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Ground reaction forces in horses trotting up an incline and on the level over a range of speeds

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Summary

Although the forces required to support the body mass are not elevated when moving up an incline, kinematic studies, *in vivo* tendon and bone studies and kinetic studies suggest there is a shift in forces from the fore- to the hindlimbs in quadrupeds. However, there are no whole-animal kinetic measurements of incline locomotion. Based on previous related research, we hypothesized that there would be a shift in forces to the hindlimb. The present study measured the force produced by the fore- and hindlimbs of horses while trotting over a range of speeds (2.5 to 5 m s^{-1}) on both level and up an inclined (10%) surface.

On the level, forelimb peak forces increased with trotting speed, but hindlimb peak force remained constant. On the incline, both fore- and hindlimb peak forces increased with speed, but the sum of the peak forces was lower than on the level. On the level, over the range of speeds tested, total force was consistently distributed between the limbs as 57% forelimb and 43% hindlimb, similar to the weight distribution of the horses during static weight tests. On the incline, the force distribution during locomotion shifted to 52% forelimb and 48% hindlimb.

Time of contact and duty factor decreased with speed for both limbs. Time of contact was longer for the forelimb than the hindlimb, a finding not previously reported for quadrupeds. Time of contact of both limbs tended to be longer when traveling up the incline than on the level, but duty factor for both limbs was similar under both conditions. Duty factor decreased slightly with increased speed for the hindlimb on the level, and the corresponding small, predicted increase in peak vertical force could not be detected statistically.

Key words: ground reaction force, limb, horse, biomechanics, force, locomotion, trotting, incline.

Introduction

Increasing speed of locomotion will require an increased ground reaction force. This is the case in humans during running, and is primarily due to the decreased contact time (Munro et al., 1987). In quadrupeds, trotting involves the simultaneous contact of diagonal fore- and hindlimbs, so that the ground reaction force is produced by the combined effort of both limbs. Do the forces produced by both limbs increase as trotting speed increases, similar to that observed in humans? Muscle–tendon stress has been shown to increase with speed in tendons of the distal joints in the forelimb but not the hindlimb (Biewener, 1998), and although ground reaction forces are not reported directly in Biewener (1998), force traces for the fore- and hindlimbs over a range of speeds that include trotting seem to indicate that force increases for the forelimb but not the hindlimb. McLaughlin et al. (1996) observed that peak vertical ground reaction forces increase with trotting speed in the forelimb but not in the hindlimb in horses. However, the results did not provide sufficient detail to describe the forces associated with trotting, and covered a slower range of trotting speeds (1.9–3.9 m s^{-1}). In contrast with both of these studies, a study of bone strain *versus* speed in horses suggested that there are no differences in the forces between fore- and hindlimbs (Rubin and Lanyon, 1982). Based on the studies presented above, we developed the hypothesis that ground reaction forces increase for the forelimb but not the hindlimb as trotting speed increases. Studies of locomotion often assume that duty factor and time of contact of the fore- and hindlimbs are the same during trotting. If force production by the forelimb increases with speed but that by the hindlimb does not, this may be because the duty factor does not change with speed in the same way in both limbs. Further, if the force generated by the hindlimb is lower than the forelimb (as indicated by reported force tracings; Biewener, 1998), then the duty factor may be lower in the hindlimb. A second question we were interested in, was how do the forces produced by the limbs relate to the observed duty factor and time of contact during trotting?

Even though total vertical forces are expected to be the same on the level and an incline, there is evidence that the forces under the fore- and hindlimbs of a quadruped may not change in the same way when trotting up an incline. One kinematic analysis (Sloet van Oldruitenborgh-Oosterbaan et al., 1997) showed that, when trotting up an incline, there was increased hyperextension of the metatarsophalangeal (MTP) joint on the hindlimb and decreased hyperextension of the metacarpophalangeal (MCP) joint of the forelimb. Because the MCP and MTP are primarily controlled by ligaments and increases in MCP range of motion have been found to positively correlate with increased ground reaction force (McGuigan and Wilson, 2003), we hypothesized that there will be smaller forces acting on the forelimb and increased forces acting on the hindlimb. Additionally, we asked whether these changes in force would produce concomitant changes in the temporal stride characteristics.

