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High-speed gallop locomotion in the Thoroughbred racehorse. I. The effect of incline on stride parameters

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SUMMARY

During locomotion up an incline, power is required to elevate the centre of mass. This is provided when the animal's limbs are in contact with the ground. Measurements of stride timing variables from multiple limbs during high speed, over-ground locomotion would enhance our understanding of locomotor powering during changes in terrain. This study measured foot-on and foot-off times from galloping horses using a previously validated system of limb-mounted accelerometers and a global positioning system data logger. A detailed track survey provided incline information from all areas of the track. Measurements were made from six horses over a speed range of 9 to 13 m s^{-1}. Foot-fall timings were used to calculate variables, which included stance duration, protraction duration, stride frequency and duty factor. The relationship between track incline and measured variables was assessed. Stride variables from horses galloping on level (0–2% incline) and incline (8–12% incline) sections of the track were compared. Fore- and hindlimb protraction durations were significantly reduced across the speed range during incline galloping (P=0.001). This resulted in a mean increase in stride frequency from 2.01 to 2.08 strides s^{-1} at 9.5 m s^{-1} and 2.10 to 2.17 strides s^{-1} at 12.5 m s^{-1} during incline galloping. Duty factor was significantly greater for the hindlimbs during incline galloping (P<0.001), increasing from 0.31 to 0.32 at 9.5 m s^{-1} and 0.28 to 0.29 at 12.5 m s^{-1}. Peak limb force was calculated from duty factor and assumed fore- to hindlimb impulse distributions. Smaller peak vertical forces were calculated in the forelimbs and increased peak vertical forces were calculated in the hindlimbs when galloping on an incline. Measured changes in stride timing variables differ from those reported in trotting horses. We propose that horses increase their stride frequency at a given speed during incline galloping to provide power for moving the centre of mass up the slope.

Key words: horse, biomechanics, incline, power, high speed locomotion, duty factor, stride frequency.

INTRODUCTION

During incline running, positive mechanical work is performed to move the animal's centre of mass (CoM) up the slope. This contrasts with level, steady speed running where the net mechanical work of each step is zero. The power required to elevate the centre of mass is provided when the animal's limbs are in contact with the ground. Changes in stride timing variables may therefore provide an insight into the mechanism of powering inclined high speed locomotion. Recent technological advances have allowed the accurate measurement of stride timing variables in galloping horses travelling at a range of speeds over ground (Parsons and Wilson, 2006; Witte et al., 2006; Witte et al., 2004). Measured variables, including stance duration, protraction duration and stride frequency, improve our understanding of the athletic ability of animals (Usherwood and Wilson, 2005; Weyand et al., 2000), the metabolic cost of locomotion (Kram and Taylor, 1990), limb forces (Alexander et al., 1979; Witte et al., 2006; Witte et al., 2004) and gait transitions (Farley and Taylor, 1991; Kram and Taylor, 1990; Weyand et al., 2000).

The effect of speed on temporal stride parameters has previously been characterised. Contact time and duty factor decrease with increasing speed in horses (Dutto et al., 2004; Hoyt et al., 2000; Witte et al., 2006), other quadrupeds (Kram and Taylor, 1990) and bipeds (Munro et al., 1987). Peak limb forces increase with speed (Alexander et al., 1979; Dutto et al., 2004; Witte et al., 2004; Witte et al., 2006). Protraction, particularly in the horse, is a largely passive process (Heglund et al., 1982; Kram and Taylor, 1990; Wilson et al., 2003) and is similar over a range of running speeds. During incline trotting in the horse (on a 10% incline), contact and protraction duration for both fore- and hindlimbs have been demonstrated to be slightly increased (Wickler et al., 2005). Stride frequency is reduced and duty factor is unchanged (Dutto et al., 2004; Wickler et al., 2005). Interestingly, these changes in stride parameters contrast with those reported in humans, where stride frequency and duty factor are both significantly higher during incline running (Minetti et al., 1994; Swanson and Caldwell, 2000).

As well as influencing positive mechanical work, exercising on an incline results in an increase in the metabolic cost of locomotion. Horses exercising at speeds up to 11 m s^{-1} will more than double their energy expenditure when on a 10% gradient (Eaton, 1994; Wickler et al., 2000). There is strong evidence that the metabolic cost of locomotion is closely correlated with the rate of force production and hence stance time on the flat (Kram and Taylor, 1990; Pontzer, 2005; Taylor, 1994). Using this relationship and previously measured contact times we would predict a small decrease in the cost of horse locomotion on an incline. The relationship between stance time and metabolic cost therefore appears less useful for estimating the metabolic cost of incline locomotion. This is not surprising as the relationship between the metabolic cost and the rate of force production was identified during, and is intended to be applied to, conditions in which the net work performed is zero (i.e. during level, steady speed locomotion). During inclined locomotion a significant amount of external work is done. It has been proposed that during trotting on an incline the increase in metabolic cost reflects a greater volume of muscle being recruited to generate power for climbing (Wickler et al., 2005). Knowledge of the mass of the animal, the degree of incline, stride timing variables and speed allows the calculation of climbing power (P_c), i.e. the energy requirement to move up a vertical distance over a given time. The recruitment of muscle to generate climbing power is compounded at higher speeds by decreasing contact times, as peak vertical ground reaction force increases and therefore the total volume of active muscle increases (Taylor, 1994; Wickler et al., 2005). The decreased contact time also results in muscles having to shorten at a greater rate to generate power. The force–velocity relationship is also likely to have a substantial effect on how much muscle must be recruited when contact time decreases.

When standing, walking, trotting and cantering on the level, total vertical impulse and peak vertical force are consistently distributed between the forelimbs and the hindlimbs with a proportion of 57% to 43% (Merkens et al., 1993; Dutto et al., 2004; Witte et al., 2004). On a 10% incline, during trot, the forelimb to hindlimb impulse distribution shifts and the distribution becomes 52% forelimb and 48% hindlimb (Dutto et al., 2004). The measured changes in force distribution are consistent with the observed decrease in the hyperextension of the forelimb metacarpophalangeal joint when trotting up an incline (McGuigan and Wilson, 2003; Sloet van Oldruitenborgh-Ooste et al., 1997). The ratios of fore- to hindlimb impulses have been shown to be independent of speed whilst trotting and cantering on level surfaces (Witte et al., 2004). The ratio has also been shown to be independent of speed whilst trotting on an incline (Dutto et al., 2004). Changes in impulse distribution during incline locomotion whilst cantering and galloping have not been quantified.

