© 2019. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2019) 222, jeb204107. doi:10.1242/jeb.204107

RESEARCH ARTICLE

Ground reaction forces of overground galloping in ridden Thoroughbred racehorses

Zoe T. Self Davies, Andrew J. Spence* and Alan M. Wilson‡

ABSTRACT

The horse has evolved to gallop economically at high speed. Limb force increases with speed but direct measures of limb ground reaction forces (GRFs) at gallop are sparse. This study reports GRFs for multiple limbs, using force plates, across seven Thoroughbred racehorses during ridden galloping. The results show peak vertical GRF values of 13.6 N kg^{-1} (non-lead hindlimb), 12.3 N kg^{-1} (lead hindlimb), 14.0 N kg^{-1} (non-lead forelimb) and 13.6 N kg^{-1} (lead forelimb) at 11.4 m s^{-1} and recorded values are consistent with those predicted from duty factor. The distribution of body weight between the forelimbs and hindlimbs is approximated to 50:50, and is variable with speed, unlike the 60:40 commonly stated for cursorial quadrupeds in the literature. An even distribution of load on all limbs may help minimise accumulation of fatigue and assist in injury avoidance. Cranio-caudal force data concur with the observation that horses apply a net accelerative impulse with the hindlimbs and a net decelerative impulse with the forelimbs. Capturing GRFs enhances our knowledge on the mechanics of galloping in fast-moving species and provides insight into injury risk and factors limiting athletic performance.

KEY WORDS: Biomechanics, Horse, Gallop, Force, Kinetics

INTRODUCTION

The horse (*Equus caballus*) has evolved to be a fast and efficient (Self Davies et al., 2019) runner with a low cost of transport (Thornton et al., 1987; Minetti et al., 1999) and a number of anatomical and physiological adaptations for high-speed locomotion (Hildebrand, 1988; Biewener, 1998; Wilson et al., 2001; McGuigan and Wilson, 2003; Wilson et al., 2003; Payne et al., 2004; Payne et al., 2005). Further selective breeding has produced the Thoroughbred racehorse, which has been highly selected for speed and endurance. In racing, Thoroughbred racehorses show top speeds of around 19 m s^{-1} (Russell and McWhirter, 1988) and use a transverse gallop gait pattern.

Understanding of the limits to maximum speed is of interest from both basic science and athletic performance perspectives. Maximum attainable speed is determined, and limited, by a number of interrelated factors, including power (Self et al., 2012) and peak limb force (Jones and Lindstedt, 1993; Alexander, 2003; Weyand and Davis, 2005), the latter of which is a major determinant of the strain placed on the musculoskeletal tissues of the limbs. The peak load that can be withstood by the limbs may limit maximum speed and it has been suggested that musculoskeletal tissue forces (strains) trigger the transition from trot to gallop in horses (Farley and Taylor, 1991). Bend running provides a useful perturbation to limb force in running as the resulting centripetal force simulates an increase in body weight. Human and equine athletes show a reduction in speed with bend running, implying a limit on limb force (Usherwood and Wilson, 2006; Bowtell et al., 2007; Tan and Wilson, 2011), though greyhounds do not (Usherwood and Wilson, 2005).

Force plate ground reaction force (GRF) data have been collected from horses in numerous studies (Merkens et al., 1986; Merkens et al., 1993a; McLaughlin et al., 1996; Dutto et al., 2004; Witte et al., 2004), though there are no force plate data in the literature for multiple limbs during overground, ridden galloping, representative of racing conditions. Instrumented horseshoes have been shown to successfully measure vertical forces during a variety of gaits (Ratzlaff et al., 1990; Roepstorff and Drevemo, 1993), though it is possible that they may affect grip and alter digital mass, and they must be customised to fit the individual. In the absence of galloping force plate data, it has been shown that vertical GRFs can be accurately estimated from duty factor at lower speeds (Alexander et al., 1979; Witte et al., 2004). Assuming that the vertical force trace follows a half-sinusoidal shape and the distribution of body weight across the forelimbs and hindlimbs remains constant, this can be used to predict forces during galloping; however, in the absence of experimental data, these predictions have not been verified. Verification of such predictions would be a valuable addition to the literature.

During standing and at low speed (up to cantering), the body weight of the horse is distributed between the forelimbs and hindlimbs with a ratio of 57:43 (Dutto et al., 2004; Witte et al., 2004), which is comparable to the weight distribution in other cursorial species (Jayes and Alexander, 1978; Alexander et al., 1979; Lee et al., 1999; Walter and Carrier, 2007; Hudson et al., 2012). As well as this front:back (vertical) loading asymmetry, there is also a left:right (more correctly a lead:non-lead) asymmetry shown in cantering horses (Merkens et al., 1993b) and galloping dogs (Walter and Carrier, 2007). From an evolutionary standpoint, these findings are counterintuitive as asymmetrical loading across limbs would probably decrease manoeuvrability, result in musculoskeletal asymmetry (Watson et al., 2003; Pearce et al., 2005) and increase injury risk. At very high speeds, the front:back loading distribution has been shown to change with speed in cheetahs and greyhounds (Hudson et al., 2012).

Here, we present a novel dataset of individual limb GRFs for ridden overground galloping in Thoroughbred racehorses. We hypothesise that peak forces will be similar in magnitude to those predicted in the literature, increasing with speed, with the implication of a force constraint to maximum speed. We also predict that horses may move more towards a 50:50 front:back impulse distribution at

Structure and Motion Lab, The Royal Veterinary College, University of London, Hawkshead Lane, North Mymms, Hatfield, Hertfordshire, AL9 7TA, UK.
*Present address: Department of Bioengineering, Temple University, 1947 N. 12th Street, Philadelphia, PA 19122, USA.

