multiplied by stride frequency and divided by the product of stride speed and body mass to calculate the linear MCT ($MCT_{lin(CoM)}$), rotational MCT ($MCT_{rot}$) and total linear plus rotational MCT ($MCT_{lin(CoM)+rot}$).

Respective negative mechanical works were calculated from the sum of the negative decrements in $ME_{lin(CoM)}$. The effect of incline on $W^{+}_{lin(CoM)}/W^{-}_{lin(CoM)}$ ratio was calculated as the percentage of the total linear work (sum of $W^{+}_{lin(CoM)}$ and $W^{-}_{lin(CoM)}$) (Minetti et al., 1993).

To assess the efficiency of energy exchange between *KE* and *PE* for each of the gaits the percentage energy recovery from $W_{KE(CoM)}$, $W_{PE(CoM)}$ and $W_{lin(CoM)}$ over the complete stride (Cavagna et al., 1977; Minetti et al., 1999) was calculated as:

$$\text{Percentage recovery} = [(W_{KE(CoM)}+W_{PE(CoM)}-W_{lin(CoM)}) / (W_{KE(CoM)}+W_{PE(CoM)})] \times 100\ .$$

Relative timing of the aerial phase with respect to inertial sensor data was estimated from plotting the sum of the vertical *KE* and *PE* (in the global coordinate system) and locating the aerial phase within the area of the curve where it is approximately constant. It was assumed that the sum of the vertical *KE* and *PE* is constant during the aerial phase (when no feet are on the ground to produce an external ground reaction force, GRF). This method has previously been assessed for reliability on a treadmill with a cantering Thoroughbred horse and has also been used in a previous study on level gallop locomotion (Pfau et al., 2006).

Foot-mounted accelerometer data were downloaded from each MP3 recorder and converted into a wave file using a custom programme written in MATLAB. The accelerometer data were imported into data transcription freeware (Barras et al., 1998) and features corresponding to foot-on and foot-off times were identified and the timings of these events recorded, as described in detail elsewhere (Witte et al., 2004). Foot-on and foot-off timings were used to determine duty factor to estimate limb force. Measured stride timing variables, including stride frequency, are presented in the companion paper (Parsons et al., 2008).

Data collected at speeds below 9 m s$^{-1}$ were discarded as these speeds were during periods of acceleration and deceleration at the start and end of the trial. For each stride the mid-point time, GPS speed and percentage incline were determined and individual strides interpolated to 100 samples for each variable: linear (craniocaudal, mediolateral, dorsoventral) displacements, velocities, accelerations and energies; rotational (roll, pitch and heading), displacements, velocities, accelerations and energies and CoM potential energy. For each stride the maximum, minimum and ranges were determined for each variable of interest. Two incline categories (defined as level (0–2% incline) and incline (10–15% incline) were identified for comparisons of estimated CoM movements.

Lines of best fit were calculated for each incline category and variable of interest for each individual. A linear line of best fit was used as it was the simplest model yielding the most consistent fit. The lines of best fit were then used to calculate values of variables in each speed and incline category for each horse. A population mean was determined and these data were then used to display ranges of displacements and maximum and minimum velocities and accelerations of selected variables.

The relationship of measured variables to speed and the effect of incline were examined. A General Linear Model (GLM) one-way between-groups analysis of covariance (ANCOVA) was conducted, using the complete dataset, to compare the effect of incline on measured variables with speed as the covariate, incline category as a fixed factor and horse identity as a random factor (SPSS 12.0 for Window, SPSS Inc.). Preliminary checks were conducted to ensure there was no violation of the assumptions of normality of the tests. A $P$ value of <0.05 was taken as showing a statistically significant difference. Multivariate multiple regression analyses were used to determine the percentage of the variance in $W_{lin(CoM)}$, $W_{rot}$, $W_{lin(CoM)+rot}$, $MCT_{lin(CoM)}$, $MCT_{rot}$ and $MCT_{lin(CoM)+rot}$ explained by speed and percentage incline.

## RESULTS

A total of 1113 strides were collected and analysed from 6 horses (range 134–294 per horse). Speed ranged from 9 m s$^{-1}$ to 12 m s$^{-1}$. Strides falling within two defined incline ranges were initially selected and analysed for comparison, these categories being 0–2% incline (classified as level) ($N$=198, mean speed=10.4 m s$^{-1}$, mean slope=1.2%) and 10–15% incline (classified as incline) ($N$=156, mean speed=10.2 m s$^{-1}$, mean slope=12.8%).

### Estimated CoM movements

Features of craniocaudal, mediolateral and dorsoventral displacement, velocity and acceleration of individual strides for both level and incline galloping were similar to those previously described (Pfau et al., 2006). Fig. 1 gives examples of the experimental data recorded in the craniocaudal direction and the integration procedure for strides recorded on the level and incline at 10 m s$^{-1}$ and 12 m s$^{-1}$ from horse 1. Overall craniocaudal and dorsoventral displacement curves showed sinusoidal behaviour. Mediolateral displacements were more variable and influenced by lead limb. Over the speed range the population mean craniocaudal and dorsoventral displacement ranges of the CoM showed a moderate decrease with speed (Fig. 2).

There was significant difference between dorsoventral displacements between horses ($P$=0.001). Analysis demonstrated that the population mean of the dorsoventral displacement decreased from 0.103 m and 0.093 m at 9 m s$^{-1}$ to 0.091 m and 0.083 m at 12 m s$^{-1}$ whilst galloping on level and inclined surfaces respectively. GLM analysis demonstrated maximum dorsoventral displacement was significantly greater during level galloping than