The direct measurement of ground reaction forces during high-speed locomotion in large animals within their natural or training environment is difficult. The use of force-plates is limited to experimental tracks where they are mounted in a runway and rely on the subject hitting the plate with one leg. At a speed of 18 m s^{-1} the stride frequency is 2.3 strides s^{-1} (Witte et al., 2006) and stride length is 8 m. This is substantially longer than the length of an average force-plate and so the number of hits per trial would be low. Force shoes have been designed and used during high speed locomotion with varying success (Kai et al., 2000; Ratzlaff et al., 1985; Ratzlaff et al., 1993; Roepstorff et al., 1999; Roland et al., 2005). Their development and design is complex and expensive as they have to meet specific design criteria, including being able to account for variations in hoof sizes. The linear relationship between metacarpophalangeal joint angle and vertical limb force can be used to predict vertical ground reaction forces (McGuigan and Wilson, 2003). This requires the collection of calibrated, high speed and high resolution optical motion capture data, which is difficult under field conditions. The view of the metacarpophalangeal joint is also impaired when protective boots are worn by exercising horses. Treadmill studies are an alternative to field studies; however, they affect kinematics, resulting in increased stance time and stride length (Buchner et al., 1994). These changes may become even more important when investigating subtle changes that may occur during variations in terrain, such as incline. Owners and trainers are also reluctant to allow elite racehorses, such as the ones used in our study, to partake in studies that involve treadmills or the attachment of equipment that may affect routine training.

Alexander and co-workers (Alexander et al., 1979) used the principle of conservation of momentum, the knowledge of the force distribution between fore and hindlimbs and an assumption of a half-sinusoidal shaped vertical ground reaction force to derive the following equation for the calculation of peak vertical ground reaction force:

$$Fz_{\max} = \pi pm\boldsymbol{g} / 4\beta \,, \tag{1}$$

where $Fz_{\max}$ is peak vertical ground reaction force (N), p is the proportion of the mass of the animal carried by the pair of legs in question, m is the mass of the animal (kg), $\boldsymbol{g}$ is the gravitational constant (9.81 m s^{-2}) and β is the duty factor.

The accuracy of this relationship relies on the shape of the vertical ground reaction force (F_z) curve (assumed to be half-sinusoidal during stance), the ratio of forelimb to hindlimb impulse and the symmetry of limb ground reaction force curves between pairs of legs in asymmetrical gaits. The equation has been shown to be reliable, even in asymmetrical gaits such as canter, with a mean error (±s.d.) in prediction of –2.3±0.27 and 2.1±0.7 N kg^{-1} for the non-lead and lead limb, respectively. The difference between lead and non-lead load, and hence the error, decreases at higher speeds (Witte et al., 2004). The prediction of peak vertical ground reaction force from duty factor relies on the accurate measurement of stride timing variables, the application of Eqn 1 and knowledge of impulse distribution between fore- and hindlimbs. Prediction of peak limb force from duty factor is the most practical method of investigating the relationship between limb force and running speed in galloping quadrupeds in the field. Measurement of ground reaction forces is also of interest as higher running speeds are achieved in humans with greater peak vertical ground reaction forces (Weyand et al., 2000). This is not true for greyhounds (Usherwood and Wilson, 2005) and may differ for horses and other quadrupeds.

The purpose of this study was to measure the temporal stride parameters of galloping Thoroughbred racehorses over a range of inclines. We aimed to (i) explore the effect of incline on stride parameters of the horse during galloping, and (ii) investigate how inclined surfaces affect estimated peak vertical ground reaction forces. We hypothesised that peak vertical forces increase in the hindlimbs and decrease in the forelimbs during incline galloping. We also tested the hypothesis that stride frequency decreases when galloping on an incline, as in trotting.

MATERIALS AND METHODS

Data collection

Six clinically sound, Thoroughbred, National Hunt racehorses of mean age 5 years (range 4–6 years), mean mass 516 kg (range 438–575 kg) and mean height at the fourth to sixth thoracic spinous processes of 1.66 m (range 1.60–1.70 m) were used in the study. The animals were stabled and trained at the same yard. Mass was measured prior to kinematic assessment using standard equine scales and the height of each horse was measured using a standard height stick. Leg length of each horse was measured to the point of the mid-scapula using a standard height stick. Mean leg length was 1.56 m (range 1.5–1.6 m). The same jockey was used for each horse. The combined mass of the jockey and riding equipment was 72 kg.

Each horse was equipped with four foot-mounted accelerometer/data acquisition units (Parsons and Wilson, 2006) and the jockey with a stand-alone global positioning system (GPS) data logger (Trine II, Emtac, Byron, MA, USA). A solid state MEMS accelerometer with a dynamic range of ±50 g (where 1 g is equal to 9.8 m s^{-2}; ADXL 150, Analog Devices, Norwood, MA, USA) was mounted on the dorsal midline of each hoof as previously described (Parsons and Wilson, 2006; Witte et al., 2006; Witte et al., 2004). Each accelerometer was encased with epoxy-impregnated Kevlar fibres and attached to the dorsal midline of each hoof using hot glue (Bostick Findley Inc., Stafford, UK) so the sensitive axis was in the proximal–distal direction. A short, fatigue-resistant cable, constructed of multi-strand copper wire helically coiled around a flexible 2 mm diameter core of climbing cord and surrounded with PVC braid, ran along the lateral aspect of the digit and metacarpal/tarsal bone and linked the accelerometer to the data recorder. Each accelerometer was logged continuously at 44.1 kHz and compressed at a bit rate of 128 kbit s^{-1} into an MP3 recorder (iAUDIO U2, Cowan, Seoul, Korea) secured within an exercise boot to the lateral aspect of the third metacarpal/metatarsal bone. The combined weight of the unit and exercise boot was 333 g (98 and 235 g, respectively). A 1.5 V pulse was simultaneously applied to the input of all the MP3 recorders prior to attachment to the horse to enable synchronisation between accelerometers. The GPS time at which the pulse was applied was manually recorded to enable subsequent synchronisation between the accelerometer and GPS data. Further information regarding the MP3/accelerometer data acquisition units can be found in a previous publication (Parsons and Wilson, 2006). The time of the pulse application was recorded to allow for subsequent synchronisation with the GPS unit.

The GPS device was configured to log speed (km h^{-1}), position (latitude and longitude, in decimal degrees) and time (hours, minutes and seconds) data once per second (Witte and Wilson, 2004; Witte and Wilson, 2005). The device was mounted on the rider's hat with a custom-made elasticated strap and was powered on 10 min before the jockey mounted the horse. Data were logged continuously from this time for the duration of exercise and then downloaded *via* Bluetooth$^{\text{TM}}$ for analysis on a personal computer (PC). The horses were ridden by their regular rider during the study and all horses 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 prior to galloping along the track (length of track 1077 m, duration of gallop approximately 90 s). The horse was then walked back to the start of the track and the exercise repeated one further time. Exercise duration was kept within the limits of the horses' usual exercise regime (typically less than 40 min total duration).