‡Author for correspondence (awilson@rvc.ac.uk)

Z.T.S.D., 0000-0003-1419-8735; A.M.W., 0000-0001-9914-3455

Received 27 March 2019; Accepted 23 July 2019

Journal of Experimental Biology (2019) 222, jeb204107. doi:10.1242/jeb.204107

the gallop, similar to other fast-moving species, in order to increase loading symmetry across limbs.

MATERIALS AND METHODS

Ethical approval for this study was granted by the Royal Veterinary College (RVC) Welfare and Ethics Committee (URN 2011 1107). Data were collected from seven Thoroughbred racehorses at the British Racing School (BRS), Newmarket, UK. All horses were in regular training and considered to be free from underlying pathologies that could affect performance. All subjects were weighed on the in-house scales (477±25 kg) (though weights for data analysis were taken as the integral of the vertical force across a stride) and limb lengths were taken to the top of the scapula (1.63±0.04 m) using a standard tape measure. The same professional jockey (mass of jockey+equipment=70.1 kg) rode all horses for all trials.

Ten 0.6×0.9 m Hall-effect force plates (AMTI, Watertown, MA, USA) were placed in series in a custom-designed steel frame [Quality Equipment, G. E. Baker (UK) Ltd, Suffolk, UK] in the racing track at the BRS on a base layer of chalk. Plates were covered with a thin layer of material membrane and custom-designed top-plates were laid over this. Approximately 0.1 m depth of oiled sand was then filled over the plates to provide a surface over which the horses could gallop safely. On the left-hand side of the track were two high-speed cameras (AOS Technologies AG, Dättwil, Switzerland), set back 5 m from the track, with a view of approximately 5 m before the plates and 5 m after the plates, with an overlap of approximately 1 m in the middle to ensure that full strides were captured. The cameras were set to 1280×560 pixels and filmed at 500 Hz. Each horse was given as much time as was required for it to become acclimatised to the setup. Temporal stride data were obtained from the videos using VirtualDub (v.1.9.11). The use of wide-angle lenses (12.5 mm) was unavoidable so in order to compensate for lens distortion and parallax, a calibration square was filmed at all points along the path. Speed data were subsequently computed from the video using a custom-written point-tracking script (Hedrick, 2008) in MATLAB (MathWorks, Natick, MA, USA).

Force data were analysed in a custom-written script in MATLAB. Individual limb stances were used in the analysis if they landed fully on the plate and no other limbs were in contact with that plate during the same period. Where a limb stance fell across two plates or there was transfer of cranio-caudal force to adjacent plates, data from the plates were summed. The outputs of the script were individual limb forces in the vertical, cranio-caudal and medio-lateral directions throughout stance for each horse, for each trial. From this, impulse was taken to be the integral of force with respect to time, for each dimension, during each stance phase. Peak forces were taken to be the maximum value in force, in each dimension, during each stance phase for the statistical analysis and were normalised to newtons per kilogram mass (horse plus jockey). Because of the damping effects of the overlying surface, no smoothing was required. The ratio of forelimb:hindlimb impulse was calculated for the trials in which all four stances were captured, by dividing the summed impulses for the limb pairs by the sum of the impulses across all four limbs.

All statistics were carried out in SPSS v.22.0 (released 2013; IBM SPSS Statistics for Windows, IBM Corp., Armonk, NY, USA). To ascertain whether there were significant differences in the peak forces and impulses between the lead and non-lead limb of each pair, a linear mixed effects model was conducted, taking speed to be a fixed effect and both horse and trial to be random effects. All data conformed to the assumptions of normality and in cases where a significant difference was established, linear hypothesis testing was applied to establish which limbs differed significantly from the others with regard to impulse and peak force. The significance level was taken to be $P<0.05$. Where all four footfalls were collected, summed forelimb and hindlimb vertical impulses were also correlated with speed.

As GRFs in galloping horses are often currently estimated from duty factor (Alexander et al., 1979; Witte et al., 2004), duty factor data from video in this study were also used to calculate predicted values for comparison with recorded values, though this was corrected for a 50:50 front:back weight distribution (see below).

RESULTS

Data were collected for seven horses across 34 trials. Horses galloped through the set-up at speeds between 9.1 and 13.7 m s^{-1}, with 3 or 4 footfalls being captured in most trials. A total of 138 single-limb stances were analysed, comprising 31 for the non-lead hindlimb (NLH), 36 for the lead hindlimb (LH), 37 for the non-lead forelimb (NLF) and 34 for the lead forelimb (LF). Mean vertical, cranio-caudal and medio-lateral forces are presented in Fig. 1 and data are summarised in Table 1.

Fig. 2 shows stance time, peak vertical force (GRF$_z$) and vertical impulse against speed. The statistical analysis revealed that speed had a significant effect on GRF$_z$ (LME; $P<0.05$) and vertical impulse. GRF$_z$ and vertical impulse were significantly greater (LME; $P<0.05$) in the NLH than in the LH, but there was no significant difference in either parameter between the LF and NLF.

There were 26 trials in which a full stride (4 sequential footfalls) was collected, which allowed calculation of the front:back impulse distribution. The mean front:back impulse distribution was 49:51, though this varied with speed, as shown in Fig. 3. There was a significant positive correlation between hindlimb vertical impulse and speed and a significant negative correlation between forelimb vertical impulse and speed.