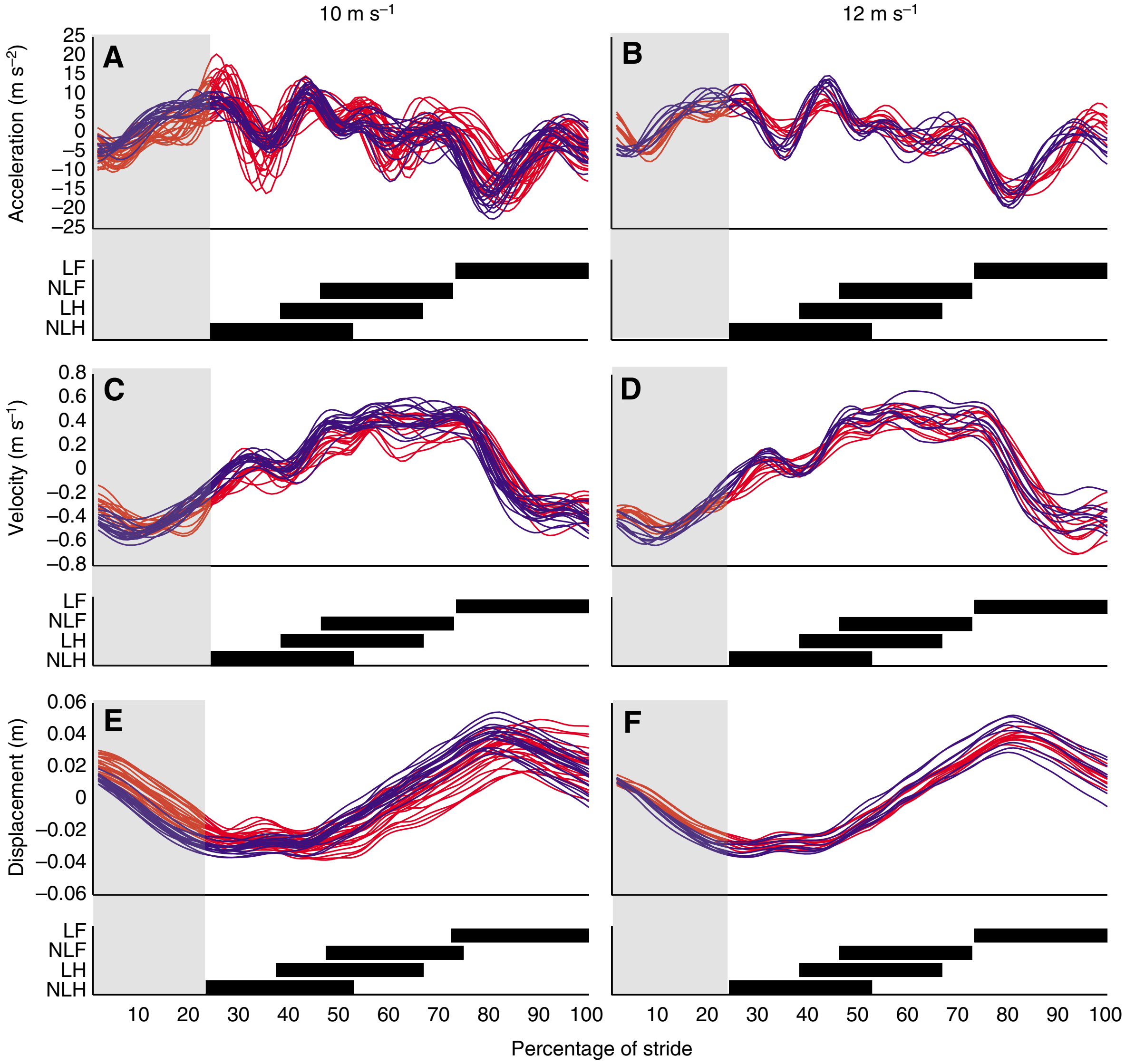


Fig. 1. Examples of experimental records at 10 m s$^{-1}$ (A,C,E) and 12 m s$^{-1}$ (B,D,F) for horse 1. Red represents incline data and blue represents level data. Craniocaudal acceleration (A,B), craniocaudal velocity (C,D) and craniocaudal displacement (E,F) of the trunk for strides recorded at each speed are presented and the figure demonstrates the integration procedure. Acceleration data is integrated to provide velocity data and displacement data for each stride. LF=lead fore; NLF=non-lead fore; LH=non-lead hind; NLH=non-lead hind.

during inclined galloping ($P$=0.047). There were no significant differences between craniocaudal or mediolateral range of trunk movement or maximal velocity when comparing level and incline galloping ($P$>0.05).

Features of roll, pitch and heading displacement, velocity and acceleration during the stride for both level and incline galloping were also similar to those previously described (Pfau et al., 2006). Mean pitch displacement range increased from 12.9° and 16.7° at 9 m s$^{-1}$ to 13.4° and 17.4° at 12 m s$^{-1}$ during level and incline galloping, respectively (Fig. 3). There was a statistically significant difference between pitch range during level and inclined galloping ($P$=0.018). Pitch range did not vary significantly between horses ($P$>0.05). Maximum pitch angular velocity was significantly greater on the incline than on the level ($P$=0.009). There were no statistically significant differences between roll or heading displacements or maximum and minimum velocities between horses or incline category ($P$>0.05).

### Mechanical energy fluctuations

Mean *PE* plus vertical kinetic energy is shown in Fig. 4. The relative timing of the aerial phase was located at the part of the curve where it was approximately constant (for details, see Pfau et al., 2006). Mean $KE_{cc}$ (Fig. 5), *PE* (Fig. 6) and $ME_{lin(CoM)}$ (Fig. 7) fluctuations during the stride for all horses galloping on level and inclined surfaces at speeds of 10 m s$^{-1}$ and 12 m s$^{-1}$ are shown. For illustrative purposes the minimum $KE_{cc}$ has been subtracted from the $KE_{cc}$ and the minimum $ME_{lin(CoM)}$ has been subtracted from the $ME_{lin(CoM)}$. Average foot fall patterns and aerial phases have been added for reference. Mean mechanical work ($ME_{lin(CoM)}$, $ME_{rot}$ and $ME_{lin(CoM)+rot}$) and MCT ($MCT_{lin(CoM)}$, $MCT_{rot}$ and $MCT_{lin(CoM)+rot}$) for the population of horses studied are shown in Fig. 8.

### $W_{lin}$

Fluctuations in the $KE_{cc}$ dominated the changes in $ME_{lin(CoM)}$ during level and inclined galloping. As the gradient of the slope increased

