Grip and limb force limits to turning performance in competition horses

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Manoeuverability is a key requirement for successful terrestrial locomotion, especially on variable terrain, and is a deciding factor in predator–prey interaction. Compared with straight-line running, bend running requires additional leg force to generate centripetal acceleration. In humans, this results in a reduction in maximum speed during bend running and a published model assuming maximum limb force as a constraint accurately predicts how much a sprinter must slow down on a bend given his maximum straight-line speed. In contrast, greyhounds do not slow down or change stride parameters during bend running, which suggests that their limbs can apply the additional force for this manoeuvre. We collected horizontal speed and angular velocity of heading of horses while they turned in different scenarios during competitive polo and horse racing. The data were used to evaluate the limits of turning performance. During high-speed turns of large radius horizontal speed was lower on the bend, as would be predicted from a model assuming a limb force limit to running speed. During small radius turns the angular velocity of heading decreased with increasing speed in a manner consistent with the coefficient of friction of the hoof–surface interaction setting the limit to centripetal force to avoid slipping.

Keywords: manoeuvrability; friction limit; muscle force limit

1. INTRODUCTION

The ability to change direction is a key requirement for animal locomotion in a natural environment and can be a deciding factor in predator–prey encounters, especially small radius turning while sprinting [1]. Our understanding of the stability and manoeuverability of terrestrial vertebrates is still limited compared with our knowledge of other aspects of their locomotion [2]. Here, we endeavour to investigate those factors that might limit the turning capacity of horses (*Equus caballus*) under field conditions.

One mechanical factor proposed as a limitation to human sprinting speed is the force experienced by the limbs during stance [3]. Compared with straight-line sprinting at similar speed, sprinting around a bend requires additional force perpendicular to the initial moving direction in order to change the direction of the velocity vector and deflect the trajectory of the centre of mass (CoM). The additional force required to negotiate a bend increases with higher speed and with turns of smaller radius (centripetal acceleration is velocity squared over radius). Greene [4] investigated the ability of human runners to run in circles and suggested that cornering speed might be limited by the ability of the musculoskeletal system to generate the required forces. Usherwood & Wilson [5] compared the times for indoor 200 m sprint races and outdoor races and showed that the decreased performance in indoor competition and the bias by lane number are consistent with the constant limb force hypothesis. Given the constant peak limb force

constraint for maximum speed sprinting, the requirement of extra force for turning is met by increasing the proportion of time each foot spends in contact with the ground, with a resultant reduction in speed. If the maximum speed of horses is similarly limited by constant peak limb force, horses will also slow down during maximum effort bend running.

In contrast, racing greyhounds do not slow down or change their stride parameters to compensate for the increased net force requirement while running on bends [6], suggesting that they apply larger forces on a bend than while running straight. The ability of greyhounds to reach similar top speeds during curve and straight sprinting was attributed to decoupling of the power generating from the weight-supporting mechanisms of quadrupeds meaning that maximum running speed on the straight is not constrained by the capacity of the limbs to resist axial force. Dogs power locomotion by torque about the hips and by back extension, whereas weight support is biased towards the forelimbs [7–9]. The centripetal force required for turning is effectively increasing body weight (but not inertia) and they do not need to slow down because the muscles that power the greyhound do not have to withstand the increases in effective weight.

Functional and anatomical decoupling of the power generating from the weight-supporting mechanisms is also evident in horses. Short-fibred pennate muscles capable of generating vertical impulse are found in the forelimb and suggest an apparent specialization for weight support and passive, spring-like behaviour [10,11]. Conversely, large muscles with long, parallel fibres capable of generating substantial net mechanical work are found in the upper hindlimb [12]. Moreover, the acceleration of both horses and greyhounds is limited

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by the requirement to balance pitch at low speed, supporting the hypothesis that they are powered by torque around the hip [9]. We are interested in whether this functional dissociation will convey the same advantage to horses during bend running manoeuvers and turning as seen in greyhounds, namely that they can maintain similar speeds while running on a bend as running on a straight line [6].

Besides the muscular ability to produce force, other mechanical constraints such as the danger of skidding/slipping may also limit manoeuverability, especially during turns of small radius and at lower speeds. Alexander [2] suggested that humans might run slower at very small radii/low speeds because of a friction limit rather than a force limit, as was shown in a study of a single subject running curves of different radii [13]. Slippery surfaces are a significant concern in equine veterinary practice during both orthopaedic evaluation and treatment, especially when horses have to trot on circles [14]. Hoof slip in the direction of motion occurs when the ratio of total horizontal to vertical components of the ground-reaction forces exceeds the static coefficient of friction of the hoof–surface interaction. The horizontal ground-reaction force may, therefore, be constrained by need to avoid slipping, which will limit the maximum centripetal acceleration during turning. Moreover, a limit in horizontal force should result in a trade-off between acceleration in the direction of movement and centripetal acceleration since as vectors they combine to a single horizontal acceleration.