Recorded GRF data were concomitant with estimates from duty factor when assuming a 50:50 front:back weight distribution. Taking predicted data as a percentage of recorded data, the predictions were a mean of 100% (interquartile range, 90–107%) of the recorded values (Fig. 4).

DISCUSSION

A general decrease in stance time with speed and an increase in GRF$_z$ with speed was seen here, in agreement with the literature (Witte

Table 1. Summary of data by individual leg

	NLH	LH	NLF	LF
Peak vertical force at 11.4 ms^{-1} (N kg^{-1})	13.6	12.3	14.0	13.6
Positive cranio-caudal impulse (N kg^{-1} s)	0.11±0.032	0.07±0.019	0.05±0.02	0.04±0.01
Negative cranio-caudal impulse (N kg^{-1} s)	−0.03±0.02	−0.03±0.01	−0.05±0.02	−0.07±0.02

Peak vertical force values, normalised to individual mass (horse plus jockey), are taken at the middle of the speed range from the model in Fig. 2; positive and negative cranio-caudal impulse values are means±s.d. N=138 single limb stances from 7 horses across 34 strides. NLH, non-lead hindlimb; LH, lead hindlimb; NLF, non-lead forelimb; LF, lead forelimb.

Journal of Experimental Biology

Journal of Experimental Biology (2019) 222, jeb204107. doi:10.1242/jeb204107

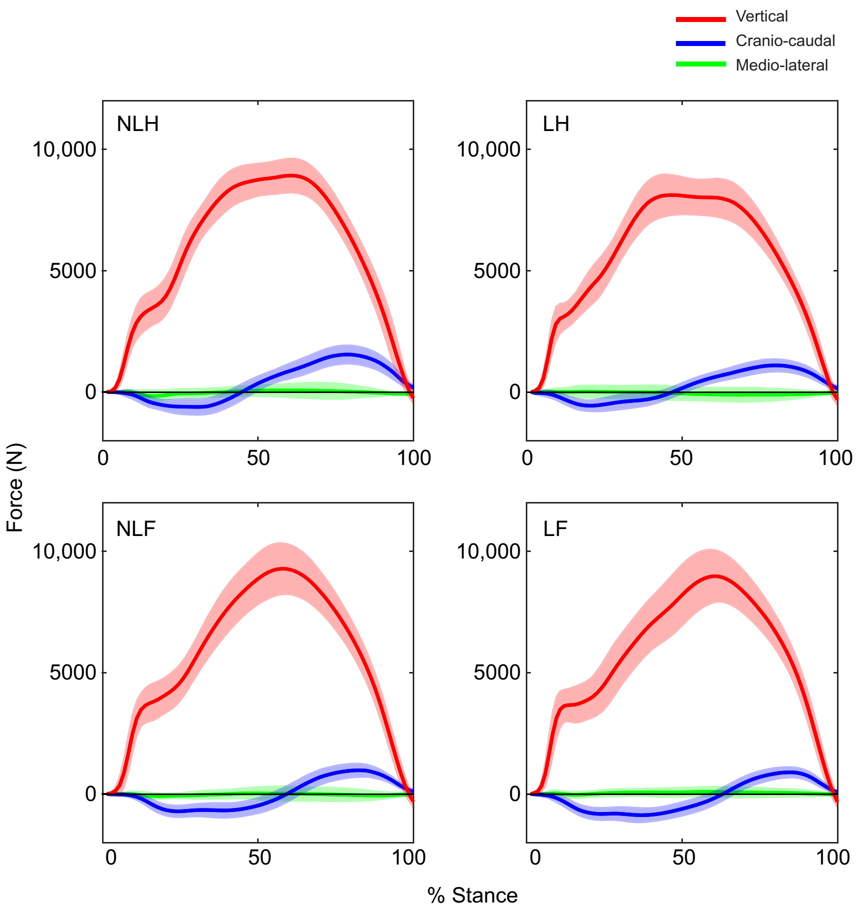

Fig. 1. Raw ground reaction force (GRF) data in the vertical, cranio-caudal and medio-lateral directions. Lines represent the mean, shaded areas represent the standard deviation. Non-lead hindlimb (NLH), 31 footfalls across 7 individuals; lead hindlimb (LH), 36 footfalls across 7 individuals; non-lead forelimb (NLF), 37 footfalls across 7 individuals; lead forelimb (LF), 34 trials across 7 individuals.

et al., 2004, 2006) and with the requirement of basic physics for the body weight to be supported under conditions of reducing duty factor. GRF_z was between 1 and 1.7 times body weight and was dependent on speed. These GRF_z data were consistent in magnitude with those predicted from duty factor, though the distribution of force between forelimbs and hindlimbs was more symmetrical than suggested in former studies. The durations for stance in this study are greater than the mean values in Witte et al. (2006) but fall within the range they observed. This is possibly due to differences in measurement techniques (accelerometers versus force plates) or to differences in the animals (elite racing versus non-competing Thoroughbred horses) and the depth of the synthetic surface. The peak forces seen here are lower, relative to body mass, than those in other galloping species such as dogs and cheetahs (Walter and Carrier, 2007; Hudson et al., 2012).