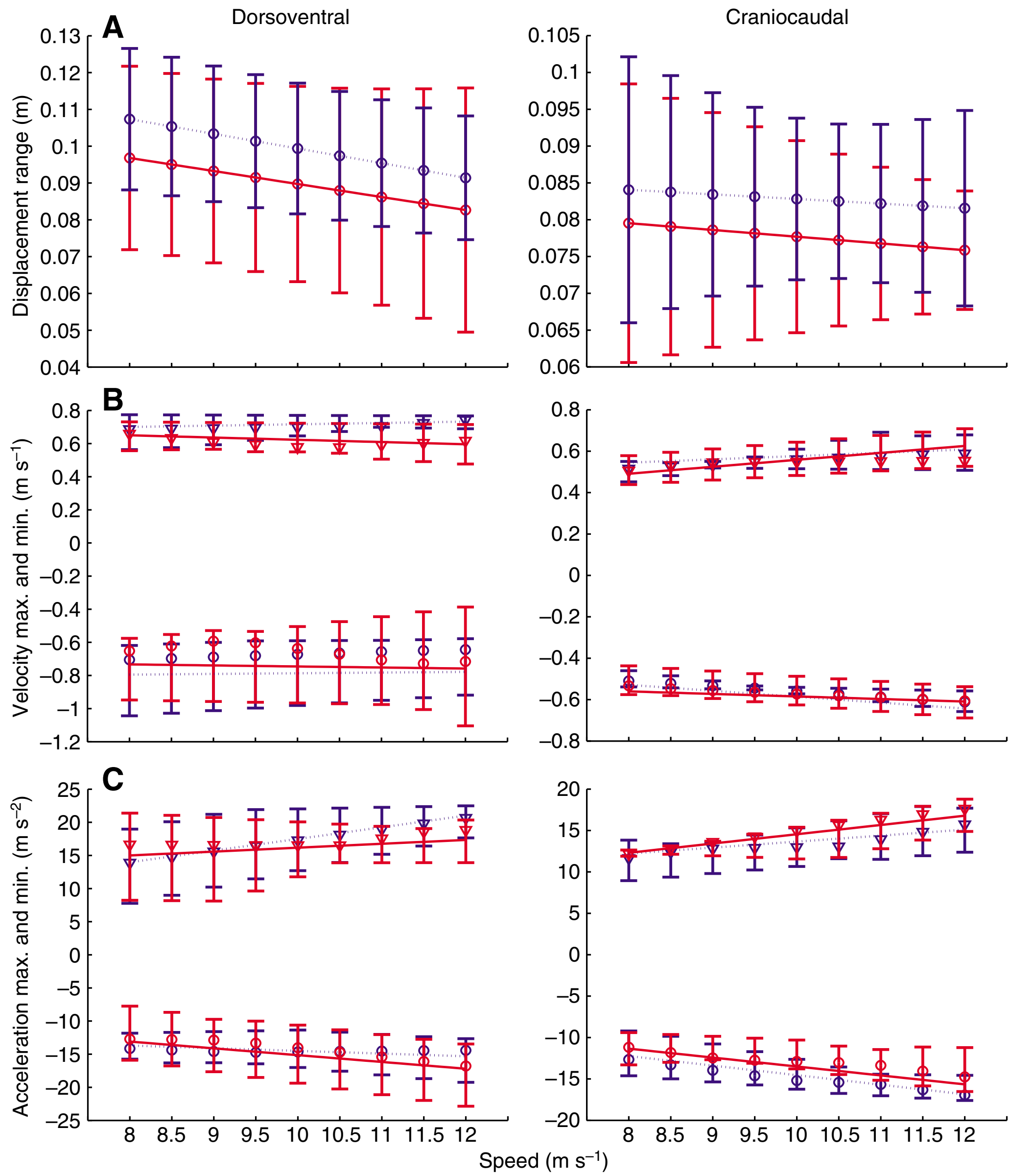


Fig. 2. Displacement range (A), minimum and maximum velocity (B) and minimum and maximum acceleration (C) from 8 m s$^{-1}$ to 12 m s$^{-1}$ for dorsoventral (left) and craniocaudal (right) movement on the level (blue triangles) and incline (red circles) for the six horses. For each speed category mean ± 1 s.e.m. (displacement) or median and interquartile range (velocity and acceleration) are calculated from all strides. A linear function was fitted to the data and is shown as a red solid line (incline data) and a blue broken line (level data).

(at a given speed) *PE* made an increasingly significant contribution to the overall $ME_{\mathrm{lin(CoM)}}$ fluctuations ($P$<0.05). The effect was that $W_{\mathrm{lin}}$ was significantly greater during inclined locomotion ($P$<0.001) (Fig. 8A). Without the increase in *PE* resulting from the slope of the track there was no statistical difference between mechanical work of galloping on level and inclined surfaces ($P$>0.05). The difference between $W_{\mathrm{ext}}$ of locomotion (equal to $W_{\mathrm{lin(CoM)}}$) on the incline compared to the level appears to be principally related and dominated by the movement of the CoM up the hill, rather than any change in trunk movement of the horse.

### $W_{\mathrm{rot}}$

Fluctuations in both the range and angular velocity of pitch resulted in a slight increase in the $KE_{\mathrm{rot}}$ during inclined locomotion (Fig. 8B). The GLM demonstrated there was no significant difference between $W_{\mathrm{rot}}$ when galloping on inclined or level surfaces ($P$=0.056). $W_{\mathrm{rot}}$ was positively correlated with speed ($P$<0.001).

### $W_{\mathrm{lin(CoM)+rot}}$

The GLM demonstrated that $W_{\mathrm{lin(CoM)+rot}}$ was statistically greater during galloping on an inclined surface than when galloping on the level ($P$<0.001) (Fig. 8C).

### Mechanical cost of transport (MCT)

$\mathrm{MCT}_{\mathrm{lin(CoM)}}$ and $\mathrm{MCT}_{\mathrm{lin(CoM)+rot}}$ were greater during inclined galloping due to the work done to move the CoM up the slope ($P$<0.001) (Fig. 8B and F). There was a significant correlation between $\mathrm{MCT}_{\mathrm{lin(CoM)+rot}}$ and speed for both level and incline galloping (from the mean population) ($P$<0.001) (Fig. 8F). There was no significant difference in $\mathrm{MCT}_{\mathrm{rot}}$ between incline categories.

