

Biomechanical and energetic determinants of the walk–trot transition in horses

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Summary

We studied nine adult horses spanning an eightfold range in body mass (M_b) (90–720 kg) and a twofold range in leg length (L) (0.7–1.4 m). We measured the horses' walk–trot transition speeds using step-wise speed increments as they locomoted on a motorized treadmill. We then measured their rates of oxygen consumption over a wide range of walking and trotting speeds. We interpreted the transition speed results using a simple inverted-pendulum model of walking in which gravity provides the centripetal force necessary to keep the leg in contact with the ground. By studying a large size range of horses, we were naturally able to vary the absolute walking speed that would produce the same ratio of centripetal to gravitational forces. This ratio, $(M_b v^2/L)/(M_b g)$, reduces to the dimensionless Froude

number (v^2/gL), where v is forward speed, L is leg length and g is gravitational acceleration. We found that the absolute walk–trot transition speed increased with size from 1.6 to 2.3 m s⁻¹, but it occurred at nearly the same Froude number (0.35). In addition, horses spontaneously switched between gaits in a narrow range of speeds that corresponded to the metabolically optimal transition speed. These results support the hypotheses that the walk–trot transition is triggered by inverted-pendulum dynamics and occurs at the speed that maximizes metabolic economy.

Key words: equine, Froude number, gait, inverted pendulum, locomotion, oxygen consumption.

Introduction

Terrestrial animals travel from one place to another by moving their limbs in characteristic patterns called gaits. Each gait is used only over a limited range of speeds. For example, horses walk at slow speeds, trot at moderate speeds and gallop at fast speeds. However, animals are not strictly constrained to a particular gait at a given speed. Horses can gallop at a walking speed, such as in the first stride of a race but, in general, animals only use one gait at a given speed. When speed is controlled, as during treadmill locomotion, animals prefer to switch gaits at specific speeds (Farley and Taylor, 1991). These gait-transition speeds are highly repeatable from one day to the next, suggesting that gait transitions are tightly regulated processes.

Gait transitions occur as the result of information the body senses or perceives. Transitions do not occur because some maximal limit is reached – animals can be trained to use a gait over a broader speed range than they normally choose to use (Farley and Taylor, 1991; Hoyt and Taylor, 1981; Wickler et al., 2003). Rather, animals naturally switch gaits when they reach some critical kinematic, kinetic or metabolic level that is relieved by changing gaits. Most investigators

seeking to identify these critical factors in terrestrial locomotion have focused on the walk–run transition of bipeds or the trot–gallop transition of quadrupeds (e.g. Biewener and Taylor, 1986; Diedrich and Warren, 1995; Farley and Taylor, 1991; Hreljac, 1993a,b, 1995a,b; Kram et al., 1997; Mercier et al., 1994; Minetti et al., 1994; Prilutsky and Gregor, 2001; Raynor et al., 2002; Rubenson et al., 2004; Thorstensson and Roberthson, 1987; Turvey et al., 1999). Our goal was to understand the determinants of the walk–trot transition in quadrupeds.

The walk–trot transition is biomechanically analogous to the bipedal walk–run transition (Cavagna et al., 1977). Walking is traditionally defined as a gait in which there is at least one leg always in contact with the ground (Howell, 1944). In contrast, an animal that runs or trots generally has periods during a stride when all the legs are off the ground. Biomechanical data also differentiate these two gaits. For walking animals, the center of mass reaches its highest position near the middle of the stance phase; whereas in running, the center of mass attains its lowest position near mid-stance (McMahon et al., 1987). These patterns reflect two different basic mechanisms of legged

locomotion – the inverted-pendulum-like mechanics of walking and the spring-like mechanics of running (Cavagna et al., 1977). The change from a walk to a trot is a critical transition in biomechanics from inverted-pendulum to spring-like mechanics.