There was a significant difference in peak GRF_z and vertical impulse between the LH and NLH but not between the LF and NLF. Slightly longer stance periods in the NLH have been shown in galloping horses (Deuel and Lawrence, 1987) and there is also a trend for this in dogs, though the difference is not significant (Walter and Carrier, 2007). Data from this study concur with these previous findings. The literature does, however, show higher peak values in GRF_z in the LH of galloping dogs (Bryant et al., 1987; Walter and Carrier, 2007) and cantering horses (Merkens et al., 1993b), which is the opposite of what was observed in this study. While in canter it has been shown that the GRF patterns are different in all four limbs (Merkens et al., 1993b), it would be of benefit that force and impulse become distributed more evenly across all four limbs as speed increases. There would be a disadvantage to an asymmetrical gallop with regard to force, which would result in significant musculoskeletal asymmetries. Galloping in the wild requires mammals to manoeuvre to escape predation and adapt to varying terrain, which would be hindered by asymmetries. Skeletal asymmetries have been demonstrated in racehorses, which are due to the turn directions of racetracks (Watson et al., 2003; Pearce et al., 2005), and there is also proposed to be a distinct disadvantage to an asymmetrical transverse gallop during bend running as the lead limbs are ipsilateral, meaning one lead will be on the outside and one will be on the inside. It is possible that some observations in this study are a result of asymmetries built up over the careers of the racehorses used.

When compared with estimates from duty factor, the recorded data are very consistent with predictions; however, the difference in vertical impulse between the forelimbs and hindlimbs is very much reduced. In the literature, predicted forces are based on the assumption of a 60:40 front:back impulse distribution (Alexander et al., 1979; Witte et al., 2004, 2006), which is not consistent with data from this study. In this study, the front:back impulse ratio is closer to 50:50, which accounts for the decreased differences between the forelimbs and hindlimbs. There are a number of factors that could account for the apparent change in impulse distribution, including changes in forelimb and hindlimb protraction and retraction angles; increased back flexion; increasing hindlimb loading; position of the jockey (see Appendix); and movement of the guts within the abdominal cavity. It must also be noted that horses accelerated slightly in each trial (mean 0.45 m s^{-2}), which could result in a pitching moment, shifting the weight towards the hindlimbs.

Journal of Experimental Biology

Journal of Experimental Biology (2019) 222, jeb204107. doi:10.1242/jeb.204107

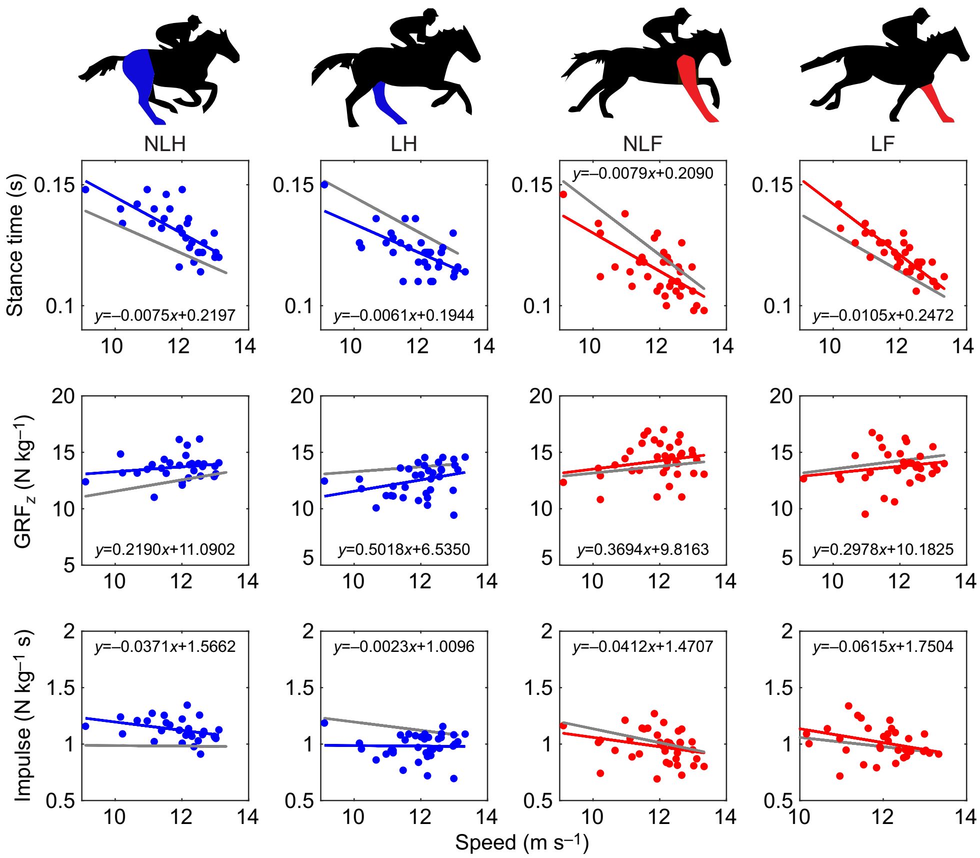

Fig. 2. Trends with speed for stance time (top), peak vertical GRF (GRF_z, middle) and vertical impulse (bottom) across the NLH, LH, NLF and LF. Blue represents the hindlimbs, red represents the forelimbs. The fit line for the other limb of the pair is superimposed in grey for comparison.

It has been proposed that the peak GRF that the limbs can withstand limits maximum speed (Jones and Lindstedt, 1993; Weyand et al., 2000; Usherwood and Wilson, 2005, 2006; Tan and Wilson, 2011). As is concomitant with the literature, data from this study show a decrease in stance time and an increase in peak force with speed. With this knowledge, it is wholly plausible that horses may reach a speed at which the musculoskeletal tissues of the limbs can no longer resist the GRFs for repeated cycles and are forced to slow down in order to avoid injury. It is possible that an increase in stride frequency would ameliorate the increase in duty factor and reduce the increase in vertical GRF; however, there is very little variation shown in swing time in galloping horses (Witte et al., 2006). The point at which such a limit comes into play is harder to determine as other limits, such as power (Self et al., 2012), may dominate before force limit-inducing speeds are reached. Speeds achieved here are, however, lower than the maximum recorded speed for a racehorse (around 19 m s^{-1}: Russell and McWhirter, 1988).