Here, we collected position and speed of horses during turns of different radius, during two competitive polo games and during 56 horse races. Both scenarios represent conditions of sustained maximum effort. Angular velocity of track and turning radii were calculated. In doing so, we endeavour to investigate what factors might limit the turning capacity of horses. We hypothesized that:

— on small radius turns the maximum speed of horses will be limited by lateral force/friction to avoid sliding; and
— on large radius turns horses will be able to maintain their straight-line speed due to not being force limited as observed in greyhounds.

2. METHODS

(a) *Data collection*
Data were collected at two scenarios.

1. Data were collected during two mid-level competitive polo games on a standard grass polo field (275×140 m). One team of four riders from each game took part in the study. Data collection occurred in the middle of the season, with riders and horses routinely taking part in competitions. The horses were judged to be clinically sound by a veterinary surgeon before data collection. Each rider rode four or five different horses during each 40 min game so a total of 17 horses were evaluated. A small ($60 \times 30 \times 10$ mm, 31 g including battery) custom-designed stand-alone Global Positioning System-Inertial Measurement Unit (GPS-IMU) module [15] was attached to the helmet of each rider. The maximum sampling frequencies for the GPS module and the inertial unit were 10 Hz and 100 Hz, respectively. Raw pseudorange data from the GPS unit were post-processed
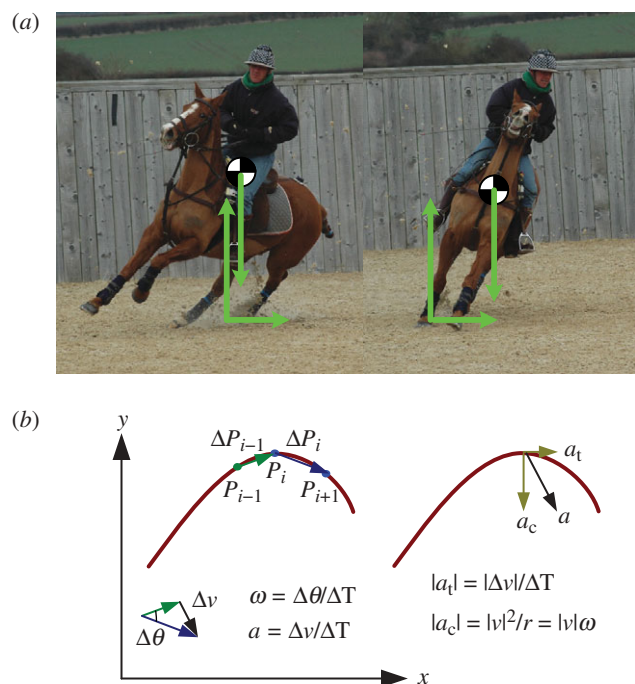
(a)

(b)

Figure 1. (a) Shows horses turning in a race, with the arrows showing the direction of gravity and ground-reaction forces. (b) Shows how change of heading, angular velocity, tangential and lateral accelerations are calculated from two-dimensional positions and horizontal speeds.

using commercial software (GRAVNAV v. 7.60; Waypoint; Calgary, Canada) with kinematic ambiguity resolution and other settings as per manufacturer's defaults. This gave measurements of position and horizontal velocity. A Kalman filter based complementary filter [15] was applied to combine speed measurements from the GPS and accelerations from the inertial sensors. The measurement error of horizontal speed after integrating the GPS and the IMU is ± 0.06 m s^{-1} (standard deviation) for cycling [15] and the measurement error of absolute position is ± 0.2 m in both east and north.

2. Races involving a bend on four different grass horserace tracks in the UK were monitored. Data from the first three winning horses of each race were used for subsequent analysis to minimize the risk of a horse being impeded by slower horses. In total, 168 horses from 56 races on a total of 28 days between June and October were used in the analysis. Location and speed were determined using a wireless radiolocation tracking system (TurfTrax, UK). This system measured the two-dimensional position and horizontal speed of each horse in each race at 4 Hz, which is then filtered to one update per second. The accuracy of this system was previously validated against high-performance differential GPS [16]. The mean distance between position measurements from the wireless radio tracking system and the GPS system ranges from 0.32 to 0.66 m. The mean ($\pm$ s.d.) difference in the speed measurement between the radio tracking system and high-performance GPS is 0.036 ± 0.11 m s^{-1}. These figures include the errors in both systems.