A survey of the outer edges of the track was made using dual frequency carrier wave differential GPS with a local base station (NovAtel OEM4, NovAtel Inc., Calgary, Canada) sampled at 20 Hz. Processed track survey data contained latitude, longitude and altitude in metres (see Data processing and statistics for further details).

Data processing and statistics

The data were downloaded from each MP3 recorder and decoded as described elsewhere (Parsons and Wilson, 2006). Synchronisation between accelerometers and GPS was obtained by using the synchronisation pulse. The accelerometer data were then imported into data transcription freeware (Barras et al., 1998). Features corresponding to foot-on and foot-off times were identified and the timing of these events recorded as described previously (Parsons and Wilson, 2006; Witte et al., 2004). Foot-on and foot-off times were used to calculate stance duration, protraction duration (defined as the time between a foot-off event and a foot-on event for an individual leg) and duty factor. A stride was defined as the interval between two foot-on events for an individual leg.

GPS data were downloaded from the GPS data logger via a Bluetooth wireless link and speed, position and time data were extracted for each position fix using a custom-made programme written in Matlab (The MathWorks Inc., Natick, MA, USA). For each stride the mid-point time was determined and GPS speed and position were identified.

The track survey was processed to provide longitude, latitude and elevation (all in metres) at each fix along the track. Raw binary data were post-processed in Waypoint software (NovAatel Inc.). This information was then used to calculate the incline of the track (in per cent slope) at each fix along the track survey. The calculation of incline was determined from 0.75 m position intervals along the track. Jockey-mounted GPS position fixes were then compared with data from the track survey to determine the incline (in per cent) at each position fix. The track was a woodchip racetrack of length 1077 m and overall elevation from start to finish of 50.5 m (Fig. 1).

Peak vertical ground reaction force was estimated from duty factor for each limb and stride using Eqn 1. The relative impulse distribution of fore- and hindlimbs was taken as 0.57 and 0.43 at 0% incline (Witte et al., 2004) and 0.52 and 0.48 at 10% incline [as reported for trotting horses by Dutto et al. (Dutto et al., 2004)]. A linear change in the shift of forelimb to hindlimb impulse ratio was assumed between 0 and 10%, e.g. 0.545:0.455 ratio at 5% incline. The effect of this assumption on our conclusions was considered by also calculating peak vertical ground reaction force assuming no shift in forelimb to hindlimb impulse ratio. Calculated forces were reported normalised to horse body mass (N kg^{-1} M_b where M_b is body mass).

GPS derived velocity data were differentiated to provide acceleration data. Stride data recorded when accelerations or decelerations were greater than 0.6 m s^{-2} were discarded from the analysis. Stride data at speeds below 9 m s^{-1} were also discarded as these occurred at the start and end of the trial and were only recorded from two of the horses. Data were divided into forelimb and hindlimb strides and then categorised into 1 m s^{-1} speed bins for analysis. Two categories were formed for initial comparisons between level and incline running. The relationship of each variable to speed and the effect of incline were examined. A one-way between-groups analysis of covariance (ANCOVA) general linear model (GLM) was conducted to compare the effect of incline on measured variables with speed as the covariate, incline as a fixed factor and horse identity as a random factor (SPSS 12.0

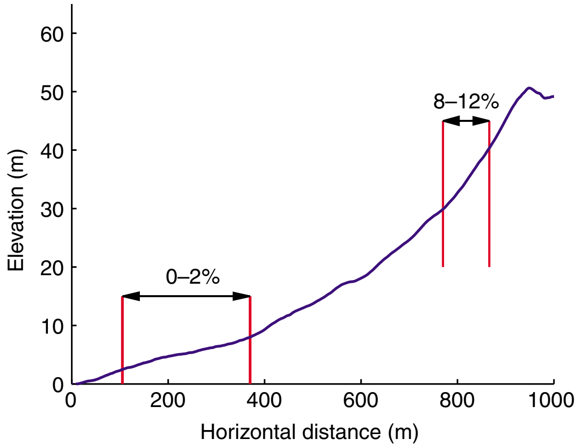

Fig. 1. Track survey showing elevation of the track from start to finish. Overall length of the track was 1077 m with an elevation of 50.5 m. The areas of the track that fell within the selected level (0–2%) and incline (8–12%) categories are indicated.

for Windows, SPSS Inc., Chicago, IL, USA). A *P* value of <0.05 was taken as a statistically significant difference. Preliminary checks were conducted to ensure there was no violation of the assumptions of normality of the test. Best-fit curves were estimated for each variable for each individual. Second order polynomial function curves were calculated for fore- and hindlimbs in both incline categories according to the quadratic function $y=b_0+b_1x+b_2x^2$. These fit equations were then used to calculate values of variables for each speed and incline category for each horse. A population mean was determined from these calculated values.

Pearson's correlation coefficients (*r* values) were determined for comparison of stride parameters (i.e. outcome) and the input variables (i.e. speed, percentage incline and leg length). Multivariate multiple regression analysis was used to determine the percentage of variance explained by each input variable for each stride parameter. Sequential multiple regressions were employed to determine the statistical significance of speed, percentage incline and leg length in explaining variance. All variables were independently considered in the regression analysis, which resulted in a ranking of the variables according to relative variance explained. Analysis was performed using SPSS regression and SPSS frequencies for evaluation of assumptions.

Mass-specific net positive vertical work (W_c) was calculated for each stride by calculating the increase in horse potential energy during each stride period (the product of gravity, $\boldsymbol{g}$, and change in height, Δh):

$$W_c = V_x S_t \boldsymbol{g} \sin\theta \, , \tag{2}$$

where V_x is velocity (overground), S_t is stride time, $\boldsymbol{g}$ is 9.81 m s^{-2} and θ is incline (in degrees).

Climbing power (in W) per hindlimb stance period was calculated [based on the assumption that the majority of propulsive muscle mass is associated with the hind legs (Payne et al., 2005) and much of the apparent power generation occurs while the hindlimbs are in stance (Pfau et al., 2006)].

RESULTS

A total of 4861 strides were analysed (range 381–1080 per horse). These were subdivided into forelimb and hindlimb categories. Strides falling within two defined incline ranges were initially analysed for comparison, these categories being 0–2% incline (mean 1.1%, classified as level) and 8–12% incline (mean 9.7%, classified as incline). Strides were divided into four speed categories (range 9.5–12.5 m s^{-1}) with a range of 9 to 150 strides per speed category per horse for the level and 4 to 72 strides per speed category per horse for the incline category. Lead and non-lead limb data were combined for analysis (Witte et al., 2006). Front and hindlimbs were analysed separately. Strides included in the two categories are shown in Table 1. The range of speeds and percentage incline of strides from different horses are shown in Fig. 2. All horses were represented in both incline categories over a range of speeds.