The mass-specific peak cranio-caudal forces observed here are low in magnitude in comparison to those of other galloping species (Walter and Carrier, 2007), though were of comparable magnitude to those seen in cantering horses (Merkens et al., 1993b), resulting in a relatively low external work (Self Davies et al., 2019). This is probably due to the shallow leg angles seen in galloping horses versus galloping dogs as a more vertical limb would experience reduced cranio-caudal forces as a result of the change in GRF vectors. Statistical analysis was not performed on the cranio-caudal forces because of the high level of variability. It is suspected that this variability is largely due to the experimental environment whereby horses were accelerating and decelerating in response to the unfamiliar situation. Although as much as possible was done to ensure that horses were acclimatised to the set-up, speed was controlled by the jockey, and the surface was even and raked between trials, there was still variability in all of these factors and horses often respond to stimuli by galloping away. The shapes of the curves reveal that the accelerative impulse was greater than the decelerative impulse in the hindlimbs and that the decelerative impulse was greater than the accelerative impulse in the forelimbs. This corroborates the theory that horses push off with the hindlimbs and brake with the forelimbs during galloping (Ruina et al., 2005) and also reflects the location of most propulsive muscle in the hindleg (Crook et al., 2008; Payne et al., 2005). This collisional perspective predicts that utilising sequential footfalls that give impulses that redirect the centre of mass (COM) velocity through equal angles is energetically advantageous (Lee et al., 2011). This is due to an assumption of pseudo-elastic collisions in which energy losses are proportional to the angle of redirection squared, and so it is advantageous to have multiple redirections through small angles as opposed to few redirections through large angles. Our finding that this occurs in horses through direct force plate measurements lends support to the notion that this mechanism may generalise from dogs (Lee et al., 2011) to larger galloping animals.

Conclusion

GRFs for multiple limbs during high-speed, ridden galloping are reported here, to our knowledge, for the first time. Data show that vertical forces are concomitant with predictions in the literature (Merkens et al., 1993b; Witte et al., 2004, 2006) in terms of magnitude; however, the distribution of the forces between the forelimbs and hindlimbs deviates from the previously reported 57:43 ratio (Dutto et al., 2004; Witte et al., 2004) and approximates to 50:50. Further validation is required to determine the cause of this change to impulse distribution though it can be suggested that a

Journal of Experimental Biology (2019) 222, jeb204107. doi:10.1242/jeb204107

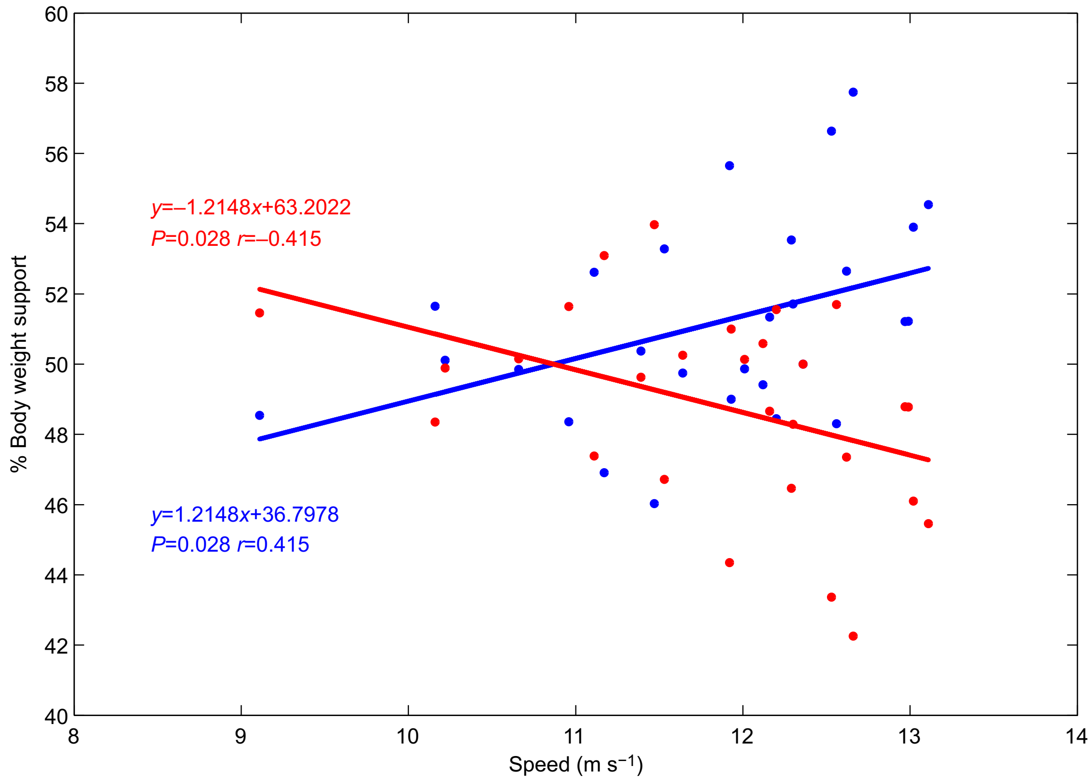

Fig. 3. Correlations between summed hindlimb (blue) and forelimb (red) vertical impulses with speed. The data demonstrate the change in front:back weight distribution with speed.

move towards symmetry is beneficial if injury is to be avoided. Peak GRF_z increased with speed, suggesting the potential for a force limit to maximum-speed running. Cranio-caudal forces were low in magnitude, showing low acceleration and deceleration within a stride, and conform to the suggestion that horses may accelerate with the hindlimbs and brake with the forelimbs (Ruina et al., 2005). This last finding may, in turn, be due to an energetic constraint imposed by the suggested collisional nature of legged locomotion.