In a simple inverted-pendulum model of walking, maximal walking speed is set by gravity and leg length (Alexander, 1977). This model simplifies the legs to ‘mass-less’ struts and body mass to a point mass located at the hip. During a step, body mass follows a curved path and to do so, it must be accelerated (centripetally) towards the ground contact point. Because legs do not stick to the ground, this acceleration must be provided by gravity. Based on this inverted-pendulum model, Alexander predicted that animals could not walk faster than the speed at which the centripetal force required to keep the body moving along the curved path exceeded the force provided by gravity (Alexander, 1989). This limit occurs when the ratio of these forces exceeds 1.0:

$$(M_b v^2 / L) / (M_b g) > 1, \quad (1)$$

where M_b is body mass, v is forward velocity, L is leg length, and g is gravitational acceleration. This (dimensionless) ratio reduces to (v^2/gL) and is commonly referred to as the Froude number (Alexander and Jayes, 1983). Although a Froude number of 1.0 predicts a theoretical maximal walking speed, animals naturally switch from a walk to a run (bipeds) or trot (quadrupeds) at Froude numbers well below one (Alexander and Jayes, 1983).

Central to the inverted-pendulum model of walking is the exchange of kinetic energy and gravitational potential energy (Cavagna et al., 1963). This exchange conserves mechanical energy by allowing forward motion to help raise the center of mass, thereby reducing muscular work. The extent to which this exchange occurs is, in part, limited by the amount of kinetic energy ($\propto M_b v^2$) available to convert into gravitational potential energy ($\propto M_b g L$). The ratio of these energies also reduces to the dimensionless Froude number. Therefore, the Froude number may link mechanical and metabolic energy-saving aspects of the inverted-pendulum mechanism across the walk–run and walk–trot transitions.

We hypothesized that quadrupeds switch from a walk to a trot at similar inverted-pendulum dynamics. We also hypothesized that quadrupeds would switch gaits at the metabolically optimal transition speed. To test these hypotheses, we studied nine adult horses spanning an eightfold range in mass and a twofold range in leg length. If horses switch gaits at the same Froude number, then given these size differences, we would expect the largest horse to switch from a walk to a trot at a speed that is 1.4 times faster than the smallest horse. We chose to study horses because they are experimentally tractable and they provided a large range of similarly shaped adult body sizes. Furthermore, by using an intra-specific size comparison, we hope to control for potential phylogenetic and morphological differences associated with inter-specific comparisons.

Materials and methods

Preliminary procedures

The Institutional Animal Care and Use Committees at U.C. Berkeley and C.S.P.U. Pomona approved the experimental methods and procedures. Data were collected from nine adult horses (*Equus caballus* L.) that ranged in body mass from 91 to 720 kg. We studied three horses for each of the three size groups: miniature horses (112±21 kg; mean ± s.d.), Arabian horses (448±22 kg) and draft horses (715±5 kg). Experiments were conducted on an equine treadmill (SÄTO I; SÄTO AB, Knivsta, Sweden). The horses quickly habituated to treadmill locomotion, and after approximately 10 training sessions over the course of two weeks we obtained consistent heart rate and stride-frequency recordings.

Morphological measurements

We performed an allometric analysis to determine whether the horses in our study were geometrically similar to one another. If different sized animals are geometrically similar, then their linear dimensions should be proportional to body mass to the $\frac{1}{3}$ power (Schmidt-Nielsen, 1984). We measured the trunk, fore limb and hind-limb lengths by palpation during quiet standing. Trunk length was measured as the cranial–caudal distance between the anterior aspect of the scapulo–humeral joint and the tuber ischii. Fore-limb length was measured in two ways: as the vertical distance between (1) the ground and the shoulder and (2) the ground and the dorsal edge of the scapula. The functional fore-limb length is probably intermediate to these two measurements because the scapula rotates during stance (Back et al., 1993). Hind-limb length was measured as the vertical distance between the ground and the greater trochanter of the femur. To estimate limb posture across body size, we calculated the relative hip (l_h) and shoulder (l_s) heights by dividing the height of the hip and shoulder joints above the ground by the sum of the segment lengths for the hind and fore limbs, respectively (Gatesy and Biewener, 1991).

We used reduced major-axis regression (model II; Sokal and Rohlf, 1995) to determine the scaling coefficient (a) and exponent (b) relating parameter length (Y) to body mass (M_b), where $Y = a M_b^b$ (Schmidt-Nielsen, 1984). The regression coefficients and confidence intervals were determined after logarithmic transformation of the data:

$$\log Y = \log a + b \log M_b. \quad (2)$$

The 95% confidence interval of the scaling coefficient (intercept, a) and exponent (slope, b) are presented along with the correlation coefficient, R . Horses were considered to be geometrically similar if the 95% confidence interval for the scaling exponent, b , included a value of 0.33.