Table 1. Number of strides (*N*), and mean and standard deviation (s.d.) of percentage incline of track in the four categories used for analysis (forelimb level, forelimb incline, hindlimb level and hindlimb incline)

	Level (0–2%)			Incline (8–12%)		
	N	Mean incline	s.d.	*N*	Mean incline	s.d.
Forelimb	472	1.11	0.56	312	9.78	1.16
Hindlimb	453	1.12	0.56	278	9.83	1.17

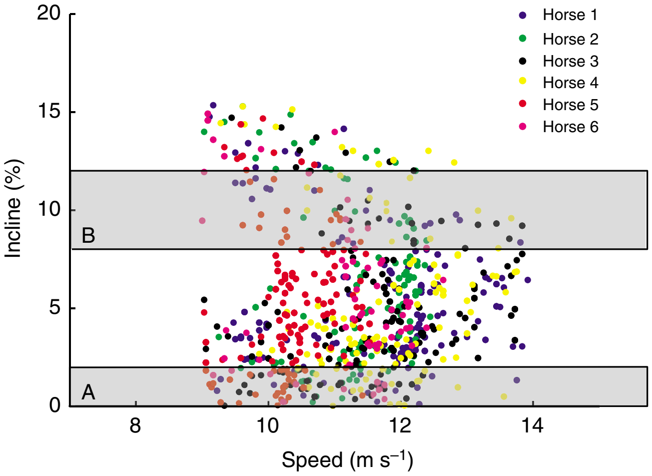

Fig. 2. Scatter plot showing speed against percentage incline for strides included in the analysis. Points are coloured according the horse number. The shaded areas represent the two incline categories that were used for the general linear model (GLM) analysis: 0–2% incline category (classified as level, A) and 8–12% incline category (classified as incline, B). NB Many of the points represent multiple numbers of strides due to superimposition.

Stride parameters

At a galloping speed of 9.5 m s^{-1}, mean forelimb stance duration was 148 ms on the level and 147 ms on the incline. Stance duration decreased to 126 ms on the level and 128 ms on the incline at 12.5 m s^{-1}. For the hindlimbs, mean stance duration was 154 ms on the level and 154 ms on the incline at 9.5 m s^{-1}. This decreased to 133 ms on the level and 134 ms on the incline at 12.5 m s^{-1}. Stance duration decreased during both level and incline running for both

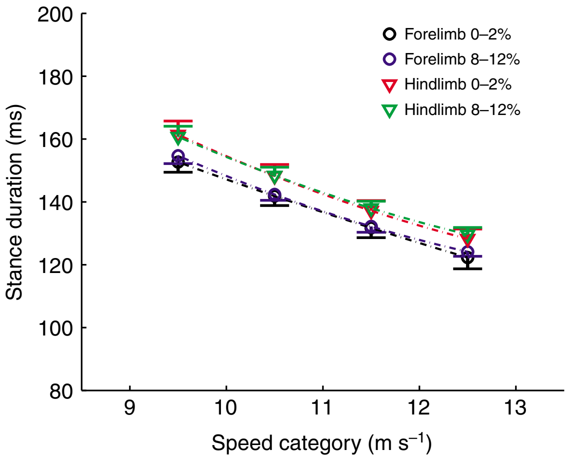

Fig. 3. Stance duration as a function of speed. Values are means + s.e.m. for hindlimbs and means – s.e.m. for forelimbs (for clarity; *N*=6 throughout) of individual horse mean data (indicated by different symbols) during level (0–2%) and incline (8–12%) galloping for the six horses. Quadratic lines of best fit (*P*<0.001) are shown. These were estimated for the population using mean data. Coefficients: forelimb level b_0=289.1, b_1=–17.59, b_2=0.34, r^2=0.75; forelimb incline b_0=377.7, b_1=–33.58, b_2=1.06, r^2=0.915; hindlimb level b_0=392.0.1, b_1=–34.32, b_2=1.06, r^2=0.75; hindlimb incline b_0=377.2, b_1=–32.22, b_2=0.99, r^2=0.82.

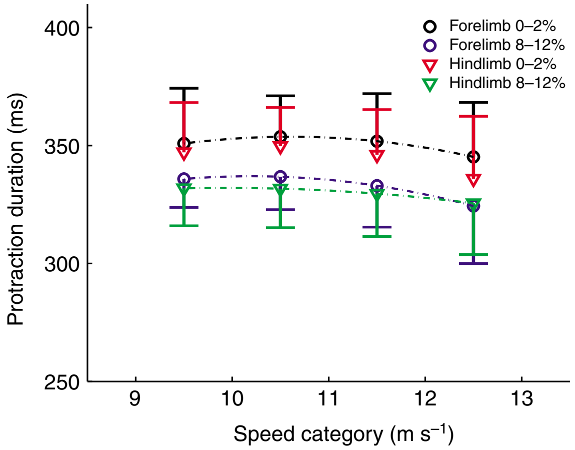

Fig. 4. Protraction duration as a function of speed. Values are means + s.e.m. for forelimb level and hindlimb level and means – s.e.m. for forelimb incline and hindlimb incline (for clarity; N=6 throughout) of individual horse mean data for fore- and hindlimbs (indicated by different symbols) during level (0–2%) and incline (8–12%) galloping for the six horses. Quadratic lines of best fit (P<0.001) are shown. These were estimated for the population using mean data. Coefficients: forelimb level b_0=86.7, b_1=50.37, b_2=–2.38, r^2=0.11; forelimb incline b_0=89.13, b_1=48.60, b_2=–2.38, r^2=0.17; hindlimb level b_0=4.02, b_1=66.39, b_2=–3.19, r^2=0.19; hindlimb incline b_0=233.59, b_1=19.81, b_2=–1.00, r^2=0.06.