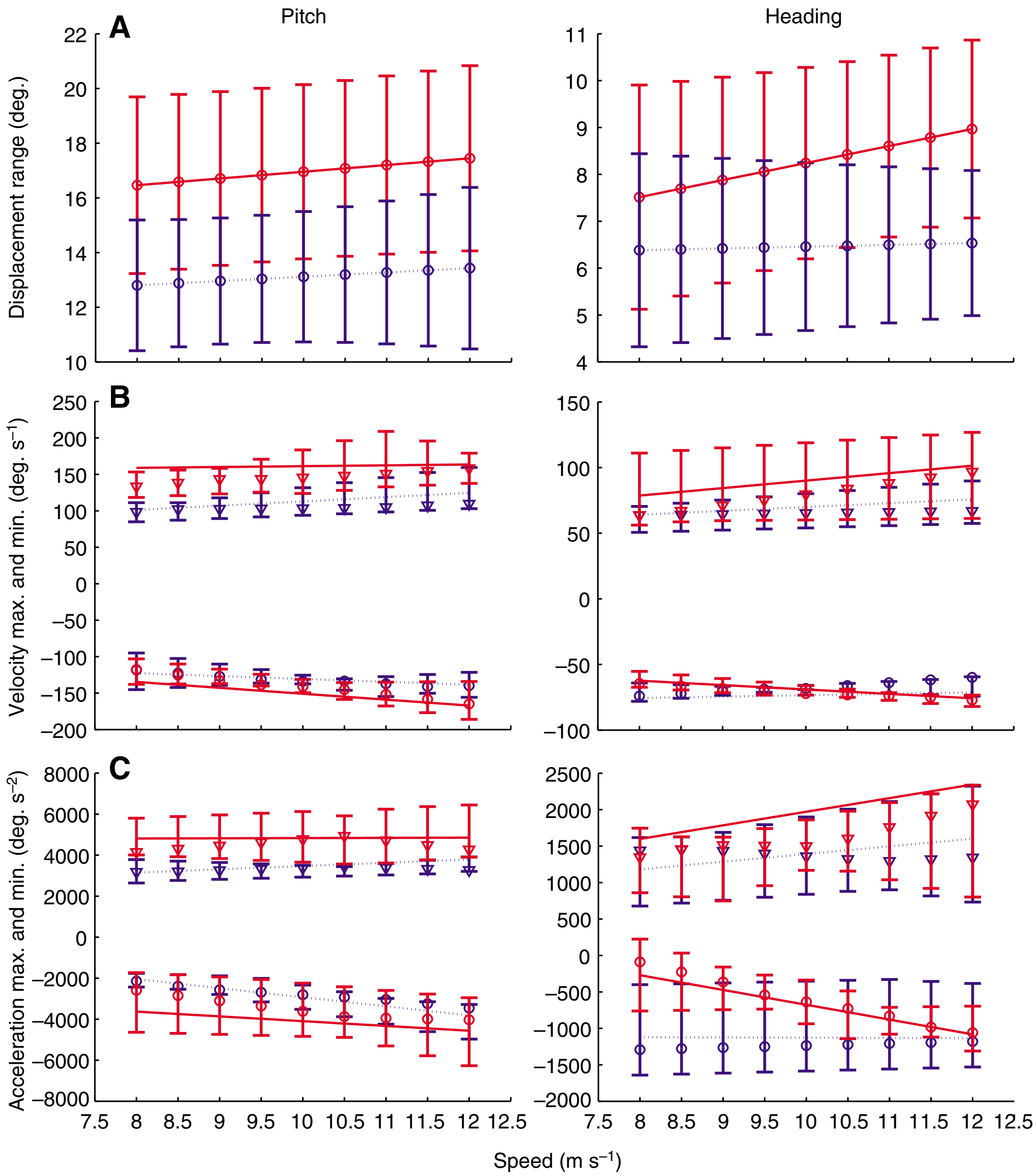


Fig. 3. Displacement range (A), minimum and maximum velocity (B) and minimum and maximum acceleration (C) from 8 m s$^{-1}$ to 12 m s$^{-1}$ for pitch (left column) and heading (right column) on the level (blue triangles) and incline (red circles) for the six horses. For each speed category mean ±1 s.e.m. (displacement) or median and interquartile range (velocity and acceleration) are calculated from all strides. A linear function was fitted to the data and is shown as a red solid line (incline data) and a blue broken line (level data).

Multiple regression analysis is presented in Table 1 and demonstrates both speed and slope make a significant contribution to the prediction of $MCT_{lin(CoM)}$ and $MCT_{lin(CoM)+rot}$ but only incline makes a significant contribution to the prediction of $MCT_{rot}$ of transport.

### Percentage recovery and $W^{+}_{lin}$ and $W^{-}_{lin}$ partitioning

Percentage recovery decreases with gallop speed on both level and incline and is greater on the incline at all speeds.

Partitioning of total work between $W^{+}_{lin(CoM)}$ and $W^{-}_{lin(CoM)}$ follow a linear trend with gradient ($R^2$=0.48) (Fig. 9).

### Positive work per stride

Fig. 8A shows $W^{+}_{lin(CoM)}$ as a function of speed for galloping on the level and incline. Figs 5 and 7 demonstrated that the majority of this work is performed during hindlimb stance.

### $W_{int}$

Increase in stride frequency would result in an increase in $W_{int}$ [reported in the companion paper (Parsons et al., 2008)]. As stride frequency increases we would expect $W_{rot}$ of trunk to increase (if we assume the same range of movement, but at an increased frequency there is less time to move through the range).

## DISCUSSION

This study is the first to demonstrate the effect of incline on the mechanical cost of over-ground inclined locomotion during gallop in the horse. The information adds to the conclusions presented in the companion paper (Parsons et al., 2008) where it was identified that whilst galloping on an inclined surface the power required for climbing appears, in contrast to trotting on an incline, to be provided partly by an increase in stride frequency.

Mechanical energy fluctuations on both the level and incline agree with those presented previously for high-speed over-ground locomotion (Pfau et al., 2006), with our data showing the minimum mechanical energy during the aerial phase and an immediate acceleration after the aerial phase. This is, however, different to previously published data (Minetti et al., 1999; Cavagna et al., 1977). During much of the aerial phase all four legs are swinging forwards thus contributing to a backward displacement and hence deceleration of the trunk (and hence sensor). Just before the hind legs, which together are about 12% of the horse's body mass (Buchner et al., 1997), hit the ground they are retracting quickly (moving the trunk forward) and since most of the propulsive musculature is found in the hind legs (Payne et al., 2005) it seems possible that they produce a substantial extensor torque at the hips, and so little or no horizontal deceleration is observed during their ground contact.

It is also possible that early in hindlimb stance dorsoventral momentum (and hence) kinetic energy is converted into craniocaudal momentum (Ruina et al., 2005). Previously published data (Pfau et al., 2006) show that the magnitude of change in dorsoventral energy is small (<10%) compared to craniocaudal energy. Such a conversion would therefore contribute only little to the increase in craniocaudal energy that is observed, but may contribute in part to the high apparent efficiency values calculated. The fluctuations in mechanical energy are dominated by horizontal *KE*, reaching a maximum at the end of hindlimb stance. The shape of the mechanical energy curves and the observation that the increases occur during hind leg stance phases suggest that the majority of this work is being performed by the hindlimb muscles. Both hind legs appear to contribute to the increase in kinetic energy during stance, which suggests that considerable work is performed by the powerful hindlimbs and hip extensors (Usherwood and Wilson, 2005).

As expected, there was very little positive work performed during the stride whilst hindlimbs were not in stance. A small difference is observed when comparing between the level and incline $ME_{\mathrm{lin(CoM)}}$ data. This occurs primarily when the non-lead forelimb is in contact with the ground (Fig. 5). This may suggest that some positive work is being performed by the forelimb. Alternatively, the increased kinetic energy may result from the contact limb diverting vertical *KE* (making it appear that the non-lead forelimb is 'generating' this energy). The latter would be consistent with a collision-based model of galloping (Ruina et al., 2005). It is important to note that the foot contact of the non-lead forelimb overlaps the foot contact of the lead hindlimb. This, combined with the limitations of the study [i.e. (i) the presented footfall data are averages from a number of horses