Materials and methods

Animals and experimental protocol

Seven horses (four Arabian, two Thoroughbred, and one Quarter Horse-cross) were used during testing, but only one horse completed both the level and incline protocols because the two studies were conducted 2 years apart. Four horses (three Arabian and one Thoroughbred) with a body mass of 491±37 kg completed the level test condition, and four horses (two Arabian, one Thoroughbred and one Quarter Horse-cross) with a body mass of 438±39 kg completed the incline protocol. Both the level and incline experimental protocols were approved by the university's Animal Care and Use Committee. Animals had been conditioned to the testing protocol for several weeks prior to testing. A surcingle with a reflective strip (Scotchlite Reflective Tape, 3M St Paul, MN, USA) was placed around the thorax of the animal. This strip was part of the system used to monitor the animal's trotting velocity over the force plate. A series of three infrared emitters and sensors were placed with 2 m between each sensor. The sensors were triggered by reflected infrared light and a timing program (Labview®, v5.1, National Instruments Inc., Austin, TX, USA) permitted instantaneous calculations of velocity through each of two consecutive timing zones, one of which included the force plate. If the speed in the two timing zones differed by more than 10%, the trial was not included in the analysis. Less than 2% of trials were excluded because of changing speed. After a brief warm-up, the animal was led through the test area, by either a trained handler running alongside (level) or by the handler sitting on the rear of a motorized cart (incline). Approximately 1–5 min elapsed between trials. The test speeds were randomly varied from trial to trial. Trotting velocities between 2.5 and 5.0 $m\ s^{-1}$ were obtained for each animal and are included in this analysis. The upper speed of 5.0 $m\ s^{-1}$ was chosen because the maximum trotting speed of these animals on the level averaged 5.1 $m\ s^{-1}$ and on the incline averaged 4.4 $m\ s^{-1}$ (Wickler et al., 2003), thus giving us top trotting speeds at the upper limit of natural trotting speeds. These speeds are near the allometrically predicted trot–gallop transition speed (5.8 $m\ s^{-1}$) for a 458 kg mammal but are much slower than the maximum trotting speeds (ca. 12 $m\ s^{-1}$) observed in some equine breeds (Heglund and Taylor, 1988).

Experimental set-up

Two runways, each 30 m in length, were built for data collection. The first runway was level and the second was sloped with a 10% gradient (5.7° relative to horizontal as measured using a transit). The cement runways (10 cm thick, 1.25 m wide) were covered by a 10 mm-thick, high density, black rubberized mat (All Weather Rollout Runway, Dodge Regupol, Lancaster, PA, USA). A 0.6 m×0.9 m force plate (model 9287BA, Kistler Instruments, Winterthur, Switzerland) was located approximately in the middle of each runway supported by a 0.9 m-thick pedestal of cement, isolated from the rest of the runway by vibration-dampening material. The same force measuring plate was used for all data collection. The top of the force plate was covered with a rubberized mat of material identical to that covering the rest of the runway to provide a continuous visual field for the animal. With the mat glued to the surface of the force plate, the natural frequency of the force plate was 384 Hz in the *z*-axis and 500 Hz in the two horizontal directions. These frequencies are somewhat lower than the original natural frequency of the plate (520 Hz and 750 Hz, respectively) but the observed decrements are within the tolerances recommended by the manufacturer. Three-dimensional force data were sampled at 1000 Hz for all tests, but only the horizontal (representing the fore–aft direction) and vertical forces were included in the study.

Data analysis

Normal and parallel forces were recorded for each trial. For the level trials, the normal force corresponded to F_z (true vertical) and the parallel force to F_y (the fore–aft force or true horizontal). For the data collected during the inclined trials, the normal and parallel forces were rotated 5.7° relative to the level condition. In order to compare level and incline data, force data recorded during the incline trials were converted to represent true vertical (parallel to the gravitational vector) and horizontal (orthogonal to the gravity vector) force. Thus, data referred to as F_z and F_y are representations of forces parallel and orthogonal to the gravitational vector. F_{brake} and F_{prop} are used in subsequent analysis of the horizontal force, where F_{brake} is indicative of a braking force, and F_{prop} of a propulsive force, and these are also orthogonal to the gravitational vector.

From each trial, the following variables were calculated: peak vertical force ($F_{z,peak}$), vertical impulse (Imp_z), peak braking and propulsive forces (F_{brake}, F_{prop}), and the total (net) horizontal impulse (Imp_h). The distribution of vertical forces between the fore- and hindlimbs was determined by calculating the average force over a stride for both the fore- and hindlimbs, and then the percentage distribution of force is simply the ratio of the average force over the stride for a particular limb and the sum of the fore- and hindlimb average forces over the stride. Time of contact (t_c) was also measured from the