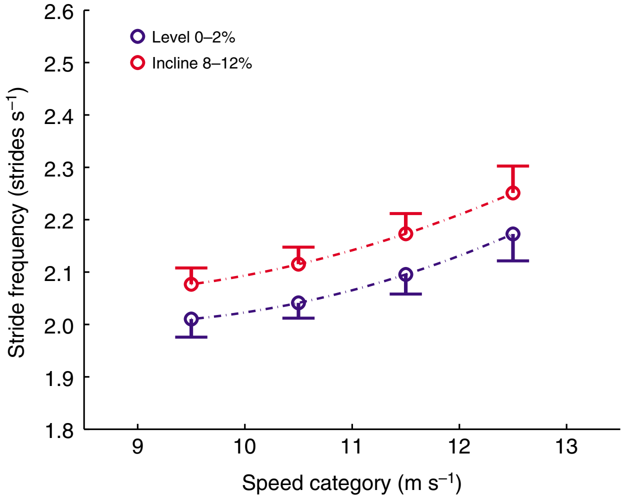

Fig. 5. Stride frequency as a function of speed. Values are means – s.e.m. for level and means + s.e.m. for incline (for clarity; N=6 throughout) of individual horse mean data for fore- and hindlimbs (indicated by different symbols) during level (0–2%) and incline (8–12%) galloping for the six horses. Quadratic lines of best fit (P<0.001) are shown. These were estimated for the population using mean data. Coefficients: level b_0=2.88, b_1=–0.202, b_2=0.012, r^2=0.44; incline b_0=2.70, b_1=–0.158, b_2=0.010, r^2=0.454.

the fore- and hindlimbs as speed increased. Hindlimbs consistently showed longer stance times than forelimbs over the speed range under both conditions (Fig. 3). This difference was statistically significant during incline (P=0.01) but not during level galloping (P=0.10).

Mean forelimb protraction duration was 351 ms on the level and 336 ms on the incline at 9.5 m s^{-1} decreasing to 352 ms on the level and 333 ms on the incline at 12.5 m s^{-1}. Hindlimb protraction duration was on average 347 ms during level and 332 ms during incline galloping at 9.5 m s^{-1}, decreasing to 346 ms during level galloping and 330 ms during incline galloping at 12.5 m s^{-1}. Protraction duration was significantly reduced across the speed range during incline galloping, when compared with level surface galloping (P<0.001 for both fore- and hindlimbs). Overall there was a moderate decrease in protraction duration over the speed range. Hindlimbs consistently showed slightly shorter protraction durations than forelimbs over the speed range under both incline conditions (Fig. 4). This was statistically significant during incline galloping (P=0.03) but not for level galloping (P=0.09).

Mean fore- and hindlimb stride frequency increased from 2.01 to 2.08 strides s^{-1} when comparing level and incline galloping at 9.5 m s^{-1} and from 2.10 to 2.17 strides s^{-1} at 12.5 m s^{-1}. Stride frequency was significantly increased during incline galloping (P<0.001; Fig. 5).

Differences in duty factor were identified when comparing level and incline galloping at both 9.5 and 12.5 m s^{-1}. Mean forelimb duty factor was 0.30 on the level and 0.31 on the incline at 9.5 m s^{-1}, reducing to 0.26 on the level and 0.28 on the incline at 12.5 m s^{-1}. Hindlimb duty factor was 0.31 on the level increasing to 0.32 on the incline at 9.5 m s^{-1} and 0.28 on the level and 0.29 on the incline at 12.5 m s^{-1}. Overall the trend was for duty factor to be greater during incline galloping compared with level galloping (Fig. 6). The difference in duty factor between level and incline galloping was not statistically significant for the forelimb (P=0.06). Duty factor was significantly greater in the hindlimbs than the forelimbs for strides during incline running (P=0.01). During level galloping there was no difference between fore- and hindlimb duty factor (P=0.10).

Calculated mass-specific peak vertical forelimb force (see Eqn 1) decreased by 11% (14.5 to 12.9 N kg^{-1}) at 9.5 m s^{-1} and 12% (16.5 to 14.5 N kg^{-1}) at 12.5 m s^{-1} when comparing incline galloping with level galloping using a change in forelimb to hindlimb impulse distribution as described in Materials and

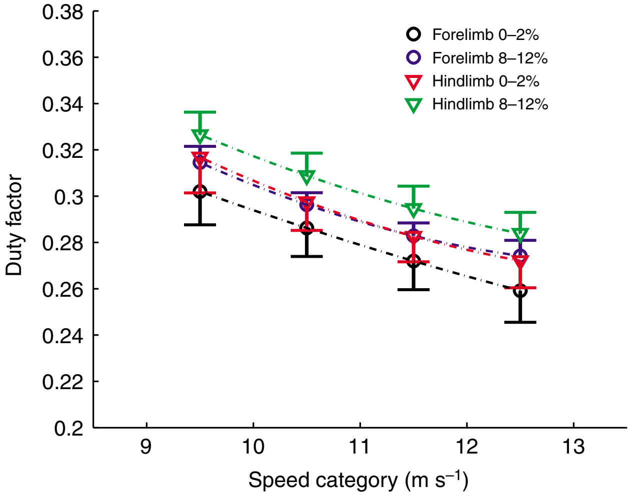

Fig. 6. Duty factor as a function of speed. Values are means + s.e.m. for forelimb level and hindlimb level and means – s.e.m. for forelimb incline and hindlimb incline (for clarity; N=6 throughout; indicated by different symbols) during level (0–2%) and incline (8–12%) galloping for the six horses. Quadratic lines of best fit (P<0.001) are shown. These were estimated for the population using mean data. Coefficients: forelimb level b_0=0.525, b_1=–0.031, b_2=0.001, r^2=0.53; forelimb incline b_0=0.727, b_1=–0.066, b_2=0.002, r^2=0.71; hindlimb level b_0=0.718, b_1=–0.063, b_2=0.002, r^2=0.54; hindlimb incline b_0=0.667, b_1=–0.052, b_2=0.002, r^2=0.69.