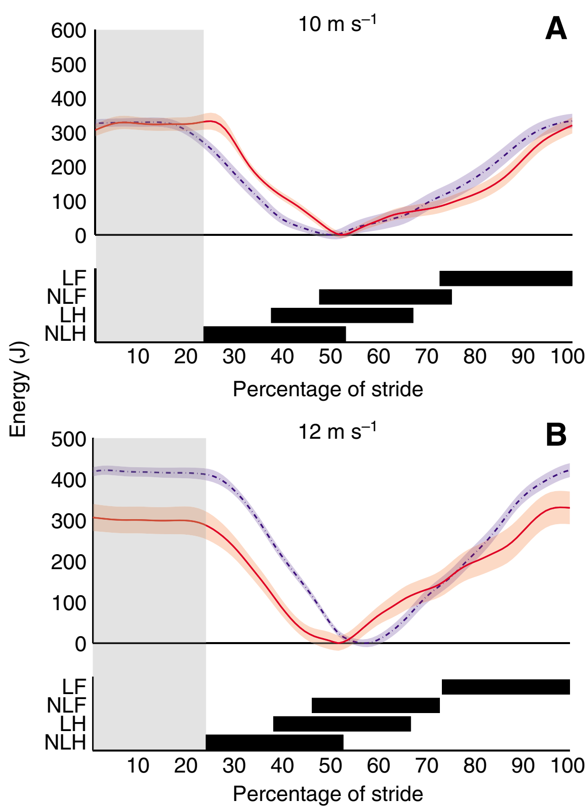


Fig. 4. Stride data (mean ± s.e.m. as shading, $N$=6) of the sum of the vertical kinetic ($KE_{\mathrm{dv}}$) and linear potential energy (*PE*) during level (blue broken line) and incline (red solid line) galloping at a mean speed of (A) 10 m s$^{-1}$ ($n$ level=56 and $n$ incline=60) and (B) 12 m s$^{-1}$ ($n$ level=60 and $n$ incline=28). Presented data are averages of all strides from all horses within the speed range. Aerial phases (vertical grey bar) were estimated to be during the time when the curve was approximately constant. Stance phases of individual feet are presented for illustrative purposes as black bars in the lower panels. LF=lead fore; NLF=non-lead fore; LH=non-lead hind; NLH=non-lead hind.

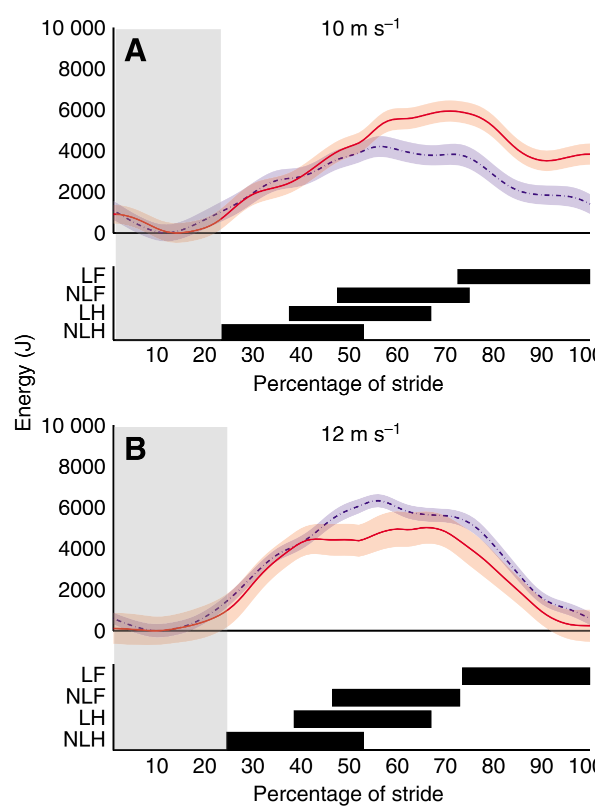


Fig. 5. Stride data (mean ± s.e.m. as shading, $N$=6) of changes in craniocaudal kinetic ($KE_{\mathrm{cc}}$) energy during level (blue broken line) and incline (red solid line) galloping at a mean speed of (A) 10 m s$^{-1}$ ($n$ level=56 and $n$ incline=60) and (B) 12 m s$^{-1}$ ($n$ level=60 and $n$ incline=28). Presented data are averages of all strides from all horses within the speed range. For illustrative purposes the minimum craniocaudal kinetic energy has been subtracted from external mechanical energy. Estimated aerial phase (vertical grey bar); stance phases of individual feet are presented for illustrative purposes as black bars in the lower panels (LF=lead fore; NLF=non-lead fore; LH=non-lead hind; NLH=non-lead hind).

at the given speed, (ii) the mechanical energy data represents averages over a large number of strides from all the horses in the study and (iii) the exact timing of the aerial phases are estimated using the method described earlier] mean that it is important not to over-interpret the findings. The increased work on the incline combined with an increase in stride frequency [presented in the companion paper (Parsons et al., 2008)] results in a higher mechanical power during inclined locomotion.

Distinct oscillations in total mechanical energy of the CoM during the stride that have been described previously (Minetti et al., 1999; Pfau et al., 2006) were not evident in Figs 5 and 7 as a result of averaging data from multiple strides. Calculation of mechanical work was made using data from each individual stride as this takes into account these fluctuations. The relationship between $W^{+}_{\mathrm{lin(CoM)}}$ and $W^{-}_{\mathrm{lin(CoM)}}$ follows a linear trend with increasing gradient and is similar to that reported in humans (Minetti et al., 1994). The gradient of the regression line is less than that reported for humans and suggests that $W^{-}_{\mathrm{lin(CoM)}}$ would only become negligible at a gradient of about 60%, which is approximately twice the slope reported for humans (Minetti et al., 1994).

On the level, MCT calculated in this study is consistently less (e.g. 1.95 J kg$^{-1}$ m$^{-1}$ *versus* 2.6 J kg$^{-1}$ m$^{-1}$ at 10 m s$^{-1}$) than reported by Minetti et al. (Minetti et al., 1999). Previously published values for the metabolic cost vary considerably, with some values exceeding 100% (Minetti et al., 1999). It is therefore interesting to estimate the efficiency. Using the metabolic values for level treadmill galloping (Eaton et al., 1995) along with our mechanical work estimates, an apparent efficiency of muscle contraction of between ~40% and ~70% is calculated. This is similar to published results (Pfau et al., 2006). On a 10% incline a metabolic cost of ~5 J kg$^{-1}$ m$^{-1}$ can be estimated (Eaton et al., 1995). Combining this with our measured MCT for incline galloping at 10 m s$^{-1}$ gives an approximate apparent efficiency of 52%. Fig. 7 shows a negative work phase separated from a positive work phase by an aerial phase. In a simple deformable object (such as a bouncing ball), no force is exerted on the ground during the aerial phase and thus elastic elements would relax. However, in a more complex system (e.g. linked segment system), energy storage is possible during the aerial phase. For example, in a galloping horse the back is fully flexed in the mid-aerial phase storing mechanical energy (Faber et al., 2001), which is subsequently released when the back extends throughout stance. This has not been measured here and may, together with energy storage in the legs and a possible overestimation of mechanical energy fluctuations (particularly linear horizontal fluctuations) of the CoM (Pfau et al., 2006), contribute to the improbably high apparent efficiencies [compared with the values obtained from the thermodynamics of muscular contraction (Woledge et al., 1985)]. An interesting observation is that the slope