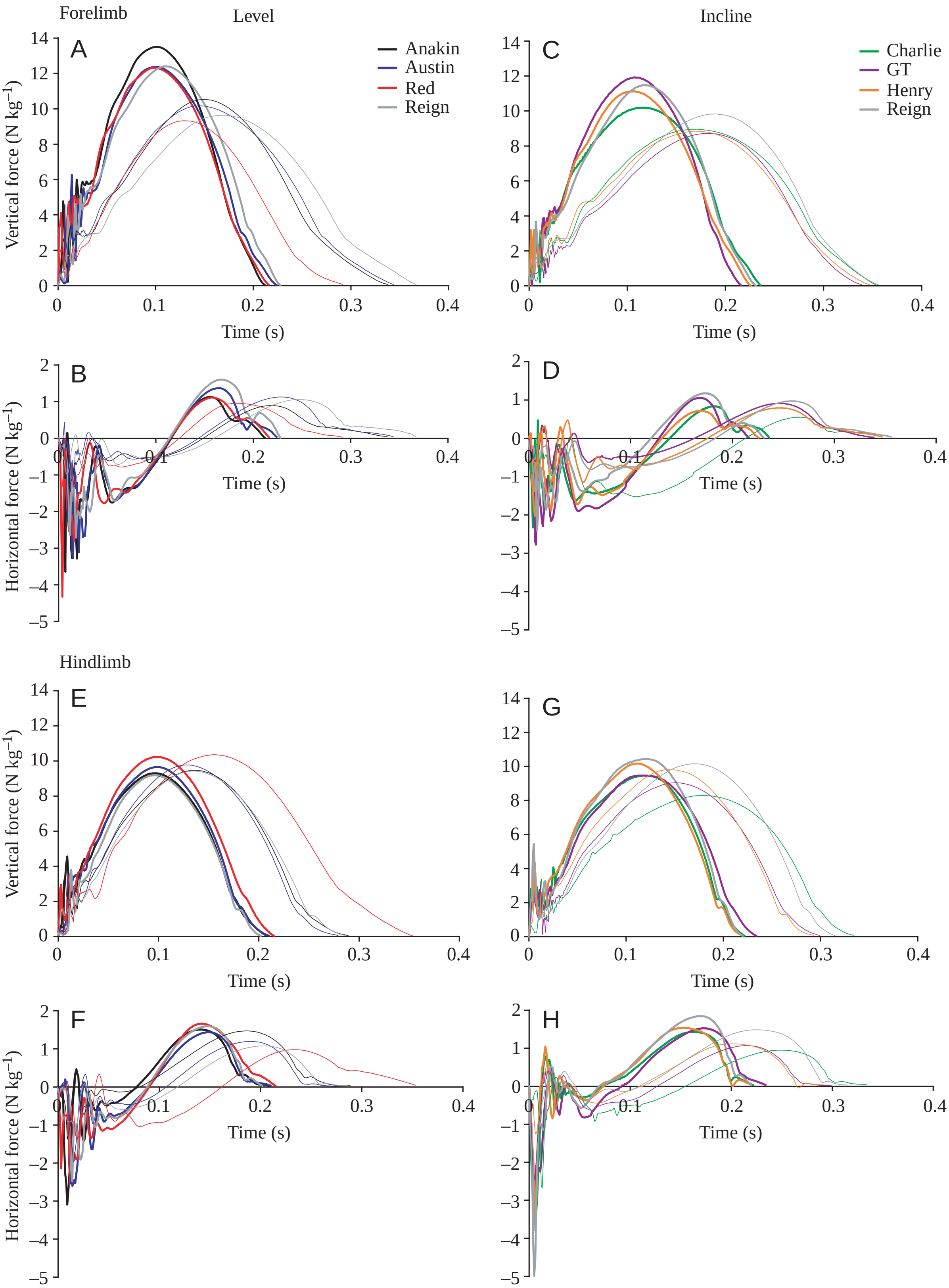

Fig. 1. Ground reaction force (GRF) patterns are similar to those typically reported for other quadrupeds. Both vertical (A,C,E,G) and horizontal (B,D,F,H) forces are depicted for the level and the incline. Thicker lines represent faster (>4.5 m s^{-1}) and the thinner lines represent slower (<2.75 m s^{-1}) speeds. Forces generated by the forelimb increased as speed increased for both the level (A) and incline (C) conditions. Hindlimb vertical forces tended to remain constant on the level (E), but increased on the incline (G). Hindlimb forces were higher on the incline than on the level.

recorded force data. From video recordings obtained simultaneously with the force recordings, stride time was measured. Duty factor (DF) was calculated as the ratio of time of contact to stride time.

It would not have been statistically valid to treat all of the ca. 120 values obtained for a given limb and condition as independent observations because they were obtained from four individual animals. Therefore, the data obtained from an individual animal were subjected to regression analysis and then the resulting regression coefficients were subjected to analysis of variance (ANOVA). For each animal, the best-fit regression line was determined for the variable of interest using speed as the independent variable. For three variables (t_c, DF and Imp_z), the best-fit lines were power functions. A log transform was applied to both speed and the variable (t_c, DF or Imp_z) to create a linear relationship, from which a linear regression was calculated. From all regression lines, two values were used for statistical analysis: the slope of the line and the predicted value at 3.5 m s^{-1}. The predicted value at 3.5 m s^{-1} was used, rather than intercept, to assess the magnitude of difference between limbs and between level and incline, because it represents a datum in the mid-range of speeds tested, and is relatively close to the preferred trotting speed of horses of this mass (Wickler et al., 2000). Differences between the fore- and hindlimb (leg) and the differences between the level and incline (condition) were assessed by a 2×2 ANOVA (P=0.05), with repeated measures used for the leg but not for the condition comparison. Repeated measures were not used for condition because only one horse was tested on both the level and incline conditions; each of the remaining six horses performed either the level or the incline test. An ANOVA was used to assess each variable of interest (one for the slope of the regression line and the second for the value at 3.5 m s^{-1}). To determine whether speed affected a particular variable, under a particular condition, the 95% confidence interval for the slope was determined. The speed effect was present if the 95% confidence interval did not include zero.