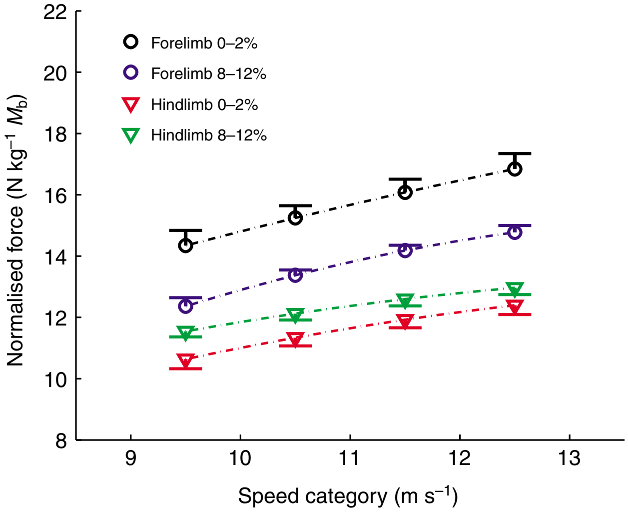

Fig. 7. Calculated peak vertical force, normalised to total mass of the subject (including mass of horse, riding tack and rider) as a function of speed assuming a shift in forelimb to hindlimb force distribution on inclined surfaces. Values are means + s.e.m. for forelimbs and means – s.e.m. (N=6 throughout) for hindlimbs (for clarity; indicated by different symbols) during level (0–2%) and incline (8–12%) galloping for the six horses. Peak forces were calculated from duty factor and Eqn 1 assuming a shift in forelimb to hindlimb impulse distribution from 57:43 on the level to 52:48 on a 10% incline (Dutto et al., 2004). Quadratic lines of best fit (P<0.001) are shown. These were estimated for the population using mean data. Coefficients: forelimb level b_0=2.40, b_1=1.578, b_2=–0.034, r^2=0.51; forelimb incline b_0=–7.68, b_1=3.100, b_2=–0.104, r^2=0.72; hindlimb level b_0=–1.73, b_1=1.846, b_2=–0.057, r^2=0.53; hindlimb incline b_0=0.870, b_1=1.617, b_2=–0.052, r^2=0.61.

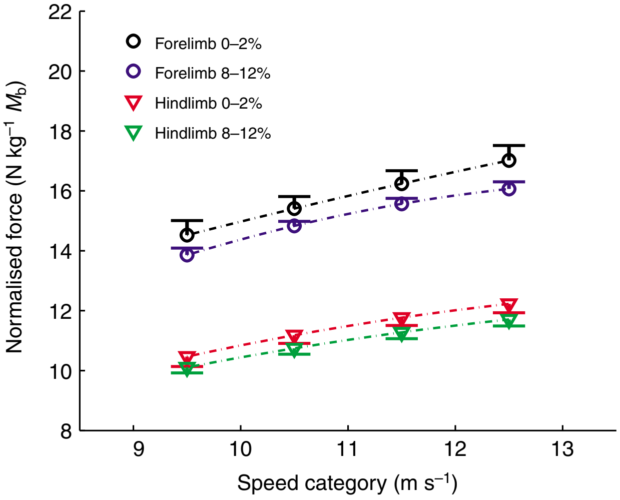

Fig. 8. Calculated peak vertical force, normalised to total mass of the subject (including mass of horse, riding tack and rider) as a function of speed – assuming no shift in forelimb to hindlimb force distribution. Values are means + s.e.m. for forelimbs and means – s.e.m. (N=6 throughout) for hindlimbs (for clarity; indicated by different symbols) during level (0–2%) and incline (8–12%) galloping for the six horses. Peak forces were calculated from duty factor and Eqn 1 assuming no shift in forelimb to hindlimb impulse distribution from 57:43 on the level and incline. Quadratic lines of best fit (P<0.001) are shown. These were estimated for the population using mean data. Coefficients: forelimb level b_0=3.358, b_1=1.436, b_2=–0.028, r^2=0.51; forelimb incline b_0=–7.271, b_1=3.355, b_2=–0.119, r^2=0.70; hindlimb level b_0=–2.615, b_1=1.978, b_2=–0.063, r^2=0.53; hindlimb incline b_0=–1.077, b_1=1.668, b_2=–0.052, r^2=0.686.

methods. Hindlimb calculated mass-specific force increased by 7% (11.0 to 11.8 N kg^{-1}) at 9.5 m s^{-1} and 6% (12.1 to 12.8 N kg^{-1}) at 12.5 m s^{-1} when comparing incline and level galloping. ANCOVA results demonstrated that calculated mass-specific force was significantly greater in the hindlimbs (P<0.001) and was significantly reduced in the forelimbs (P<0.001) during incline galloping. Calculated peak vertical forelimb force with an assumed shift in fore- to hindlimb impulse distribution of 52:48 is presented in Fig. 7. For comparison Fig. 8 shows calculated values for peak vertical force assuming no shift in impulse distribution from level running whilst galloping on the incline (i.e. using the 57:43 fore- to hindlimb impulse ratio).

Multiple regression analysis

Results from regression analysis are presented in Table 2. Speed was the most important determinant variable in explaining stance duration in the fore- and hindlimbs, with percentage incline not making a statistically significant contribution.

Percentage incline was the most important determinant variable for explaining protraction duration. It also made a statistically significant contribution to stride frequency, duty factor and peak vertical ground reaction force.

Work per stride and climbing power

Fig. 9 shows regression lines (and confidence intervals) of stride frequency *vs* work per stride (W_c) for measured strides (calculated from Eqn 2). Data were categorised into 1 m s^{-1} stride bins with each line representing one speed category. All regression lines for galloping horses show a positive correlation between W_c and stride frequency within stride bins. Stride frequency against W_c of data from trotting horses [data from figure 8 of Wickler et al. (Wickler

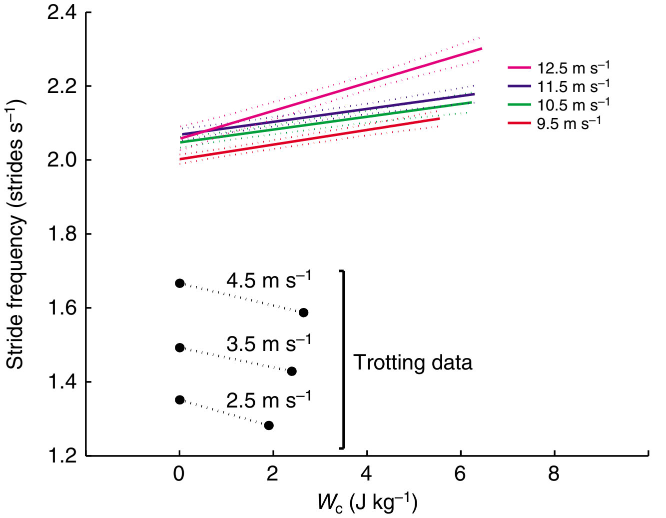

Fig. 9. Stride frequency *vs* mass-specific work per stride (W_c) for galloping horses (coloured lines). Data were categorised into 1 m s^{-1} speed bins, and linear regression lines (solid lines) and 95% confidence intervals (broken lines) have been plotted. Each colour represents data from a 1 m s^{-1} speed bin. Calculated work per stride and stride frequency from figures and data from Wickler et al. (Wickler et al., 2005) measured from trotting horses are also presented (black data points). As data are categorised into speed bins, moving from left to right represents an increase in incline.