(b) *Data analysis*
The angular velocity of the heading was calculated based on the two-dimensional position measurements, as shown in figure 1.

First, the displacements of consecutive samples were calculated.

$$\Delta \vec{P}_i = \vec{P}_i - \vec{P}_{i-1}$$
and
$$\Delta \vec{P}_{i+1} = \vec{P}_{i+1} - \vec{P}_i, \qquad (2.1)$$

where $\vec{P}_i$ and $\Delta \vec{P}_i$ are the vector of position and displacement at sample i, respectively. The displacement vector also gives the heading.

Then the change of heading can be calculated as the angle between the displacement vector of two consecutive samples and the angular velocity can be calculated:

$$\Delta \theta_i = \angle (\Delta \vec{P}_{i+1}, \Delta \vec{P}_i)$$
and
$$\omega_i = \frac{\Delta \theta_i}{\Delta T}, \qquad (2.2)$$

where ΔT is the sampling interval.

The tangential acceleration ($a_{T,i}$), centripetal or lateral acceleration ($a_{C,i}$) and instantaneous radius of the curvature (r_i) at each sampling point are calculated as:

$$a_{T,i} = \frac{v_{i+1} - v_i}{\Delta T},$$
$$a_{C,i} = \omega_i \cdot v_i$$
and
$$r_i = \frac{v_i}{\omega_i}. \qquad (2.3)$$

In scenario 1, the GPS/IMU unit was mounted to the rider's helmet. During a polo game, the rider can move a lot relative to the horse while leaning forward or sideways to hit the ball. Therefore data from scenario 1 were low pass filtered to 1 Hz with a simple moving average with a window size of 10 to remove any artefact introduced by the movement of the rider relative to the horse (stride frequency is about 2 Hz). Besides, the measurement error associated with the change of heading and angular velocity calculated from two-dimensional position over time increases as the distance between two consecutive samples reduces. Thus measurement error increases as the sampling interval and as the horizontal speed reduces. Therefore, a time interval of 1 s was used to calculate heading and change of heading for the polo data in order to reduce measurement error associated with heading.

To evaluate different theoretical models, the experimental data were grouped according to either horizontal speed or turning radius, the 99th percentile (i.e. 99% point of the angular velocity or horizontal speed) for each data group was then calculated. The correlation between the model and the 99 per cent percentiles was then calculated and the average absolute difference between the 99 per cent percentile and those predicted from the theoretical models in percentage of the experimental data are defined as the error of the model.

3. RESULTS
(a) *Angular velocity decreased with increasing speed in a polo game*
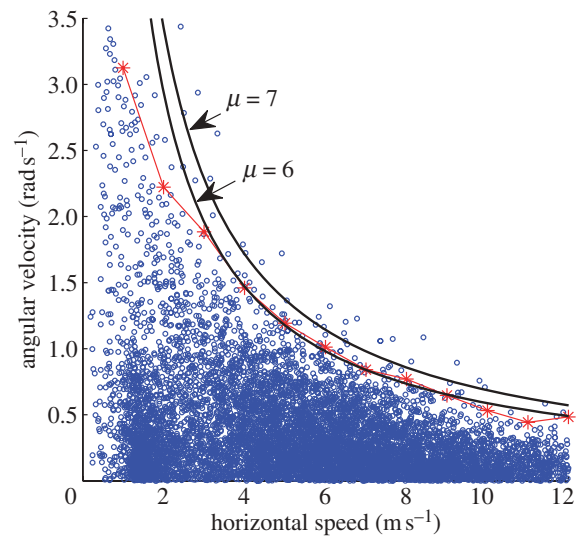During a competitive polo game, horses are required to change heading and perform turns of different radius as

Figure 2. Data from 17 horses turning during two competitive polo games. The red stars show 99% percentile of the angular velocity while grouping the data by horizontal speed with the bin width of 1 m s^{-1}. Larger heading angular velocity occurred at low horizontal speed and the angular velocity was lower at higher horizontal speed. The black lines show the relationship between angular velocity and horizontal speed predicted by a friction limit/lateral force limit model with a static coefficient of friction of 0.6 and 0.7, respectively. The larger the static coefficient friction, the further the line is from the *x*-axis and *y*-axis.

a result of the interaction between the horses and the tactics of riders during a game (as shown in electronic supplementary material, video).