Results

Patterns of force generation

The ground reaction force (F_z and F_y) patterns remained fairly consistent (Fig. 1), regardless of speed and condition. Both the fore- and hindlimb had similar patterns, even though the magnitude and timing of these forces were different.

Temporal characteristics as a function of speed

Time of contact (t_c) for both limbs decreased with speed for level and incline, and the t_c for the forelimb decreased at a faster rate than the hindlimb (Table 1). At the higher speeds (>4.5 m s^{-1}), t_c tended to converge for both limb and condition (Fig. 2A,B), indicating that both limbs were spending roughly equivalent time periods on the ground at higher speeds. Because the stride times were essentially the same for fore- and hindlimbs, duty factor exhibited the same pattern as time of contact. Duty factor also decreased with speed for both limbs during level and incline trotting (Table 1), and duty factor of the forelimb decreased at a greater rate than that of the hindlimb. At higher speeds, the DF of the fore- and hindlimbs converged.

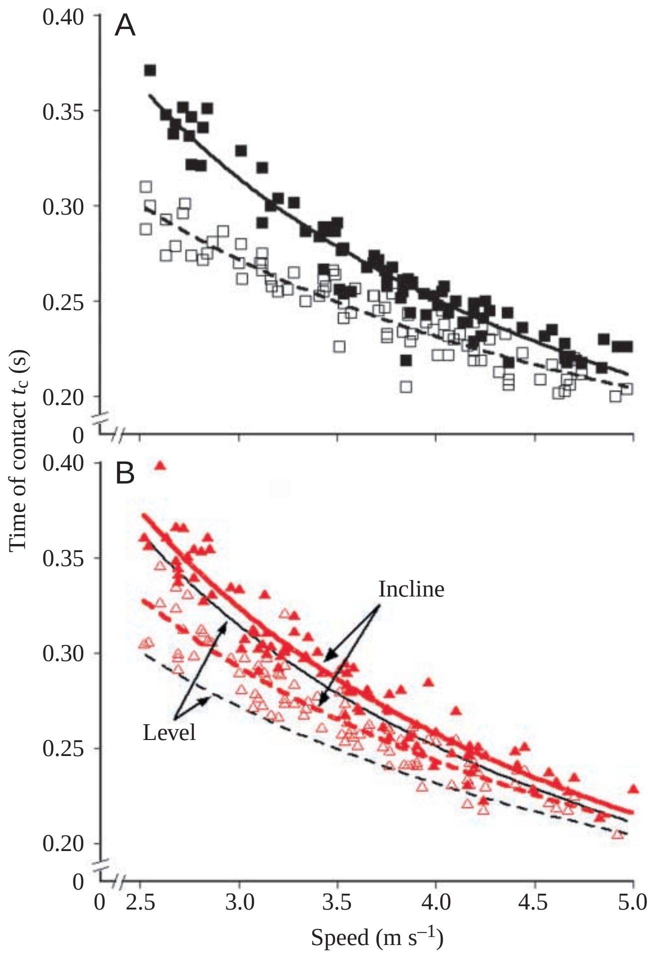

Fig. 2. Temporal characteristics decreased with speed, and were the same for the forelimb on level and incline conditions, but higher for the hindlimb on the incline. In this and subsequent figures the following symbols and lines are used: black, level; red, incline; forelimb on the level, filled squares; forelimb on the incline, filled triangles; hindlimb on the level, open squares; hindlimb on the incline, open triangles; solid lines, forelimb; broken lines, hindlimb. (A) Time of contact on the level decreased with speed as a power function (see Table 1). Time of contact t_c was lower for the hindlimb, but values converged at higher speeds. (B) Time of contact of the forelimb was essentially the same on the incline as on the level, but slightly higher for hindlimb than on the level. For easy reference, the black lines represent the data on the level.

Forces as a function of speed

Peak vertical ground reaction force ($F_{z,peak}$) generated under the forelimb increased with speed for both the level (Fig. 3A) and incline conditions (Fig. 3B). The $F_{z,peak}$ under the hindlimb did not change with speed on the level, but did on