Table 2. Results of multivariable linear regression models evaluating the effect of incline, speed and leg length on measured and calculated variables

	B	β	Sr^2 (incremental)	Sig. *B*		*B*	β	Sr^2 (incremental)	Sig. *B*
FL stance					HL stance				
Speed	–8.138	–0.849	0.577	0.000	Speed	–7.389	–0.801	0.492	0.000
Incline	–0.062	–0.017	0.000	0.086	Incline	0.173	0.049	0.003	0.000
LL	138.161	0.320	0.095	0.000	LL	149.968	0.367	0.125	0.000
Intercept	2.073				Intercept	–20.631			
r^2			0.672		r^2			0.620	
Adjusted r^2			0.671		Adjusted r^2			0.620	
r			0.820		r			0.787	
FL protraction					HL protraction				
Speed	–3.784	0.251	0.089	0.000	Speed	–4.344	–0.290	0.089	0.000
Incline	–1.527	0.267	0.075	0.000	Incline	–1.818	–0.321	0.075	0.000
LL	–154.046	0.227	0.047	0.000	LL	–131.838	–0.199	0.047	0.000
Intercept	638.922				Intercept	605.167			
r^2			0.212		r^2			0.250	
Adjusted r^2			0.211		Adjusted r^2			0.249	
r			0.460		r			0.500	
FL stride frequency					HL stride frequency				
Speed	0.053	0.611	0.367	0.000	Speed	0.052	0.612	0.355	0.000
Incline	0.007	0.215	0.047	0.000	Incline	0.007	0.228	0.052	0.000
LL	0.091	0.023	0.001	0.089	LL	–0.052	–0.014	0.000	0.330
Intercept	1.348				Intercept	1.584			
r^2			0.414		r^2	0.407		0.407	
Adjusted r^2			0.413		Adjusted r^2	0.406		0.406	
r			0.643		r	0.638		0.638	
FL duty factor					HL duty factor				
Speed	–0.010	–0.659	0.299	0.000	Speed	–0.009	–0.554	0.194	0.000
Incline	0.001	0.132	0.021	0.000	Incline	0.001	0.238	0.061	0.000
LL	0.294	0.429	0.170	0.000	LL	0.298	0.454	0.190	0.000
Intercept	1.348				Intercept	–0.101			
r^2			0.491		r^2			0.445	
Adjusted r^2			0.490		Adjusted r^2			0.445	
r			0.700		r			0.667	
FL force (57:43)					HL force (57:43)				
Speed	0.572	0.645	0.287	0.000	Speed	0.315	0.542	0.181	0.000
Incline	–0.043	–0.129	0.020	0.000	Incline	–0.052	–0.235	0.060	0.000
LL	–16.757	–0.420	0.162	0.000	LL	–11.995	–0.467	0.201	0.000
Intercept	36.544				Intercept	27.408			
r^2			0.470		r^2			0.442	
Adjusted r^2			0.469		Adjusted r^2			0.441	
r			0.685		r			0.665	
FL force (52:48)					HL force (52:48)				
Speed	0.543	0.557	0.232	0.000	Speed	0.338	0.545	0.160	0.000
Incline	–0.177	–0.479	0.240	0.000	Incline	0.075	0.318	0.095	0.000
LL	–15.998	–0.365	0.123	0.000	LL	–12.665	–0.462	0.197	0.000
Intercept	35.633				Intercept	35.633			
r^2			0.595		r^2			0.452	
Adjusted r^2			0.595		Adjusted r^2			0.451	
r			0.771		r			0.672	

FL, forelimb; HL, hindlimb; Incline, percentage incline; *LL*, leg length; *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.

et al., 2005)] have also been plotted. A negative correlation is seen between W_c and stride frequency whilst trotting. Mass-specific climbing power (W kg^{-1}) *vs* stride frequency has been plotted in Fig. 10.

DISCUSSION

This is the first study measuring the effect of incline on stride timing variables of racehorses during over-ground gallop locomotion. This information can be used to make predictions of peak limb forces experienced whilst horses are undergoing high speed exercise within their normal environment. Data presented add to those already published from horses during high speed over-ground galloping (Witte et al., 2006). Our results also provide an opportunity to identify relationships between stride timing variables and the power required by the horse to move up an incline.

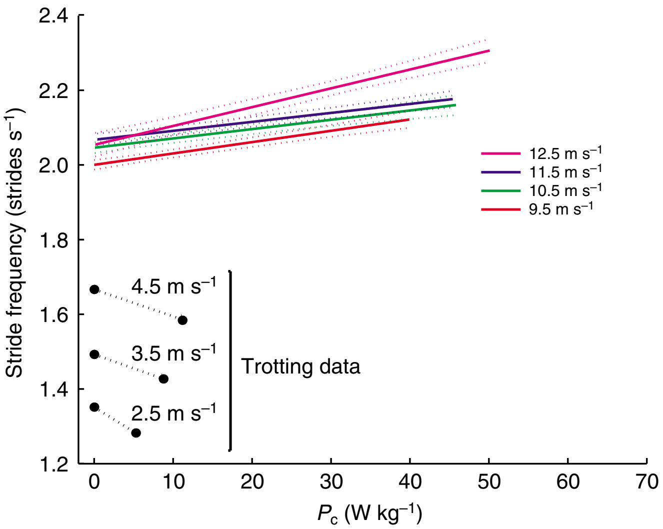

Fig. 10. Stride frequency *vs* mean stance climbing power (P_c) per stride cycle for galloping horses (coloured lines). P_c was calculated assuming the work was performed during the hindlimb stance period. Data were categorised into 1 m s^{-1} speed bins and linear regression lines (solid lines) and 95% confidence intervals (broken lines) have been plotted. Each colour represents data from a 1 m s^{-1} speed bin. Calculated P_c and stride frequency from figures and data of Wickler et al. (Wickler et al., 2005) measured from trotting horses are also presented (black data points). As data are categorised into speed bins, moving from left to right represents an increase in incline.

Protraction duration has been reported to be significantly longer when horses are trotting on a 10% incline surface (Hoyt et al., 2002). This is in contrast to this study where measurements were made from galloping horses and protraction duration was significantly shorter when on an incline surface. The GLM showed a 5% reduction in forelimb and hindlimb protraction duration when comparing level and incline galloping groups at 11 m s^{-1}. Multiple regression analysis identified percentage incline as a stronger predictor of protraction duration than the speed of the animal. Protraction is largely related to passive properties of the limb rather than muscular work (Heglund et al., 1982; Kram and Taylor, 1990; Wilson et al., 2003), although some muscle action is required to swing each leg forward to begin the next step (Kram, 2000). Horses cannot achieve the high power output required for rapid limb protraction by muscle contraction alone (Wilson et al., 2003). A passive biceps muscle tendon unit ‘catapult’ mechanism has been described in detail in the forelimb and a similar mechanism is suspected to exist in the hindlimb (Wilson et al., 2003). Changes in the kinematics of the limb during incline galloping may result in increased energy storage within the ‘catapult’ mechanism and so give rise to a reduced protraction duration. Protraction duration may also be reduced due to the surface interrupting the limb’s arc during repositioning for the next stance period so it occurs earlier because of the incline of the ground. Decreased protraction duration resulted in reduced stride time and hence an increase in stride frequency.