APPENDIX

These data were collected using ridden horses, with approximately 13% of the total mass being the rider who, in racing posture, is not tightly connected to the horse and so added weight but limited inertia. The rider can move horizontally relative to and potentially out of phase with the horse's COM (Pfau et al., 2009), so the horse can reduce the horizontal work on the rider whilst still supporting their weight. The position of the jockey on the horse's back could potentially influence the front:back weight distribution. Using Fig. A1, the following equations can be derived for a static situation.

Vertically:

$$2F_{zH} + 2F_{zF} = -\boldsymbol{g}(m_{\text{horse}} + m_{\text{jockey}}), \tag{A1}$$

where F_{zH} is the vertical force of the hindlimb, F_{zF} is the vertical force of the forelimb, m_{horse} is the mass of the horse and m_{jockey} is the mass of the jockey.

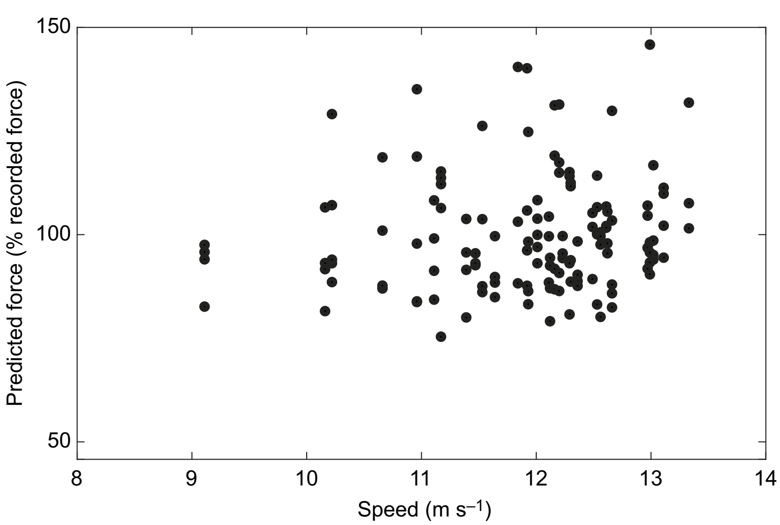

Fig. 4. GRF_z predicted from duty factor as a percentage of recorded GRF_z. Duty factor data from video in this study were used to predict GRF (see Alexander et al., 1979; Witte et al., 2004), shown as a percentage of recorded force values from this study (force plates). The data demonstrate that force predictions from duty factor (taking into account the 50:50 front:back weight distribution) can be relied upon. The mean percentage is 100%.

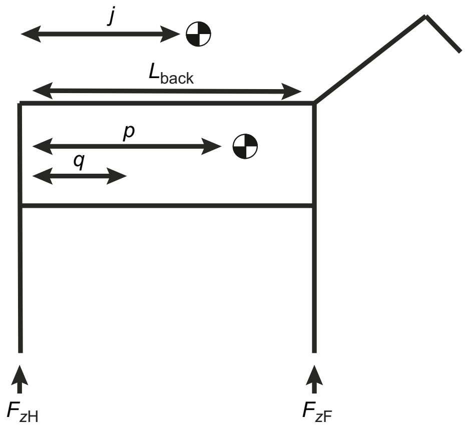

Fig. A1. Effect of jockey position on front:back weight distribution. Static reductionist model showing the position of the jockey on the horse's back. L_{back} is the length of the horse's back; j is the proportion of L_{back} at which the jockey is positioned; p is the proportion of L_{back} at which the horse's COM is located; q is p when taking into account the jockey's mass; F_{zH} is the vertical ground reaction force on the hindlimbs and F_{zF} is the vertical ground reaction force on the forelimbs.

Moment about hips:

$$2F_{z\mathrm{F}} \cdot L_{\mathrm{back}} = -\boldsymbol{g}L_{\mathrm{back}}(m_{\mathrm{horse}} \cdot p + m_{\mathrm{jockey}} \cdot j), \quad \text{(A2)}$$

where L_{back} is the length of the horse's back, p is the proportion of L_{back} at which the COM is located and j is the proportion of L_{back}, from the hips, at which the jockey is positioned.

From Eqn A2:

$$2F_{z\mathrm{F}} = -\boldsymbol{g}(m_{\mathrm{horse}} \cdot p + m_{\mathrm{jockey}} \cdot j). \quad \text{(A3)}$$

From Eqns A1 and A3, q, the 'new' p when taking into account the jockey's mass, can be derived:

$$q = \frac{2F_{z\mathrm{F}}}{2F_{z\mathrm{F}} + 2F_{z\mathrm{H}}} = \frac{-\boldsymbol{g}(m_{\mathrm{horse}} \cdot p + m_{\mathrm{jockey}} \cdot j)}{-\boldsymbol{g}\,(m_{\mathrm{horse}} + m_{\mathrm{jockey}})}. \quad \text{(A4)}$$

j can be calculated as follows:

$$j = \frac{-m_{\mathrm{horse}} \cdot p + m_{\mathrm{horse}} \cdot q + m_{\mathrm{jockey}} \cdot q}{m_{\mathrm{jockey}}}. \quad \text{(A5)}$$

This shows that for a 500 kg horse with a 60 kg jockey and p=0.6 (60:40 front:back weight distribution), to see q=0.5 (50:50 front: back weight distribution), the jockey would have to be at j=−0.33 of L_{back}, i.e. behind the tail of the horse. Thus, the presence and position of the jockey's COM on the back of the horse cannot account for the change in front:back weight distribution seen in this study. This is further supported in studies which suggest that the rider does not influence the distribution of forces in lower speed gaits (Merkens et al., 1986, 1993a,b).