The horizontal speeds of horses taking a turn in a polo game ranged from 0 m s^{-1} to 12 m s^{-1}. Turns with high angular velocity heading occurred at low horizontal speed. Maximum angular velocity achieved decreased at higher horizontal speed, as is shown in figure 2. The black lines in figure 2 show the relationship between angular velocity and horizontal speed determined by a friction limit. The 99 per cent angular velocity percentile of data grouped by horizontal speed correlates well with the friction limit model assuming a friction coefficient of 0.6 with $r = 0.96$, $p = 1.3 \times 10^{-6}$, $n = 12$. The mean absolute error of the friction model is 14.0 per cent with the horizontal speed between 1 and 12 m s^{-1} and the model error reduced to 4.7 per cent when only considering data with horizontal speed between 3 and 12 m s^{-1}.

(b) *Racehorses slowed down on bends during racing*
During racing, horses are mainly ridden to achieve maximum performance, i.e. to cover a fixed distance in minimal time and even pace is acknowledged to be tactically advantageous. For all the data used for analysis, the bends were in the middle of relatively short races and all horses exceeded a speed of 15 m s^{-1} before they reached the bend. Our data show that horses were slower around the bend in racing, even when the trajectory was smooth with a large radius. Figure 3 shows the speeds of the top three horses from each race on two of the four racetracks with bends of different radius. Slowing down on the bend was consistent across horses and races on different days.
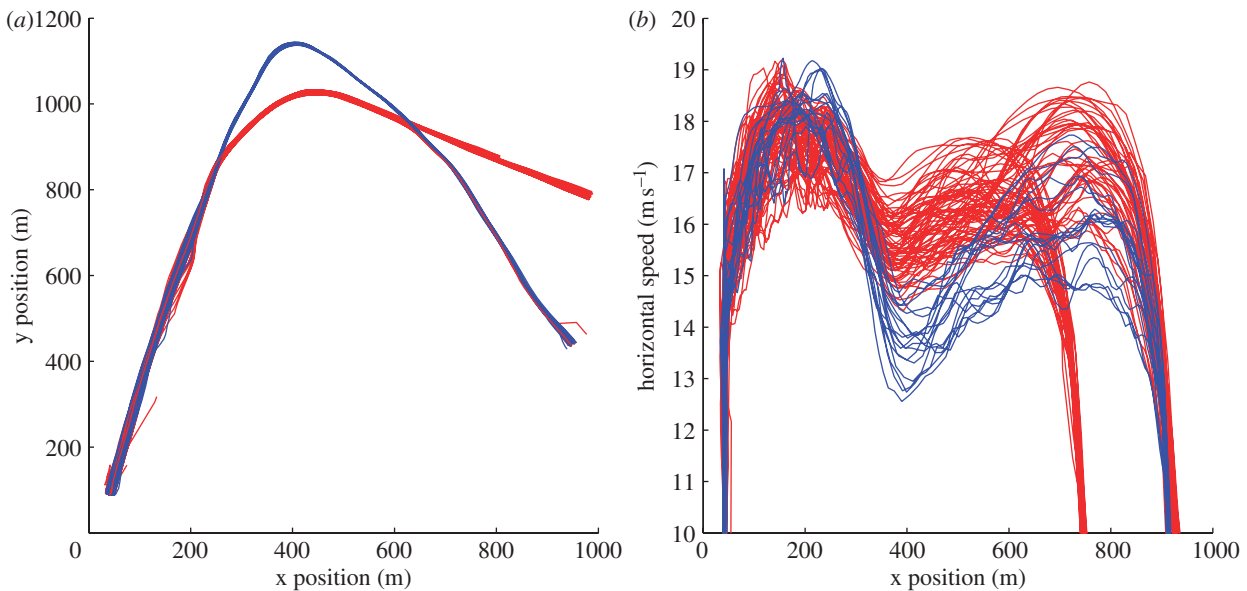
Figure 3. Data from the first three winning horses of races on two tracks of different radius. (a) Shows the location trajectories and (b) shows how speed varies with position. Blue lines in (b) are speeds from horses racing on the blue track with a tighter bend shown in (a). Red lines in (b) are speeds from horses racing on the red track in (a). It was shown that all horses slowed down while approaching the bend. Horses running on a tighter bend slowed down more than those on a smoother bend.

Horses also slowed down more on small radius bends than on large radius bends.

4. DISCUSSION

(a) *What limits turning performance of horses?*

Two factors that might limit turning performances are evaluated: peak limb force and friction.