Table 1. *Stride parameters and forces as a function of speed and incline*

	Level		Incline		RM-ANOVA	
Variable	3.5 m s^{-1}	Slope	3.5 m s^{-1}	Slope	3.5	Slope
logt_c (s)						
Fore	0.276 (0.008)	–0.75 (0.04)*	0.285 (0.008)	–0.75 (0.04)*	a	a,b
Hind	0.249 (0.006)	–0.56 (0.03)*	0.264 (0.006)	–0.66 (0.03)*		
logDF						
Fore	0.41 (0.01)	–0.38 (0.04)*	0.42 (0.01)	–0.43 (0.04)*	a	a,b
Hind	0.37 (0.01)	–0.21 (0.02)*	0.38 (0.01)	–0.30 (0.02)*		
$F_{z,peak}$ (N kg^{-1})						
Fore	11.31 (0.14)	1.14 (0.10)*	10.04 (0.14)	1.12 (0.10)*	a,c	a
Hind	9.50 (0.21)	0.05 (0.13)	9.73 (0.21)	0.27 (0.13)*		
logImp_z (Ns kg^{-1})						
Fore	1.82 (0.03)	–0.32 (0.03)*	1.72 (0.03)	–0.35 (0.03)*	a,c	a
Hind	1.37 (0.04)	–0.42 (0.05)*	1.58 (0.04)	–0.51 (0.05)*		
Load (%)						
Fore	56.99 (0.64)	0.08 (0.06)	52.28 (0.64)	0.06 (0.06)	a,c	a
Hind	43.01 (0.60)	–0.09 (0.05)	47.72 (0.60)	–0.19 (0.05)*		
F_{brake} (N kg^{-1})						
Fore	–2.47 (0.15)	–0.57 (0.13)*	–1.92 (0.15)	–0.99 (0.13)*	c	
Hind	–1.97 (0.20)	–0.45 (0.19)	–2.83 (0.20)	–0.71 (0.19)*		
F_{prop} (N kg^{-1})						
Fore	1.10 (0.07)	0.24 (0.05)*	0.90 (0.07)	–0.06 (0.05)	a,c	b
Hind	1.31 (0.17)	0.25 (0.04)*	1.61 (0.17)	0.15 (0.04)*		
Imp_h (Ns kg^{-1})						
Fore	–0.02 (0.01)	–0.01 (0.009)	–0.07 (0.01)	–0.02 (0.009)*	a,c	
Hind	0.05 (0.01)	–0.01 (0.003)*	0.10 (0.01)	–0.004 (0.003)		

Values are the means (S.E.M.) obtained from regressions fit to the data of the four individual horses. Comparisons were made for each variable at 3.5 m s^{-1} and between the slopes from the regression line (Slope).

The regression coefficients for t_c, DF and Imp_z were performed on log-transformed data as these variables were best fit by power functions.

For the statistical comparisons 'leg' refers to the test between the fore- and hindlimb and 'condition' refers to the test between level and incline.

*95% confidence interval does not include 0.

a, leg (P<0.05); b, condition (P<0.05); c, leg × condition (P<0.05).

the incline (Table 1). As speed increased, the decreasing t_c counteracted the increasing $F_{z,peak}$ and resulted in a net decrease in Imp_z for both limbs and both conditions (Fig. 4A). Forces tended to be distributed consistently between the limbs with increased speed, with a 57%/43% split to fore/hindlimbs, respectively, on the level and 52%/48% on the incline (Fig. 4B). The average force produced by the limbs was not significantly different than 9.8 N kg^{-1}, for individual animals at all speeds tested (Fig. 4B), despite the appearance from the regression line that the total average force might be less, particularly at lower speeds.

Peak braking force tended to increase with speed for both limbs and both conditions (Table 1). Peak propulsive force increased with speed for both limbs on the level but only for the hindlimb on the incline (Table 1). The total horizontal impulse remained essentially unchanged with speed for both limbs under both conditions (Table 1). While average slopes different from zero were found for the horizontal impulse of the hindlimb on the level and the forelimb on the incline, the magnitude of these slopes is so close to zero that they probably have no biological significance.

Comparison of temporal characteristics on the level and incline

On the incline, t_c of the forelimb was no different from the value on the level both in terms of the relationship with speed and in the average magnitude at 3.5 m s^{-1} (Table 1). For the hindlimb on the incline, however, t_c decreased at a greater rate with speed (Fig. 2), and tended to be longer (than on the level) at 3.5 m s^{-1}. As speed increased t_c tended to converge, regardless of condition or limb. Duty factor of the hindlimb decreased at a greater rate with speed on an incline (Table 1). The magnitude of the duty factor of both limbs at 3.5 m s^{-1} was not different between conditions (Table 1), but it was for the hindlimb at 2.75 m s^{-1} (level, 0.392±0.008; incline, 0.409±0.008).