Transition speed

The walk–trot transition speed was determined by changing speed in incremental steps and observing the horse’s gait. Transition speeds were measured prior to the measurement of

oxygen consumption. Horses began each treadmill session with a warm-up that consisted of moderate-speed walking for 2 min followed by another 2 min of moderate-speed trotting. We obtained a preliminary estimate of the walk–trot transition speed on an animal's first session by beginning at a moderate walking speed and steadily increasing the speed until the horse switched to a trot. To determine the transition speed more precisely we then adjusted the treadmill speed to 0.5 m s^{-1} slower than the estimated transition speed. Speed was increased in incremental steps (0.1 m s^{-1} steps every 1 min), and we observed the animal's gait. We defined the walk–trot transition speed as the slowest speed at which the horse trotted continuously for a minute. The treadmill speed was increased by another two steps to be sure that we identified the correct transition speed. We also noted the fastest speed at which the horse walked continuously for one minute so we could consider how alternative definitions of the transition speed would affect our conclusions. We repeated this process over a period of about two weeks for a total of 15 observations per horse.

Some investigators of the human walk–run transition have noted that the transition speed varies whether it is approached from faster (run to walk) or slower (walk to run) speeds (Diedrich and Warren, 1995; Hreljac, 1993b; Li and Hamill, 2002; Raynor et al., 2002). We measured the trot–walk transition speed in the Arabian horses and found that the trot–walk transition speed ($1.96 \pm 0.12 \text{ m s}^{-1}$; mean \pm S.D.) was numerically greater, but not statistically different, from the walk–trot transition speed ($1.91 \pm 0.14 \text{ m s}^{-1}$; $P=0.14$; two-tailed paired Student's *t*-test). A *post hoc* analysis of these data indicated that more than nine horses in each size class would be needed to have at least an 80% chance of detecting this difference to a significance level of $P<0.05$. Our sample size was limited for each size group so we did not further examine the trot–walk transition speed.

Oxygen consumption

The metabolically optimal walk–trot transition speed was determined by measuring the rate of oxygen consumption (\dot{V}_{O_2}) over a range of walking and trotting speeds, including trotting speeds that were slower than normally used. \dot{V}_{O_2} was measured with an open-flow system (Fedak et al., 1981). The system and methods used in this study have been described previously (Wickler et al., 2000). Briefly, animals wore a loose-fitting facemask, and air was drawn past the mask at $\sim 400\text{--}4700 \text{ l min}^{-1}$ depending on the animal's size and locomotor speed. Flow rates were calibrated at the end of each experimental session using the nitrogen flow technique (Fedak et al., 1981). Oxygen content from a sample of the gas exiting the mask was analyzed downstream of the flowmeter after CO_2 and water vapor were removed (FC-1B O_2 analyzer[®]; Sable Systems, Las Vegas, NV, USA). We used a commercial data-acquisition program (Datacan[®]; Sable Systems) to simultaneously record analog data from the O_2 analyzer, flowmeter and treadmill speed. All gases were corrected to STP

and \dot{V}_{O_2} ($\text{ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$) was calculated using equation 4b of Withers (1977):

$$\dot{V}_{\text{O}_2} = \frac{\dot{V}_E (F_{\text{I}\text{O}_2} - F'_{\text{E}\text{O}_2})}{1 - F_{\text{I}\text{O}_2} + \text{RQ} (F_{\text{I}\text{O}_2} - F'_{\text{E}\text{O}_2})}, \quad (3)$$

where \dot{V}_E is the rate of airflow out of the mask (STP), $F_{\text{I}\text{O}_2}$ is the fractional concentration of O_2 entering the mask, $F'_{\text{E}\text{O}_2}$ is the fractional concentration of O_2 leaving the mask after CO_2 has been removed and RQ is the respiratory quotient. A value of 0.8 was used for RQ. However, equation 3 is nearly independent of RQ because $1 - F_{\text{I}\text{O}_2}$ is much greater than $\text{RQ} (F_{\text{I}\text{O}_2} - F'_{\text{E}\text{O}_2})$. We then divided \dot{V}_{O_2} by the treadmill speed to obtain the cost of transport (i.e. oxygen consumed to travel a unit distance; $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$).