Friction limits the total horizontal force the horse can apply, resulting in a trade-off between forward acceleration and centripetal acceleration. Meanwhile, the maximal horizontal force also determines the relationship between horizontal speed and the angular velocity of heading or turning radius:

$$\left.\begin{array}{l} \sqrt{a_{\mathrm{T}}^2 + a_{\mathrm{C}}^2} \leq \mu \cdot g \\[1em] \text{and} \\[1em] |a_{\mathrm{C}}| = \dfrac{v_{\mathrm{T}}^2}{r} = |v_{\mathrm{T}} \cdot \omega| \leq \mu \cdot g, \end{array}\right\} \qquad (4.1)$$

where a_{T} and a_{C} are tangential and centripetal acceleration, respectively; g is the gravitational acceleration; v_{T} and ω are the horizontal speed and angular velocity of heading during turning, respectively; r is the radius of the turn and μ is the static coefficient of friction between the surface and the hoof.

On the other hand, if maximum limb force limits the maximum speed of horses, horses will negotiate the bend at a slower speed due to the requirement for a higher average force and hence duty factor [17]. In this case, the maximum speed on a bend of a certain radius can be calculated as follows given the stride timings, the maximum speed on a straight line, and with some assumptions [5]:

While galloping at constant speed on a straight line,

$$F_{\mathrm{limb}} \cdot t_{\mathrm{stance}} = c \cdot m \cdot g \cdot (t_{\mathrm{stance}} + t_{\mathrm{swing}}), \qquad (4.2)$$

where F_{limb} is the maximum limb force, c is a constant, which is determined by the shape of the limb force, t_{stance} and t_{swing} are the stance time and the swing time at maximum speed straight-line galloping, respectively. Therefore, F_{limb} can be estimated based on t_{stance} and t_{swing}:

$$F_{\mathrm{limb}} = c \cdot m \cdot g \cdot \frac{t_{\mathrm{stance}} + t_{\mathrm{swing}}}{t_{\mathrm{stance}}}. \qquad (4.3)$$

During galloping on a bend, the horse has to sustain centripetal force which is v_{T}^2/r, i.e.:

$$F_{\mathrm{limb}} \cdot t'_{\mathrm{stance}} = c \cdot m \cdot \sqrt{g^2 + \left(\frac{v_{\mathrm{T}}^2}{r}\right)^2} \cdot (t'_{\mathrm{stance}} + t'_{\mathrm{swing}}), \qquad (4.4)$$

where F_{limb} is the same as in straight sprinting, t'_{stance} and t'_{swing} are the stance time and the swing time, respectively.

Similar to the previous model [5], we assume that the swing time (t_{swing}) between each stance period for a leg and the distance the horse travelled during stance time (L_{stance}) are constant for sprinting around bends of different radii. By keeping t_{swing} constant, we assume that the leg is protracted in minimum time under all conditions. By keeping L_{stance} constant, we assume that the leg sweep angle is the same under all conditions. The constant t_{swing} and L_{stance} assumption in maximally performing human sprinters is broadly supported by a range of empirical data [3,4]. Measurements of stride parameters of racehorses galloping in field conditions showed that the duration of aerial phase was independent of speed [18]. The stride frequency of horses during galloping also remains almost constant across a range of speeds [19,20]. Therefore, we feel that the assumptions of constant t_{swing} and L_{stance} are justifiable. Thus:

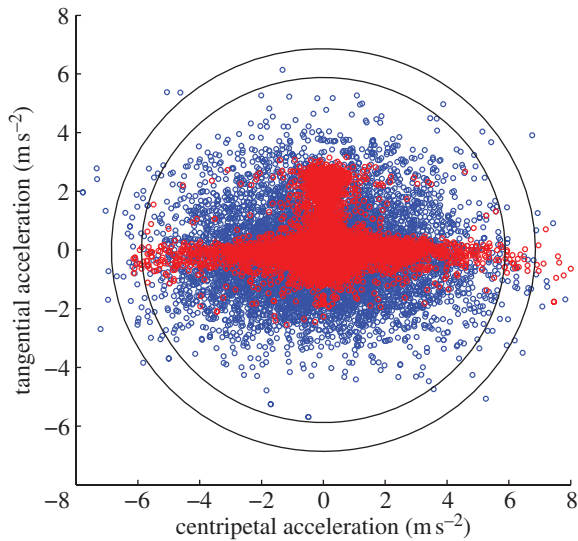$$t'_{\mathrm{swing}} = t_{\mathrm{swing}} \qquad (4.5)$$