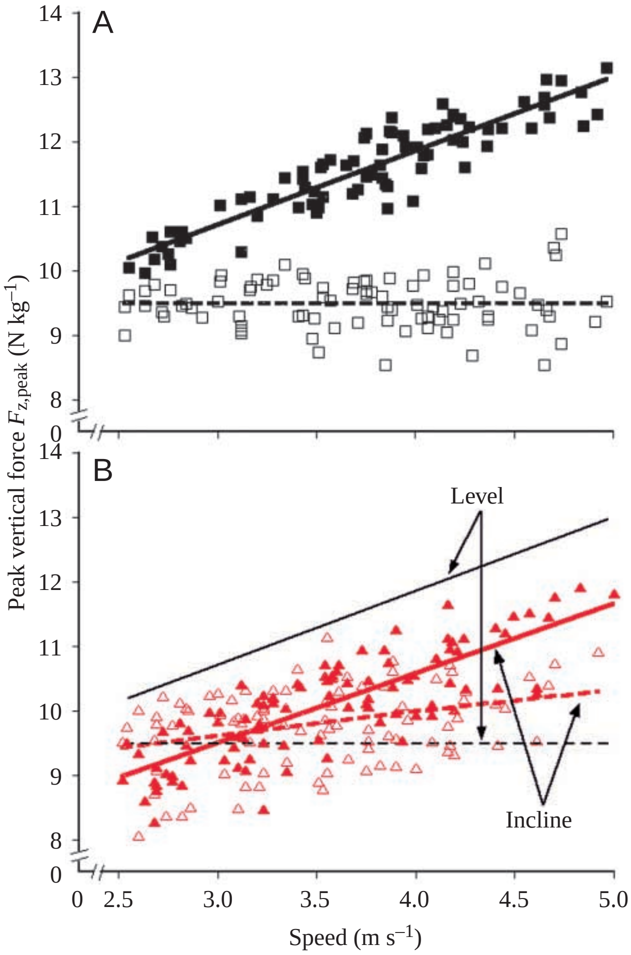

Fig. 3. On the level, peak vertical force $F_{z,peak}$ under the forelimb increased as a function of speed but the forces under the hindlimb remained constant at all trotting speeds (A). On an incline (B), force increased with speed in both limbs but was lower in the forelimb than on the level. The bottom figure shows the incline condition with the regression lines from the level condition. Symbols and lines are explained in the legend to Fig. 2.

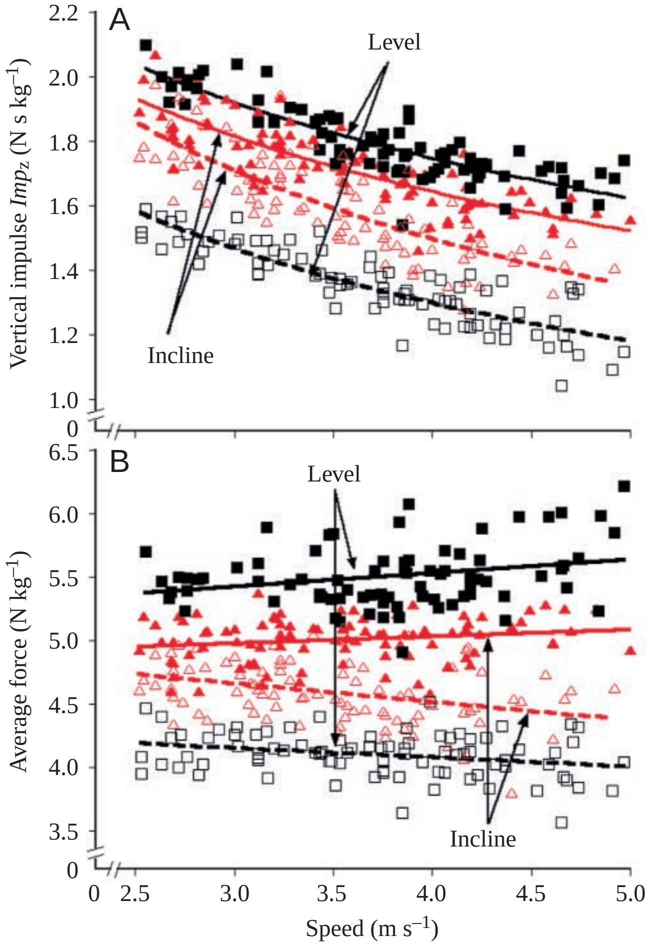

Fig. 4. Vertical impulse Imp_z decreased with increased speed for both limbs in both conditions (A). Vertical impulse generated by the forelimb was lower on the incline than on the level but vertical impulse generated by the hindlimb was higher on the incline than on the level. Using the vertical impulse to determine the average force generated over a stride (B) shows that on the level the force is distributed so that the force distribution is 57%/43% fore/hind (the values in the figure are force values, but expressed as a percentage in Table 1). On the incline the average force distribution was 52%/48% fore/hind respectively. Symbols and lines are explained in the legend to Fig. 2.

Forces on the level and incline

$F_{z,peak}$ when trotting up an incline was reduced on the forelimbs when compared to the level (Fig. 3), but increased with speed in a similar manner for both conditions (Table 1, Fig. 3). On the incline, $F_{z,peak}$ for the hindlimb was higher than that of the forelimb at the low speeds (<3.0 m s^{-1}) and increased with speed, in contrast to a constant hindlimb peak force on the level. The effect of incline was to make the $F_{z,peak}$ of the two limbs more similar. Imp_z (Fig. 4) was lower for the forelimb and higher for the hindlimb on the incline.

Comparing conditions, the forelimb tended to apply less braking force and the hindlimb more braking force on the incline, as indicated by F_{brake} at 3.5 m s^{-1} (Table 1). F_{prop} was greater for the hindlimb and less for the forelimb on the incline. On the level, Imp_h for the forelimb was slightly negative and for the hindlimb was slightly positive (Table 1). On the incline, the Imp_h became larger for both limbs, with the forelimb creating a net braking and the hindlimb a net propulsive impulse. The net effect is that horizontal impulse across both limbs was slightly positive on both the level and the incline.