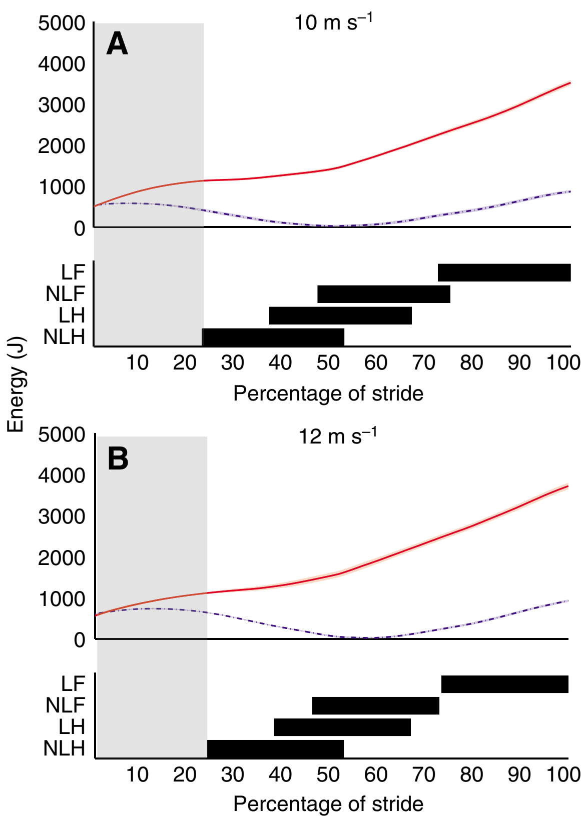


Fig. 6. Stride data (mean ± s.e.m. as shading) of changes in total potential energy (*PE*) during level (blue broken line) and incline (red solid line) galloping at a mean speed of (A) 10 m s$^{-1}$ (*n* level=56 and *n* incline=60) and (B) 12 m s$^{-1}$ (*n* level=60 and *n* incline=28). Aerial phase (vertical grey bar); stance phases of individual feet are presented for illustrative purposes as black bars in the lower panels (LF=lead fore; NLF=non-lead fore; LH=non-lead hind; NLH=non-lead hind). Note s.e.m. shading is not clearly visible as the standard errors are small.

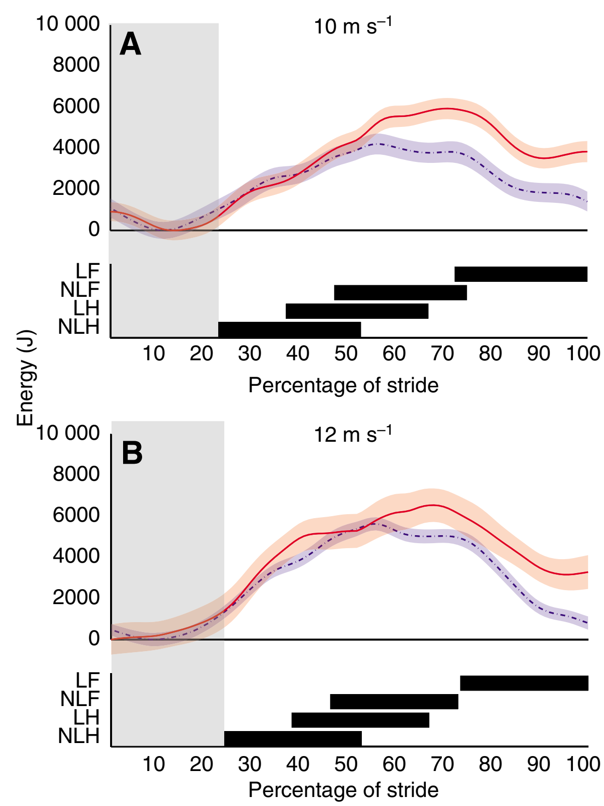


Fig. 7. Stride data (mean ± s.e.m. as shading) of changes in total linear mechanical energy $ME_{\mathrm{lin(CoM)}}$ during level (blue broken line) and incline (red solid line) galloping at a mean speed of (A) 10 m s$^{-1}$ (*n* level=56 and *n* incline=60) and (B) 12 m s$^{-1}$ (*n* level=60 and *n* incline=28). For illustrative purposes the minimum total energy has been subtracted from external mechanical energy. Estimated aerial phase (vertical grey bar); stance phases of individual feet are presented for illustrative purposes as black bars in the lower panels (LF=lead fore; NLF=non-lead fore; LH=non-lead hind; NLH=non-lead hind).