Acknowledgements
The authors would like to thank members of the Structure and Motion Laboratory for their assistance in data collection, with particular thanks to Jim Usherwood for his support and for his help with the model in the Appendix, and Jeffery Rankin for his help in data analysis. We also thank the jockey Richard Perham, and the staff at the British Racing School for their time and extensive contribution to this work.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: Z.T.S.D., A.J.S., A.M.W.; Methodology: Z.T.S.D., A.J.S., A.M.W.; Formal analysis: Z.T.S.D., A.J.S., A.M.W.; Resources: Z.T.S.D., A.M.W.; Writing - original draft: Z.T.S.D., A.M.W.; Writing - review & editing: Z.T.S.D., A.J.S., A.M.W.; Visualization: A.M.W.; Supervision: A.J.S., A.M.W.; Project administration: Z.T.S.D.; Funding acquisition: A.M.W.

Funding
This study was funded by the Biotechnology and Biological Sciences Research Council UK CASE studentship to Z.T.S.D., sponsored by Turftrax Ltd.

Data availability
Data and example high-speed videos are available from the figshare repository: https://figshare.com/s/81d8a009cc1c5568587d, https://figshare.com/s/af09a3804e3c27140aee

References

Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton University Press.

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.* **189**, 135-144. doi:10.1111/j.1469-7998.1979.tb03956.x

Biewener, A. A. (1998). Muscle-tendon stresses and elastic energy storage during locomotion in the horse. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **120**, 73-87. doi:10.1016/S0305-0491(98)00024-8

Bowtell, M., Spence, A., Wilson, A., Kerwin, D., Irwin, G. and Bezodis, I. (2007). Limitation to maximal speed human sprinting-Insights from bend running and fatigue. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **146**, S109-S109. doi:10.1016/j.cbpa.2007.01.181

Bryant, J. D., Bennett, M. B., Brust, J. and Alexander, R. M. (1987). Forces exerted on the ground by galloping dogs (Canis-Familiaris). *J. Zool.* **213**, 193-203. doi:10.1111/j.1469-7998.1987.tb03693.x

Crook, T. C., Cruickshank, S. E., Mcgowan, C. M., Stubbs, N., Wakeling, J. M., Wilson, A. M. and Payne, R. C. (2008). Comparative anatomy and muscle architecture of selected hind limb muscles in the Quarter Horse and Arab. *J. Anat.* **212**, 144-152. doi:10.1111/j.1469-7580.2007.00848.x

Deuel, N. R. and Lawrence, L. M. (1987). Kinematics of the equine transverse gallop. *JEVS* **7**, 375-382. doi:10.1016/S0737-0806(87)80008-4

Dutto, D. J., Hoyt, D. F., Cogger, E. A. and Wickler, S. J. (2004). Ground reaction forces in horses trotting up an incline and on the level over a range of speeds. *J. Exp. Biol.* **207**, 3507-3514. doi:10.1242/jeb.01171

Farley, C. T. and Taylor, C. R. (1991). A mechanical trigger for the trot-gallop transition in horses. *Science* **253**, 306-308. doi:10.1126/science.1857965

Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001. doi:10.1088/1748-3182/3/3/034001

Hildebrand, M. (1988). *Analysis of Vertebrate Structure*. John Wiley and Sons.

Hudson, P. E., Corr, S. A. and Wilson, A. M. (2012). High speed galloping in the cheetah (Acinonyx jubatus) and the racing greyhound (Canis familiaris): spatio-temporal and kinetic characteristics. *J. Exp. Biol.* **215**, 2425-2434. doi:10.1242/jeb.066720

Jayes, A. S. and Alexander, R. M. (1978). Mechanics of locomotion of dogs (Canis-Familiaris) and sheep (Ovis-Aries). *J. Zool.* **185**, 289-308. doi:10.1111/j.1469-7998.1978.tb03334.x

Jones, J. H. and Lindstedt, S. L. (1993). Limits to maximal performance. *Annu. Rev. Physiol.* **55**, 547-569. doi:10.1146/annurev.ph.55.030193.002555

Lee, D. V., Bertram, J. E. A. and Todhunter, R. J. (1999). Acceleration and balance in trotting dogs. *J. Exp. Biol.* **202**, 3565-3573.

Lee, D. V., Bertram, J. E. A., Anttonen, J. T., Ros, I. G., Harris, S. L. and Biewener, A. A. (2011). A collisional perspective on quadrupedal gait dynamics. *J. R. Soc. Interface* **8**, 1480-1486. doi:10.1098/rsif.2011.0019

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. doi:10.1242/jeb.00254

Mclaughlin, R. M., , Jr, Gaughan, 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.