The training programme of the horses meant that they all galloped at a steady speed along the whole track – starting with the level section and then the incline section. The duration of each gallop was approximately 90 s. This exercise was repeated twice, with a short rest period between consisting of walking and trotting. The horses were all race-fit elite Thoroughbreds and the length of the track, and the duration of the gallop, was short compared with that used in competitive races. Horses were therefore unlikely to have experienced significant fatigue. Fatigue has been shown to decrease stride frequency (Colborne et al., 2001; Johnston et al., 1999; Schuback et al., 1999). This contrasts with our findings and supports the conclusion that our observed changes in stride parameters are not related to fatigue. There were no significant differences in stride timing variables when comparing the first and second period of exercise. This also supports the conclusion that measured variables were not being influenced by fatigue.

Calculated mass-specific peak vertical forelimb force decreased and calculated hindlimb force increased during incline galloping. During gallop, peak vertical ground reaction forces vary between lead and non-lead limbs. This difference decreases at higher speeds (Witte et al., 2004). It has been demonstrated that there is no significant difference between duty factor when comparing lead and non-lead limbs (Witte et al., 2006). The increase in duty factor and a change in the distribution of impulses between forelimbs and hindlimbs on different inclines resulted in changes in calculated peak vertical ground reaction force between incline conditions. The result of the duty factor increase in the hindlimbs would be to counteract the change in fore- to hindlimb impulse distribution. Forelimb to hindlimb impulse distribution was assumed to range between 57:43 on the level and 52:48 on a 10% incline (Dutto et al., 2004). A linear change in the impulse distribution was assumed between 0 and 10%. To validate this assumption over a range of inclines at canter and gallop would require force-plate measurements within a training surface. This would obviously be difficult due to the limitations of force-plate use in the field during high speed locomotion. Treadmill studies would be an alternative method; however, there are limitations that have been discussed previously. The change in fore- to hindlimb impulse distribution is reported not to be consistent with the static measurement of horses on the incline, where impulse distribution was maintained at 57:43 (Dutto et al., 2004). Even if impulse distribution remained unchanged from level galloping we would predict a small decrease in the hindlimb mass-specific peak vertical ground reaction force (Fig. 7). This is a result of the increase in duty factor measured from the hindlimbs during incline galloping. Only a small shift in impulse distribution would have to occur to cause the calculated peak vertical ground reaction force to increase. The rider may also alter the front to hind ratio of forces. The jockey in this study was experienced and was positioned over the centre of mass (Fig. 11). During level ridden canter it has

Fig. 11. A fully instrumented galloping horse. At gallop the jockey stands and their centre of mass is positioned over the estimated position of the horse’s centre of mass.

previously been shown that the jockey has a minimal effect on vertical limb force distribution (Merkens et al., 1986; Merkens et al., 1993). When galloping on an incline the jockey appeared to maintain a similar standing position in the stirrups compared with on the level. Any change in position of the jockey relative to the centre of mass will be influenced by the attachment point of the stirrups to the saddle. This point is positioned dorsal to the centre of mass. Any small changes that occur in the jockey's position are therefore likely to result in a small increase in the shift of the impulse distribution towards the hindlimbs.

The changes in measured stride parameters that occurred whilst galloping on the incline are consistent with those reported during human incline running. This contrasts with the changes reported in trotting horses (Dutto et al., 2004). It has previously been identified that most of the speed-related and size-related differences in the metabolic cost of level locomotion are accounted for by the inverse relationship with contact time, or the rate of force application (Kram and Taylor, 1990; Roberts et al., 1998). Increasing the gradient by 10% can result in an increase in the metabolic rate by more than a factor of two. Our results showed that stance duration was unchanged and duty factor was slightly increased when the gradient of the surface was increased. The relationship between stance time and metabolic cost that applies during locomotion when the net work done is zero (i.e. level, steady speed locomotion) (Kram and Taylor, 1990) therefore requires modification when estimating the total metabolic cost of incline locomotion. Determination of a correction factor for this modification requires further investigation; however, it is likely to involve the additional mechanical work needed to increase the potential energy of the animal's centre of mass whilst moving up a slope and an efficiency factor for the musculature to perform this work.

Mechanical work is required to elevate the centre of mass during locomotion on inclined surfaces. Interestingly, during incline trotting, stance time remains constant and stride frequency decreases (Hoyt et al., 2002; Wickler et al., 2005). Peak vertical ground reaction force increases in the hindlimbs due to a shift in forelimb to hindlimb impulse distribution and little change in duty factor (Dutto et al., 2004). From changes in stride parameters and limb forces we would expect a greater volume of muscle to be recruited in the hindlimbs during incline trotting. This is supported by electromyography (EMG) findings (Wickler et al., 2005). Our results demonstrate that across all speed categories there is a statistically significant increase in stride frequency and a small increase in measured duty factor on the incline. Fig. 9 shows that stride frequency is negatively correlated with W_c per stride for trotting and positively correlated with W_c per stride for galloping. Our results suggest that during galloping, in contrast to trotting, changes to stride frequency are important for providing W_c per stride and hence P_c. The differences observed here may reflect the fact that there is little or no further muscle available for recruitment as it is already in use due to the higher forces experienced during galloping. Further power may, in this situation, only be provided by increasing stride frequency. This explanation is clearly not the complete solution to the questions raised – stride frequency does vary when horses trot on inclined surfaces and the work per stride will vary whilst galloping – but it shows an interesting and fundamental difference between trotting and galloping. EMG studies, force-plate analysis and full inverse dynamics during galloping would be necessary to support and confirm our suggested hypothesis. The availability of further muscle for recruitment of power may be a factor influencing trot/gallop transitions during incline locomotion. If further muscle recruitment becomes a limiting factor for the generation of power for climbing during trotting a gait transition may occur and increasing stride frequency may become the dominant provider of additional power.

Conclusion

In this study we tested two hypotheses. We have demonstrated that stride frequency is significantly increased when horses gallop on an incline compared with a level track. During incline galloping we calculated smaller peak vertical forces acting on the forelimbs and increased peak vertical forces acting on the hindlimbs. We propose that horses provide the power necessary to elevate their centre of mass up an inclined surface by increasing muscle recruitment at low speeds and hence work per stride cycle increases. At high speeds stride frequency increases to provide power for moving up the slope, perhaps indicating that the limb muscles may be fully recruited during galloping.

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