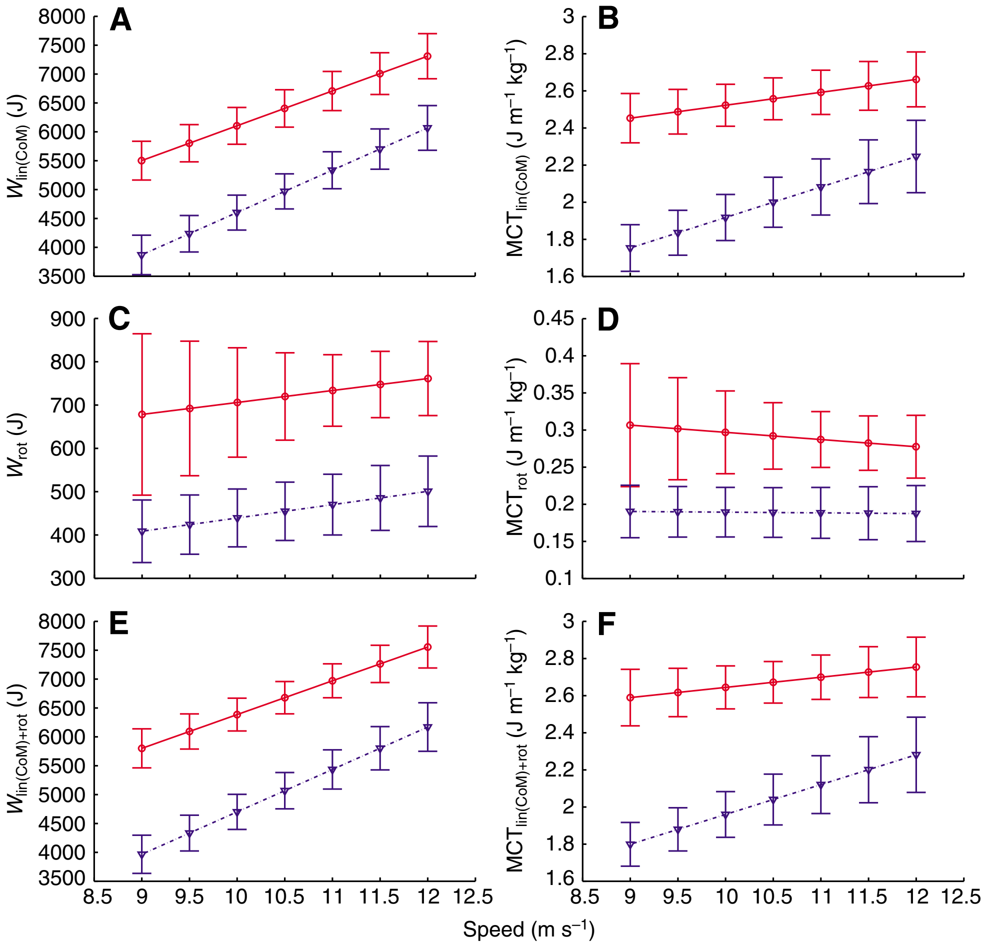


Fig. 8. Linear mechanical work $W_{lin(CoM)}$ (A), Linear mechanical cost $MCT_{lin(CoM)}$ (B), rotational mechanical work $W_{rot}$ (C), rotational mechanical cost $MCT_{rot}$ (D), linear + rotational mechanical work $W_{lin(CoM)+rot}$ (E) and linear + rotational mechanical cost $MCT_{lin(CoM)+rot}$ (F) for six galloping horses on the level (blue triangles) and incline (red circles) at a speed range of 8 m s$^{-1}$ to 12 m s$^{-1}$. For each speed category values are mean ±1 s.e.m. ($N$=6) for individual horses. A linear function was fitted to the data and is shown as a red solid line (incline data) and a blue broken line (level data).

of MCT *versus* speed graph is smaller on the incline than on the level (Fig. 8F) whereas the slope of mechanical work per stride is approximately the same for the two categories (Fig. 8E shows a constant absolute offset between the two curves). When calculating MCT from mechanical work, on the incline the smaller relative increase in mechanical work (an effect of the higher absolute values of mechanical work) together with the increase in stride frequency (Parsons et al., 2008) over the speed range is almost completely cancelled out by the increase in speed, resulting in only a small increase in MCT on the incline.

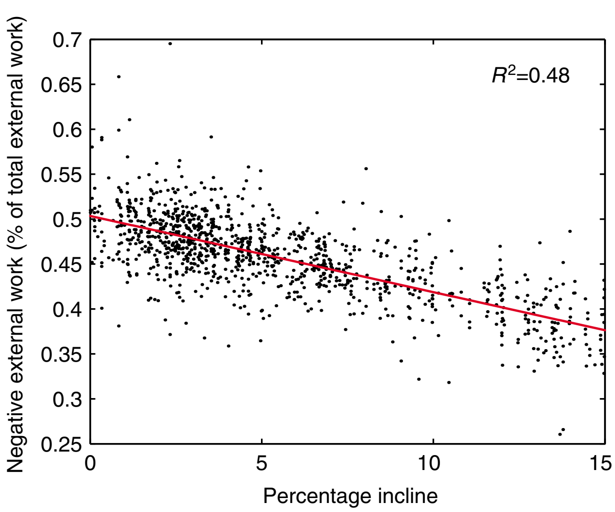


Fig. 9. Negative linear work ($W^{-}_{lin(CoM)}$) (percentage of total linear work) as a function of gradient. A linear regression line (red) has been fitted to the data.

Calculated percentage recovery values for level galloping agree with those previously published (Minetti et al., 1999). Values are higher during incline galloping. This is a result of the increase in *PE* that occurs throughout the whole stride. The decrease in *KE* during forelimb stance is therefore out of phase with *PE* contributing to *PE*–*KE* transduction.

The mechanical work performed per stride is higher during inclined locomotion than on the level at a given speed and suggests that as well as increasing stride frequency [as discussed in the companion paper (Parsons et al., 2008)] the amount of mechanical work per stride cycle increases when galloping on an inclined surface. Assuming this work is performed solely during the combined hindlimb stance period we estimate total maximal power output to be around 40 kW. This is equal to a maximal power of 60 W kg$^{-1}$ horse and 400 W kg$^{-1}$ of hindlimb musculature.

CoM displacement can be estimated from overall trunk movement using a fixed landmark [for example a marker attached over trochanter major of Th16 (Buchner et al., 2000)]. It has been shown that this leads to an overestimation of displacement but agreement increases with increasing speed (Buchner et al., 2000). In addition our method does not take into account movement of body parts (most importantly legs, head, neck) relative to the trunk or movement of lungs and gut contents within the trunk. Mass of the legs is relatively

Table 1. Results of multivariable linear regression models evaluating the effect of incline and speed on external, rotational and total work and mechanical cost of transport

| | B | β | $Sr^2$ (incremental) | Sig B |
|---|---|---|---|---|
| $W_{lin(CoM)}$ | | | | |
| Speed | 665 | 0.510 | 0.187 | 0.000 |
| Incline (%) | 149 | 0.649 | 0.415 | 0.000 |
| Intercept | –2199 | | | 0.000 |
| $r^2$ | | | 0.602 | |
| Adjusted $r^2$ | | | 0.600 | |
| $r$ | | | 0.776 | |
| $W_{rot}$ | | | | |
| Speed | 18 | 0.069 | 0.001 | 0.197 |
| Incline (%) | 15 | 0.329 | 0.107 | 0.000 |
| Intercept | 290 | | | 0.048 |
| $r^2$ | | | 0.107 | |
| Adjusted $r^2$ | | | 0.102 | |
| $r$ | | | 0.328 | |
| $W_{lin(CoM)+rot}$ | | | | |
| Speed | 664 | 0.51 | 0.19 | 0.000 |
| Incline (%) | 150 | 0.64 | 0.415 | 0.000 |
| Intercept | –2199 | | | 0.000 |
| $r^2$ | | | 0.65 | |
| Adjusted $r^2$ | | | 0.60 | |
| $r$ | | | 0.776 | |
| $MCT_{lin(CoM)}$ | | | | |
| Speed | 0.076 | 0.165 | 0.008 | 0.000 |
| Incline (%) | 0.053 | 0.653 | 0.428 | 0.000 |
| Intercept | 1.096 | | | 0.000 |
| $r^2$ | | | 0.428 | |
| Adjusted $r^2$ | | | 0.425 | |
| $r$ | | | 0.654 | |
| $MCT_{rot}$ | | | | |
| Speed | –0.011 | 0.092 | 0.015 | 0.089 |
| Incline (%) | 0.006 | 0.264 | 0.068 | 0.000 |
| Intercept | 0.323 | | | 0.000 |
| $r^2$ | | | 0.084 | |
| Adjusted $r^2$ | | | 0.078 | |
| $r$ | | | 0.289 | |
| $MCT_{lin(CoM)+rot}$ | | | | |
| Speed | 0.105 | 0.020 | 0.017 | 0.000 |
| Incline (%) | 0.061 | 0.693 | 0.473 | 0.000 |
| Intercept | 0.816 | | | 0.000 |
| $r^2$ | | | 0.490 | |
| Adjusted $r^2$ | | | 0.487 | |
| $r$ | | | 0.700 | |