Figure 4. Relationship between tangential acceleration and centripetal acceleration for data collected from horses racing (red circles, 165 horses, 24 333 samples) and polo games (blue circles, 17 horses 8512 samples). During turning in polo games, horses were able to change horizontal speed while changing heading. During racing, the horses are dominantly experiencing centripetal acceleration during the turns, and they only accelerate again when the centripetal acceleration is small. Most data lie within the black circles, which are defined by the friction limit model with a static coefficient of friction of 0.6 and 0.7, respectively. The larger the static coefficient friction, the larger is the radius of the black line.

and

$$t'_{\text{stance}} \cdot v_{\text{T}} = t_{\text{stance}} \cdot v_{\text{max}}. \qquad (4.6)$$

Substituting equations (4.3), (4.5) and (4.6) into equation (4.4), the latter can be rewritten as:

$$c \cdot m \cdot g \cdot \left(\frac{t_{\text{stance}} + t_{\text{swing}}}{t_{\text{stance}}} \right) \cdot \left(\frac{t_{\text{stance}} v_{\text{max}}}{v_{\text{T}}} \right)$$
$$= c \cdot m \cdot \sqrt{g^2 + \left(\frac{v_{\text{T}}^2}{r} \right)^2} \cdot \left(\frac{t_{\text{stance}} v_{\text{max}}}{v_{\text{T}}} + t_{\text{swing}} \right). \qquad (4.7)$$

Given t_{stance} and t_{swing} measured at high speed straight galloping [18], equation (4.7) provides a closed-form solution for maximum speed (v_{T}) on a bend of a certain the radius (r).

Figures 4 and 5 summarize all the data we collected on both the polo game and horses races, and also show how observed data compares with predictions from the friction limit model and limb force limit model.

Figure 4 shows that horses were able to change horizontal speed while turning during polo games (blue circles), whereas racing horses are dominantly experiencing only centripetal acceleration during turns in racing (red circles). They slowed down while approaching the turn and they only accelerate again when the centripetal acceleration is small, i.e. when they come out of the turn. In both cases, the tangential accelerations and centripetal accelerations lie within the circle defined by a friction limit of 0.7 (outer circle, equation (4.1)). This value was consistent with those measured in a previous
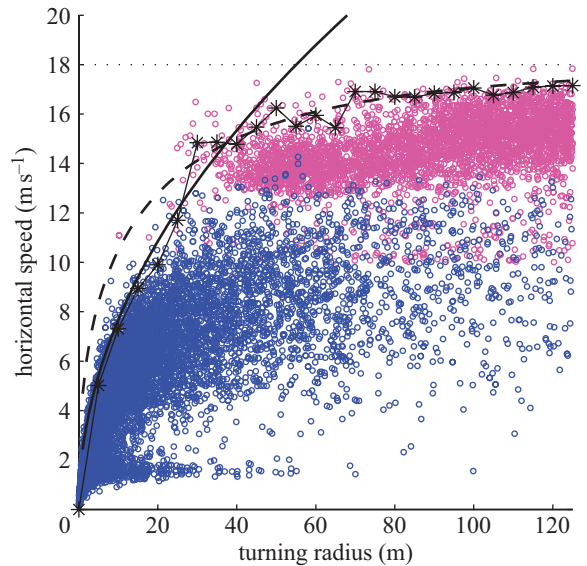

Figure 5. Data collected from racing horses (pink circles) and those from polo horses (blue circles). The black stars show 99% percentile of the horizontal speed while grouping the data by turning radius with the bin width of 5 m. The solid black line shows the maximum horizontal speed given a certain radius constrained by friction, with $\mu = 0.6$. The dashed black line shows the limit imposed by constraining peak limb force, assuming duty factor $= 0.2$, swing time $= 0.33$ s with maximum speed $= 18 \text{ m s}^{-1}$ on straight [18]. The dotted line is the assumed maximum speed on straight. The friction limit model accounts for data collected with horses turning at smaller radii. Data from horse racing at higher speed and smooth bends are in agreement with the constrained peak limb force model.

study, which tried to determine the coefficient of friction between the equine foot and different ground surfaces by measuring the forces required to pulled the hoofs horizontally [21,22]. They measured the static friction coefficient of 0.68 between shod equine digits and smooth rubber tiles, 0.69 for rough rubber tiles and 0.58 for small concrete bricks. Estimating an equivalent for turf is difficult as it will depend on whether the foot will penetrate the surface or plough through it but similar values are feasible. In comparison, racing greyhounds [6] can experience very high centripetal accelerations during turning. This can be related to banking of the track and the fact that the greyhounds digits penetrate into the surface to increase grip.