Animals were warmed-up on the treadmill prior to \dot{V}_{O_2} measurements by walking and trotting for 8–10 min. Steady-rate \dot{V}_{O_2} was measured during the last minute of 3–5 min bouts at the selected experimental speeds. This time period was sufficient to obtain steady-rate \dot{V}_{O_2} . The average \dot{V}_{O_2} during the last 60 s in the first 3 min was not significantly different from the lowest 2 min mean over a 15 min time period (Wickler et al., 2000). \dot{V}_{O_2} was collected at 4–5 speeds spaced between $\sim 0.5 \text{ m s}^{-1}$ and the fastest normal walking speed, and another 4–6 speeds between the slowest normal trotting speed and a fast trotting speed. We obtained additional walking and trotting \dot{V}_{O_2} data near the walk–trot transition by training the horses to extend their gaits beyond the speeds normally used for these gaits. No more than six trials were collected on any one sampling day to minimize potential fatigue effects and speeds were varied randomly. We collected two trials per speed condition for each horse and we averaged the \dot{V}_{O_2} from these trials.

We defined the optimal metabolic transition speed as the speed above which the walking cost of transport was more than trotting and below which the trotting cost of transport was more than walking. We calculated this speed for each animal by fitting separate 2nd order polynomial equations (Kaleidagraph[®] 3.0; Synergy Software, Reading, PA, USA) to the walking and trotting cost of transport *versus* speed data, and solving for the speed where the two curves intersected. However, for the miniature and draft horses, we were not able to obtain walking and trotting \dot{V}_{O_2} data at the same speeds in the transition zone, so we had to extrapolate the polynomial curve fits beyond the data. For the miniature horses, this involved extrapolating the walking and trotting curve fits by 0.13 m s^{-1} and 0.10 m s^{-1} , respectively (mean values). For the draft horses, this only involved extrapolating the walking curve fit (mean = 0.26 m s^{-1}).

To assess the potential errors of extrapolating the polynomial curves, we used the Arabian horse data to determine how excluding the data points for the extended walking speeds would affect the calculation of the optimal metabolic transition speed. We were able to train the Arabian horses to extend their walking gait to speeds faster than they would normally use for prolonged time periods by an average

of 0.20 m s^{-1} . If we excluded these data and relied on an extrapolated curve fit, we would have underpredicted the optimal metabolic transition speed by an average of 0.06 m s^{-1} . This value is small relative to the range of speeds in which horses spontaneously switch between walking and trotting ($0.28 \pm 0.07 \text{ m s}^{-1}$, mean \pm s.d.). Therefore, it is likely that extrapolating the curve fits beyond the data do not lead to substantial errors because the curve fits were only extrapolated by a small amount and the R^2 values of the walking curve fits were >0.96 .

Statistical analysis

We tested for statistical differences among the miniature, Arabian and draft horse values using one-way analysis of variance (ANOVA) (JMP[®], 4.0.2; SAS Institute, Cary, NC, USA). Horse groups were treated as ordinal categories, ordered by increasing body size. If a significant difference was found (i.e. $P < 0.05$), we then performed a Tukey–Kramer Honestly Significant Difference (HSD) test to determine which groups were significantly different from each other.

Results

Morphology

Trunk, fore-limb and hind-limb lengths scaled according to geometric similarity (Table 1). The allometric exponent for trunk length (0.33) matched the exponent predicted for geometric similarity and the mean limb-length scaling exponents (0.37) were not significantly different from 0.33. The correlation coefficients for these values were all ≥ 0.98 . To calculate the Froude number, it is necessary to estimate leg length (L). We used hind-limb length as this estimate. This is the traditional choice, and it seemed appropriate since hind-limb length was intermediate between our two measures of fore-limb length (Table 1). The relative hip and shoulder

heights were not significantly different across size, suggesting that limb posture was similar among all of the horses ($l_h = 0.85 \pm 0.05$, $l_s = 0.90 \pm 0.05$, mean \pm s.d.; one-way ANOVA $P = 0.87$ for l_h and $P = 0.10$ for l_s).