B, unstandardised coefficient (used to generate equation); β, standardised coefficient; denotes the contribution of the individual parameters to the models, $Sr^2$ (incremental), incremental $r^2$ after addition of independent parameter; Sig B denotes whether the contribution of the individual parameter to the model is significant.

small compared to the mass of the trunk [5.5% and 5.8%, respectively, for a front- and hindlimb (Buchner et al., 1997)], and during gallop leg movements are out of phase for a part of the stride. It also needs to be considered that the trunk movements with respect to the CoM resulting from movement of the hind legs will exaggerate the fluctuation in horizontal kinetic energy and hence the mechanical work done. The movement of the head neck segment has been shown to be slightly out of phase compared to trunk movement in cantering horses and fluctuations of power have been shown to be small in comparison to those of the body centre of mass (Gellman and Bertram, 2002). Naturally, the approach taken here (based on movement of an external landmark) cannot take into account the movement of the lungs or gut movement. This could be achieved by deriving CoM motion from force plate data; however, this was not possible under the experimental conditions with racehorses during routine high-speed training.

Sensitivity analysis to estimate the influence of the assumed position of the CoM on estimates of mechanical energy has been previously performed (Pfau et al., 2006). Those results produced a similar estimated position of the CoM to that reported previously (Buchner et al., 2000). The fixed-point estimate of the CoM position used here was 250 mm below and 200 mm behind the sensor position. During inclined trotting it has been shown that there is a shift in fore–hind impulse distribution (Dutto et al., 2004). Kinematic analysis demonstrated this redistribution of force is likely because the horse becomes re-orientated to the angle of the slope (Dutto et al., 2004) and may be a direct effect of the change in trunk orientation and/or a change in the CoM position within the body. A fixed-point estimate system may therefore have limitations. Sensitivity analysis has demonstrated a greater change in calculated external mechanical work when deviating from the assumed position in the dorsoventral direction compared to a deviation in the craniocaudal direction (Pfau et al., 2006). Therefore if the CoM position does move caudally during inclined locomotion the error in our mechanical energy calculation will be comparatively small. The position of the jockey may also influence the CoM position. When galloping on an incline the jockey subjectively maintained a similar standing position in the stirrups compared to on the level. Any change in position of the jockey relative to the CoM will be influenced by the attachment point of the stirrups to the saddle. The attachment point is positioned dorsal to the CoM. Any small changes that occur in the jockey's position are therefore likely to result in a small shift of the impulse distribution towards the hindlimbs. The effect of this on calculated external mechanical work is therefore also likely to be small as the jockey was highly experienced. A rider was necessary in this study so that the horses would reach the speeds of interest. As 3D force plate data for complete strides are not available from galloping horses on the level or incline the fixed point estimate is considered the only feasible estimate of CoM position.

## CONCLUSION

In this study we tested two hypotheses regarding mechanical energy fluctuations and work performed during level and inclined galloping. The results showed that the effect of incline on trunk motion during galloping was small, as hypothesised. Changes in trunk motion only contributed a small amount to the change in total mechanical work of the trunk during inclined galloping. Increases in linear mechanical work and MCT were primarily explained by an increased work required to move the animal up a slope (and increase the *PE* of the CoM). The majority of the work done was during the period of hindlimb stance.

Results presented in the companion paper (Parsons et al., 2008) show there was an increase in the stride frequency during inclined galloping. The data presented in this study adds to this and indicates that galloping horses also modulate power production by increasing the work per stride. Power therefore appears to be modulated by two mechanisms: (i) increasing the work per cycle and (ii) increasing the number of cycles. This contrasts with trotting on an inclined surface where power supply is modulated by increasing only the work per cycle (Wickler et al., 2005), and the difference may be due to muscles reaching the limits of the work they can perform during galloping; so as well as increasing the work per stride, there is also a drive to increase in the number of cycles. Mechanical work per stride during incline galloping has been calculated to be near the maximum estimated for horse musculature (assuming it operates within optimal physiological limits).

## LIST OF ABBREVIATIONS

| | |
|---|---|
| CoM | centre of mass |
| $\Delta E$ | sum of the positive increments of mechanical energy (J) |
| *EES* | potential elastic energy storage in the limbs (J) |
| $\boldsymbol{g}$ | gravitational constant=9.81 m s$^{-2}$ |
| GLM | general linear model |
| GPS | global positioning system |
| GRF | ground reaction force (N) |
| $\Delta h$ | change in vertical position |
| $I$ | moment of inertia (kg m$^{-1}$) |
| *KE* | kinetic energy (J) |
| $KE_{cc}$ | craniocaudal kinetic energy (J) |
| $KE_{dv}$ | dorsoventral kinetic energy (J) |
| $KE_{ml}$ | mediolateral kinetic energy (J) |
| $KE_{rot}$ | rotational kinetic energy (J) |
| $M_b$ | mass (kg) |
| MCT | mechanical cost of transport (J m$^{-1}$ kg$^{-1}$) |
| $MCT_{lin(CoM)}$ | mechanical cost of transport of linear energies of the CoM (J m$^{-1}$ kg$^{-1}$) |
| $MCT_{lin(CoM)+rot}$ | mechanical cost of transport of linear energies plus rotational energies of the CoM (J m$^{-1}$ kg$^{-1}$) |
| $MCT_{rot}$ | rotational MCT |
| *ME* | mechanical energy (J) |
| $ME_{lin(CoM)}$ | linear mechanical energy of the CoM (J) |
| $ME_{rot}$ | rotational mechanical energy (J) |
| $ME_{tot}$ | total mechanical energy |
| *PE* | potential energy of the centre of mass (J) |
| $V$ | velocity (m s$^{-1}$) |
| $W$ | mechanical work (J) |
| $W_{ext}$ | external mechanical work (J) |
| $W^+_{ext}$ | positive external work (J) |
| $W^-_{ext}$ | negative external work (J) |
| $W^+_{lin(CoM)}$ | positive linear work of the centre of mass per stride (J)=$W^+_{ext}$ |
| $W_{int}$ | internal mechanical work (J) |
| $W_{KE(CoM)}$ | the total increase in linear kinetic energy per stride (J) |
| $W_{lin(CoM)}$ | linear work of the centre of mass per stride (J) |
| $W_{lin(CoM)+rot}$ | linear work of the centre of mass plus rotational per stride (J) |
| $W^-_{lin(CoM)}$ | negative linear work of the centre of mass per stride (J)=$W^-_{ext}$ |
| $W_{PE(CoM)}$ | the total increase in potential energy per stride (J) |
| $W_{rot}$ | rotational work of the centre of mass per stride (J) |
| $W_{tot}$ | total work done (J) |
| $\theta$ | slope angle (degrees) |
| $\omega$ | Angular velocity (rad s$^{-1}$) |

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