Figure 5 shows that while turning at small radii of smaller than 30 m, the friction model with friction coefficient of 0.6 correlates well with the 99 per cent points of the horizontal speed while grouping the data by turning radius ($r = 0.99$, $p = 4.0 \times 10^{-5}$, $n = 7$). The average absolute error of the friction model is much lower than that of the limb force limit model (5.8% compared with 19.5%). While turning with radii larger than 30 m, horses slowed down more than predicted by the friction model on the bends, but in agreement with the limb force limit model. In this case, the limb force limit model correlates well with the 99 per cent points of data ($r = 0.92$, $p = 6.3 \times 10^{-9}$, $n = 20$) with the average absolute difference between the data and the model 1.8 per cent.

Therefore, we conclude that the horizontal speed of horses during turning is limited by friction at small radii and limited by limb force with larger radii. The model also suggests that in order to avoid the friction limit, which can be potentially dangerous for the horse and the rider, the radius of any turn negotiated by racehorses in training or racing should be larger than 30 m. The increase in limb force on tight turns may also be implicated in racehorse injuries.

It should be noted that there are some other factors besides the maximum limb force that might affect the speed of the horse during turning. For example, fatigue may change muscle force generation [23], therefore, the location of the turn (either in the beginning or in the end of the course) and how fresh the horse is during the race on the day might both have effects on the maximum turning speed. The effects of these factors need further investigation where manipulation and control of these factors are possible.

(b) Difference between horses and dogs

Our data showed that horses had to slow down (and presumably increase duty factor) on a bend to satisfy the requirement for extra mean force, and that the maximum speeds of horses during turning at large radii are in agreement with those predicted by the constant limb force model. In contrast, greyhounds were shown to maintain speed on the bend compared with straight sprinting [6], which may be the outcome of having been bred to race on oval tracks. It is interesting to speculate why greyhounds differ from horses in their turning capacity.

Our previous study showed that greyhounds and horses experience similar limiting factors in their acceleration. The pitch limit for acceleration at lower speed suggests that both greyhounds and horses are powered by torques around the hip. Differences in their turning capacity suggests that the decoupled mechanism for weight support and generating power is a necessary but not sufficient condition for quadrupeds to maintain maximum speed on during bend running. Compared to greyhounds as a carnivorous predator, horses are herbivorous prey and they tend to carry larger viscera. Viscera represent about 34 per cent of body weight in horses [24] and about 13 per cent of body weight in dogs (D. Carrier 2010, unpublished data) though these values may be lower in racing animals. The viscera are less tightly coupled to the skeleton than other elements, which may have two effects on locomotion.

Firstly, the viscera may deflect in the direction of the leg force, thus dissipating energy [25] that would need to be replaced by leg work. Increased peak leg force in turning would increase this dissipation and the loss would be greater in the horse because of larger visceral volume. The deflection may not be completely lossey as the abdominal wall comprises of several layers of elastic tendinous sheet.

Secondly, the viscera may not follow the within stride movements of the horse skeleton around its mean CoM trajectory. This means that the horse would have to support the weight of the viscera but it would not need to perform the leg work to make the viscera follow the movements of the horse. This loose coupling has been demonstrated as a performance benefit for standing jockeys who isolate themselves from the movement of their mount [26]. The tendinous (and hence elastic) abdominal wall would store and return energy returning the skeleton towards its mean location and reducing the external mechanical work below that which would be calculated from external kinematic measures [27]. This hidden spring could account for the apparently high metabolic efficiency of mechanical work observed in Minetti's study [28], the relatively low cost of transport in the horse and its speed endurance capacity.

So the larger viscera in the horse may increase locomotor cost on a bend owing to increased force and deflection, and produce an energetic constraint and/or the horse may have adapted by allowing the viscera to move and be coupled to the trunk by springs meaning the cost of carrying them is less than an equivalent amount of bone or muscle.

5. CONCLUSION

Examination of the horizontal and rotational speeds of polo horses and racehorses during turns of various radii showed that at small radii the horizontal speed of horses during turning is likely to be limited by friction while at larger radii horses slow down on the turn, in agreement with a peak limb force limit to maximum speed. The slowing of racehorses when turning at high speed is contrary to our hypothesis and may demonstrate a previously hidden force limit or an energetic constraint.

REFERENCES

1 Howland, H. C. 1974 Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350. (doi:10.1016/0022-5193(74)90202-1)

2 Alexander, R. M. 2002 Stability and manoeuvrability of terrestrial vertebrates. *Integr. Comp. Biol.* **42**, 158–164. (doi:10.1093/icb/42.1.158)

3 Weyand, P. G., Sternlight, D. B., Bellizzi, M. J. & Wright, S. 2000 Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991–1999.