Merkens, H. W., Schamhardt, H. C., Hartman, W. and Kersjes, A. W. (1986). Ground reaction force patterns of dutch warmblood horses at normal walk. *Equine Vet. J.* **18**, 207-214. doi:10.1111/j.2042-3306.1986.tb03600.x

Merkens, H. W., Schamhardt, H. C., Van Osch, G. J. and Van Den Bogert, A. J. (1993a). Ground reaction force patterns of Dutch warmblood horses at normal trot. *Equine Vet. J.* **25**, 134-137. doi:10.1111/j.2042-3306.1993.tb02923.x

Merkens, H. W., Schamhardt, H. C., Vanosch, G. J. V. M. and Hartman, W. (1993b). Ground reaction force patterns of dutch warmbloods at the canter. *Am. J. Vet. Res.* **54**, 670-674.

Minetti, A. E., Ardig, O. L., Reinach, E. and Saibene, F. (1999). The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* **202**, 2329-2338.
Payne, R. C., Veenman, P. and Wilson, A. M. (2004). The role of the extrinsic thoracic limb muscles in equine locomotion. *J. Anat.* **205**, 479-490. doi:10.1111/j.0021-8782.2004.00353.x
Payne, R. C., Hutchinson, J. R., Robilliard, J. J., Smith, N. C. and Wilson, A. M. (2005). Functional specialisation of pelvic limb anatomy in horses (Equus caballus). *J. Anat.* **206**, 557-574. doi:10.1111/j.1469-7580.2005.00420.x
Pearce, G. P., May-Davis, S. and Greaves, D. (2005). Femoral asymmetry in the Thoroughbred racehorse. *Aust. Vet. J.* **83**, 367-370. doi:10.1111/j.1751-0813.2005.tb15636.x
Pfau, T., Spence, A., Starke, S., Ferrari, M. and Wilson, A. (2009). Modern riding style improves horse racing times. *Science* **325**, 289. doi:10.1126/science.1174605
Ratzlaff, M. H., Hyde, M. L., Grant, B. D., Balch, O. and Wilson, P. D. (1990). Measurement of vertical forces and temporal components of the strides of horses using instrumented shoes. *JEVS* **10**, 23. doi:10.1016/S0737-0806(06)80079-1
Roepstorff, L. and Drevemo, S. (1993). Concept of a force-measuring horseshoe. *Acta Anat (Basel)* **146**, 114-119. doi:10.1159/000147431
Ruina, A., Bertram, J. E. and Srinivasan, M. (2005). A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *J. Theor. Biol.* **237**, 170-192. doi:10.1016/j.jtbi.2005.04.004
Russell, A. and McWhirter, N. D. (1988). *The Guinness Book of Records 1988*. London: Guinness Books.
Self, Z. T., Spence, A. J. and Wilson, A. M. (2012). Speed and incline during thoroughbred horse racing: racehorse speed supports a metabolic power constraint to incline running but not to decline running. *J. Appl. Physiol.* **113**, 602-607. doi:10.1152/japplphysiol.00560.2011
Self Davies, Z. T., Spence, A. J. and Wilson, A. M. (2019). External mechanical work in the galloping racehorse. *Biol. Lett.* **15**, 20180709. doi:10.1098/rsbl.2018.0709
Tan, H. and Wilson, A. M. (2011). Grip and limb force limits to turning performance in competition horses. *Proc. Biol. Sci.* **278**, 2105-2111. doi:10.1098/rspb.2010.2395
Thornton, J., Pagan, J. and Persson, S. (1987). The oxygen cost of weight loading and inclined treadmill exercise in the horse. *Equine Exerc. Physiol.* **2**, 206-215.
Usherwood, J. R. and Wilson, A. M. (2005). Biomechanics: no force limit on greyhound sprint speed. *Nature* **438**, 753-754. doi:10.1038/438753a
Usherwood, J. R. and Wilson, A. M. (2006). Accounting for elite indoor 200 m sprint results. *Biol. Lett.* **2**, 47-50. doi:10.1098/rsbl.2005.0399
Walter, R. M. and Carrier, D. R. (2007). Ground forces applied by galloping dogs. *J. Exp. Biol.* **210**, 208-216. doi:10.1242/jeb.02645
Watson, K. M., Stitson, D. J. and Davies, H. M. S. (2003). Third metacarpal bone length and skeletal asymmetry in the Thoroughbred racehorse. *Equine Vet. J.* **35**, 712-714. doi:10.2746/042516403775696348
Weyand, P. G. and Davis, J. A. (2005). Running performance has a structural basis. *J. Exp. Biol.* **208**, 2625-2631. doi:10.1242/jeb.01609
Weyand, P. G., Sternlight, D. B., Bellizzi, M. J. and Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991-1999. doi:10.1152/jappl.2000.89.5.1991
Wilson, A. M., Mcguigan, M. P., Su, A. and Van Den Bogert, A. J. (2001). Horses damp the spring in their step. *Nature* **414**, 895-899. doi:10.1038/414895a
Wilson, A. M., Watson, J. C. and Lichtwark, G. A. (2003). Biomechanics: a catapult action for rapid limb protraction. *Nature* **421**, 35-36. doi:10.1038/421035a
Witte, T. H., Knill, K. and Wilson, A. M. (2004). Determination of peak vertical ground reaction force from duty factor in the horse (Equus caballus). *J. Exp. Biol.* **207**, 3639-3648. doi:10.1242/jeb.01182
Witte, T. H., Hirst, C. V. and Wilson, A. M. (2006). Effect of speed on stride parameters in racehorses at gallop in field conditions. *J. Exp. Biol.* **209**, 4389-4397. doi:10.1242/jeb.02518