Discussion

Temporal stride characteristics (time of contact and duty factor) decreased as speed increased for both level and incline conditions. In the forelimb, peak forces increased with speed on both the level and 10% incline. In the hindlimb, peak forces were unchanged with speed on the level, but increased with speed on the incline. The amount of vertical impulse during contact decreased with speed, but the distribution of force between the limbs remained constant throughout the range of speeds. Peak horizontal forces and impulses were independent of speed on the level, but increased with speed on the incline.

The decrease in time of contact with speed was similar to observations recorded from previous studies on horses (Hoyt et al., 2000; McLaughlin et al., 1996; Robert et al., 2002), other quadrupeds (Kram and Taylor, 1990) and bipeds (Munro et al., 1987; Roberts et al., 1997). Interestingly, the time of contact was longer for the forelimb than the hindlimb, a fact not previously reported for quadrupeds. Duty factor decreased as speed increased, similar to bipeds (Gatesy and Biewener, 1991) and horses (Biewener, 1983; Hoyt et al., 2000). Contact time and duty factor for the fore- and hindlimbs converged and decreased less rapidly at higher speeds (Fig. 2).

On the level, the contact time and duty factor of the hindlimb decreased with increasing speed, but there was no change in peak vertical force. The relatively small changes in DF were not of sufficient magnitude to effect a change in hindlimb peak force. The observation in the present study that hindlimb peak forces are independent of speed is not consistent with reported increased stress on both the tibia and metatarsus (Biewener et al., 1988), but is consistent with observations of an absence of change in muscle–tendon stresses in the hindlimb (Biewener, 1998) and constant tibial compressive strain (Rubin and Lanyon, 1982). On the incline, peak forces in the hindlimb were greater and they increased with increasing speed due to the greater decrease in duty factor of the hindlimb and a rearward distribution of force compared to the level. That forces on the incline were increased is consistent with the reported increased hyperextension of the metatarsophalengeal joint on the incline (Sloet van Oldruitenborgh-Oosterbaan et al., 1997; McGuigan and Wilson, 2003).

Because of the inversely proportional relationship between duty factor and speed, one might expect peak force to increase due to the requirement of maintaining a consistent vertical impulse over the stride (Alexander et al., 1979). This relationship certainly holds true for the forelimb and the increases in peak force with speed were consistent with measured stress increases on the muscle–tendon units with speed of trotting in horses (Biewener, 1998). However, on the incline, due to the shift of force distribution to hindlimb (from 57%/43% on the level to 52%/48% on the incline, fore/hind, respectively), peak forces were decreased. This decrease in measured peak force is consistent with the kinematic data of Sloet van Oldruitenborgh-Oosterbaan et al. (1997). They observed that hyperextension of the metacarpophalangeal joint decreased when trotting up an incline and the extension of this joint is a function of the amount of force placed on the limb (McGuigan and Wilson, 2003). Also, the increased peak force generated by the forelimb with increased speed was not consistent with an absence of change in radial compressive strain (Rubin and Lanyon, 1982), but was with measured stress increases on the muscle–tendon units with increased speed of trotting (Biewener, 1998).

Based on the observations that, as a function of speed on the level, contact time for both limbs decreased, contact time was lower for the hindlimb and force was higher for the forelimb, one might conclude that the distribution of force used to support the mass of the animal against gravity might shift forward. However, the distribution of total force remained the same (57% fore, 43% hind) across all speeds (Fig. 4B). The 57% of total force under the forelimb on the level was slightly less than that reported by Jayes and Alexander (1978) for sheep and dogs (which was 60%/40%), but the same as reported by Knill et al. (2002) for horses. The measured 57%/43% force distribution during locomotion was also consistent with subsequent static weight measurements of each animal. When trotting on an incline, support shifted slightly to the hindlimb (52% fore/48% hind). This redistribution of force to the hindlimb may seem plausible since the long axis of the horse becomes oriented to an angle similar to that of the slope. However, later static measurements of several of the horses on the incline revealed that each animal's posture (slightly leaning into the slope) was such that a 57%/43% fore/hind distribution of weight was maintained, so that the observed force distribution (52%/48% fore/hind) during trotting up the hill was different from that during standing. Kinematic analysis of the hindlimb (Hoyt et al., 2002) suggests very little change in hindlimb positioning during trotting up an incline, and the small changes that were found may be due to a slight backward or downward shift of the torso of the animal on the incline, which is consistent with the changes in force distribution observed in the current study.