4 Greene, P. R. 1985 Running on flat turns: experiments, theory, and applications. *J. Biomech. Eng.* **107**, 96–103. (doi:10.1115/1.3138542)

5 Usherwood, J. R. & Wilson, A. M. 2006 Accounting for elite indoor 200 m sprint results. *Biol. Lett.* **2**, 47–50. (doi:10.1098/rsbl.2005.0399)

6 Usherwood, J. R. & Wilson, A. M. 2005 Biomechanics: no force limit on greyhound sprint speed. *Nature* **438**, 753–754. (doi:10.1038/438753a)

7 Alexander, R. 1974 The mechanics of jumping by a dog (*Canis familiaris*). *J. Zool. Lond.* **173**, 549–573. (doi:10.1111/j.1469-7998.1974.tb04134.x)

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

9 Williams, S. B., Tan, H., Usherwood, J. R. & Wilson, A. M. 2009 Pitch then power: limitations to acceleration in quadrupeds. *Biol. Lett.* **5**, 610–613. (doi:10.1098/rsbl.2009.0360)

10 McGuigan, M. P. & 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)

11 Wilson, A. M., McGuigan, M. P., Su, A. & van den Bogert, A. J. 2001 Horses damp the spring in their step. *Nature* **414**, 895–899. (doi:10.1038/414895a)

12 Payne, R. C., Hutchinson, J. R., Robilliard, J. J., Smith, N. C. & 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)

13 McMahon, T. A. 1984 *Muscles, reflexes and locomotion.* Princeton, NJ: Princeton University Press.

14 Dyson, S. J. 2000 Lameness and poor performance in the sports horse: dressage, show jumping and horse trials (eventing). *Proc. Am. Vet. Med. Assoc.* **46**, 308–315.

15 Tan, H. L., Wilson, A. M. & Lowe, J. 2008 Measurement of stride parameters using a wearable GPS and inertial measurement unit. *J Biomech.* **41**, 1398–1406. (doi:10.1016/j.jbiomech.2008.02.021)

16 Spence, A. J., Tan, H. & Wilson, A. M. 2008 Accuracy of the TurfTrax racing data system for determination of speed and position. *Equine Vet. J.* **40**, 680–683. (doi:10.2746/042516408X330338)

17 Witte, T. H., Knill, K. & 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)

18 Witte, T. H., Hirst, C. V. & 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)

19 Heglund, N. C. & 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.

20 Heglund, N. C., Taylor, C. R. & McMahon, T. A. 1974 Scaling stride frequency and gait to animal size: mice to horses. *Science* **186**, 1112–1113. (doi:10.1126/science.186.4169.1112)

21 Vos, N. J. & Riemersma, D. J. 2006 Determination of coefficient of friction between the equine foot and different ground surfaces: an *in vitro* study. *Equine Comp. Exerc. Physiol.* **3**, 191–198. (doi:10.1017/S1478061506617234)

22 McClinchey, H. L., Thomason, J. J. & Runciman, R. J. 2004 Grip and slippage of the horse's hoof on solid substrates measured ex vivo. *Biosyst. Eng.* **89**, 485–494. (doi:10.1016/j.biosystemseng.2004.08.004)

23 Higham, T. E. & Biewener, A. A. 2009 Fatigue alters *in vivo* function within and between limb muscles during locomotion. *Proc. R. Soc. B* **276**, 1193–1197. (doi:10.1098/rspb.2008.1734)

24 Lemus, C., Casas-Garcia, C., Mota-Rojas, D., Gonzalez, H. G. & Toca-Ramirez, J. 2006 Horse meat for human consumption in México: slaughter performance and carcass morphometry. *J. Food Technol.* **4**, 106–110.

25 Daley, M. A. & Usherwood, J. R. 2010 Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. *Biol. Lett.* **6**, 418–421. (doi:10.1098/rsbl.2010.0175)

26 Pfau, T., Spence, A. J., Starke, S., Ferrari, M. & Wilson, A. M. 2009 Modern riding style improves horse racing times. *Science* **325**, 289. (doi:10.1126/science.1174605)

27 Minetti, A. E., Ardigo, L. P., Reinach, E. & Saibene, F. 1999 The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* **202**, 2329–2338.

28 Pfau, T., Witte, T. H. & Wilson, A. M. 2006 Centre of mass movement and mechanical energy fluctuation during gallop locomotion in the thoroughbred racehorse. *J. Exp. Biol.* **209**, 3742–3757. (doi:10.1242/jeb.02439)