Horizontal forces increased in magnitude with speed on the level, and peak braking forces increased more than peak propulsive forces (Table 1). These increases in horizontal forces produced slight increases in the braking and propulsive impulses and this resulted in a small, net positive horizontal impulse at lower speeds and a net horizontal impulse of zero at higher speeds. Using the regression equations to predict the net horizontal impulse at 2.0 m s^{-1} indicates the change in velocity will be 0.06 m s^{-1}, a 3% increase in speed, and at more intermediate speeds the net positive impulse would increase velocity by only 0.8% (0.03 m s^{-1} at a trotting speed of 3.5 m s^{-1}). This small acceleration at intermediate speeds may not be biologically significant given the variability around the regression lines; however, it was beyond the resolution of our system of monitoring speeds and would not have caused trials to be excluded, because our standard was to exclude trials in which speed changed by more than 10% between the two timing zones. Increases in braking and propulsive peak forces and impulse were more pronounced on the incline so that the forelimb produced greater braking and the hindlimb greater propulsion when trotting up an incline.

The mechanics of the fore- and hindlimbs appeared to be different and speed-dependent. Despite differences in temporal and force measures, the horse maintained a consistent distribution of weight. Trotting up an incline was produced through increased propulsive and vertical force of the hindlimb, while force decreased for the forelimb. Both duty factor and time of contact are different between the limbs, which may have implications for previous research relating force and energy cost of locomotion to these parameters.

List of symbols

DF	duty factor
F_{brake}	braking force
F_{prop}	propulsive force
F_y	horizontal force
F_z	vertical force
$F_{z,peak}$	peak vertical force
Imp_h	horizontal impulse
Imp_z	vertical impulse
T_c	time of contact

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References

Alexander, R. M., Maloiy, G. M. O., Hunter, B., Jayes, A. S. and Nturibi, J. (1979). Mechanical stresses in fast locomotion of buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*). *J. Zool. Lond*. **189**, 135-144.

Biewener, A. A. (1983). Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. *J. Exp. Biol*. **105**, 147-171.

Biewener, A. A., Thomason, J. J. and Lanyon, L. E. (1988). Mechanics of locomotion and jumping in the horse (*Equus*): *in vivo* stress in the tibia and metatarsus. *J. Zool. Lond.* **214**, 547-565.

Biewener, A. A. (1998). Muscle–tendon stresses and elastic energy storage during locomotion in the horse. *Comp. Biochem. Physiol.* **120B**, 73-87.

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

Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool. Lond.* **224**, 127-147.

Heglund, N. C. and Taylor, C. R. (1988). Speed, stride frequency, and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318.

Hoyt, D. F., Wickler, S. J. and Cogger, E. A. (2000). Time of contact and step length: the effect of limb length, running speed, load carrying, and incline. *J. Exp. Biol.* **203**, 221-227.

Hoyt, D. F., Molinari, M., Wickler, S. J. and Cogger, E. A. (2002). Effect of trotting speed, load and incline on hindlimb stance-phase kinematics. *Equine Vet. J.* **Suppl. 34**, 330-336.

Jayes, A. S. and Alexander, R. M. (1978). Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool. Lond.* **185**, 289-308.

Knill, K., McGuigan, M. P., Witte, T. H. and Wilson, A. M. (2002). Determination of peak limb force from duty factor. In *Proceedings of IVth World Congress of Biomechanics, Calgary, Canada*.

Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.

McGuigan, M. P. and Wilson, A. M. (2003). The effect of gait and digital flexor muscle activation on limb compliance in the forelimb of the horse *Equus caballus*. *J. Exp. Biol.* **206**, 1325-1336.

McLaughlin, R. M. Jr, Gaughen, E. M., Roush, J. K. and Skaggs, C. L. (1996). Effects of subject velocity on ground reaction force measurements and stance times in clinically normal horses at the walk and trot. *Am. J. Vet. Res.* **57**, 7-11.

Munro, C. F., Miller, D. I. and Fuglevand, A. J. (1987). Ground reaction forces in running: a reexamination. *J. Biomech.* **20**, 147-155.

Robert, C., Valette, J. P., Pourcelot, P., Audigie, F. and Denoix, J. M. (2002). Effects of trotting speed on muscle activity and kinematics in saddle horses. *Equine Vet. J.* **Suppl. 34**, 295-301.

Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, C. R. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113-1114.

Rubin, C. T. and Lanyon, L. E. (1982). Limb mechanics as a function of speed and gait: a study of functional strains in the radius and tibia of horse and dog. *J. Exp. Biol.* **101**, 187-211.

Sloet van Oldruitenborgh-Oosterbaan, M. M., Barnevald, A. and Schamhardt, H. C. (1997). Effects of treadmill inclination on kinematics of the trot in Dutch Warmblood horses. *Equine Vet. J.* **Suppl. 23**, 71-75.

Wickler, S. J., Hoyt, D. F., Cogger, E. A. and Hirschbein, M. H. (2000). Preferred speed and cost of transport: the effect of incline. *J. Exp. Biol.* **203**, 2195-2200.

Wickler, S. J., Hoyt, D. F., Cogger, E. A. and Myers, G. (2003). The energetics of trot–gallop transition. *J. Exp. Biol.* **206**, 1557-1564.