Walk–trot transition speed

Larger horses switched from a walk to a trot at faster absolute speeds, but all the horses switched gaits at approximately the same Froude number (Table 2; Fig. 1). The miniature horses switched from a walk to a trot at $1.63 \pm 0.10 \text{ m s}^{-1}$ (mean \pm s.d.), which corresponded to a Froude

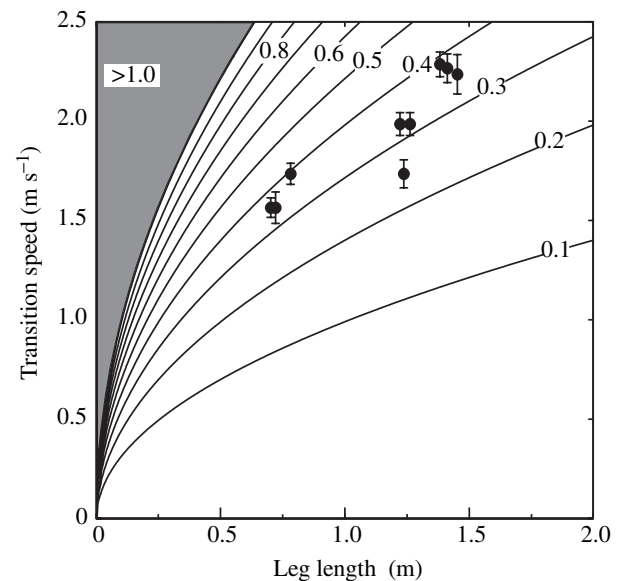


Fig. 1. Walk–trot transition speed (closed circles) versus leg length for different-sized horses. Isolines represent speed and leg length combinations for specific Froude numbers. The walk–trot transition occurs at faster absolute speeds in horses with longer legs but at nearly the same Froude number (0.35). Values are means \pm s.d.

Table 1. Allometric equation values for $Y = aM_b^b$ determined by reduced major axis regression where Y is parameter length (m) and M_b is body mass (kg) ($N = 9$)

Lengths (Y)	a	b	R
Trunk	0.19 (0.15–0.23)	0.33 (0.29–0.37)	0.99
Fore limb (ground–shoulder)	0.10 (0.07–0.14)	0.37 (0.31–0.43)	0.98
Fore limb (ground–dorsal scapula)	0.15 (0.12–0.19)	0.37 (0.33–0.41)	0.99
Hind limb (ground–hip)	0.12 (0.09–0.16)	0.37 (0.33–0.41)	0.99

The 95% confidence intervals are given in parentheses. Coefficient values (a) have been corrected for statistical bias due to log-transformation (Sprugl, 1983).

Table 2. Leg length and gait transition data for the three size groups of horses

	Miniature	Arabian	Draft	P -value
Leg length (m)	0.73 ± 0.04	1.24 ± 0.02	1.41 ± 0.04	< 0.001
W–T transition speed (m s^{-1})	1.63 ± 0.10	1.91 ± 0.14	2.27 ± 0.03	< 0.001
Froude no. at W–T transition	0.37 ± 0.02	0.30 ± 0.04	0.37 ± 0.02	0.055

Values are mean \pm s.d., $N = 3$ for each size group. P -value is for a one-way ANOVA. *Denotes a statistically significant difference between the two adjacent columns ($P < 0.05$; Tukey–Kramer HSD test).

number (v^2/gL) of 0.37 ± 0.02 . The next size group, the Arabian horses, switched gaits at $1.91\pm 0.14\text{ m s}^{-1}$ and a Froude number of 0.30 ± 0.04 . The largest horses, the draft horses, transitioned to a trotting gait at $2.27\pm 0.03\text{ m s}^{-1}$, corresponding to a Froude number of 0.37 ± 0.02 . Froude number at the walk–trot transition speed did not change across size ($P=0.87$, ANOVA) because the transition speed increased with the square root of limb length.

Oxygen consumption

The mass-specific oxygen consumed to travel a given

distance (i.e. the cost of transport) was least at moderate speeds within each gait and was greater for speeds near the walk–trot transition (Fig. 2). This pattern was similar for all the horses in our study. The optimal metabolic transition speed (i.e. the speed at which the cost of transport for walking intersected that for trotting) occurred at faster absolute speeds in the larger horses (miniature horses = $1.50\pm 0.04\text{ m s}^{-1}$, Arabian horses = $1.87\pm 0.09\text{ m s}^{-1}$ and draft horses = $2.16\pm 0.07\text{ m s}^{-1}$; mean \pm s.d.).

The optimal metabolic transition speeds corresponded closely to the observed transition speeds (Figs 2, 3). The

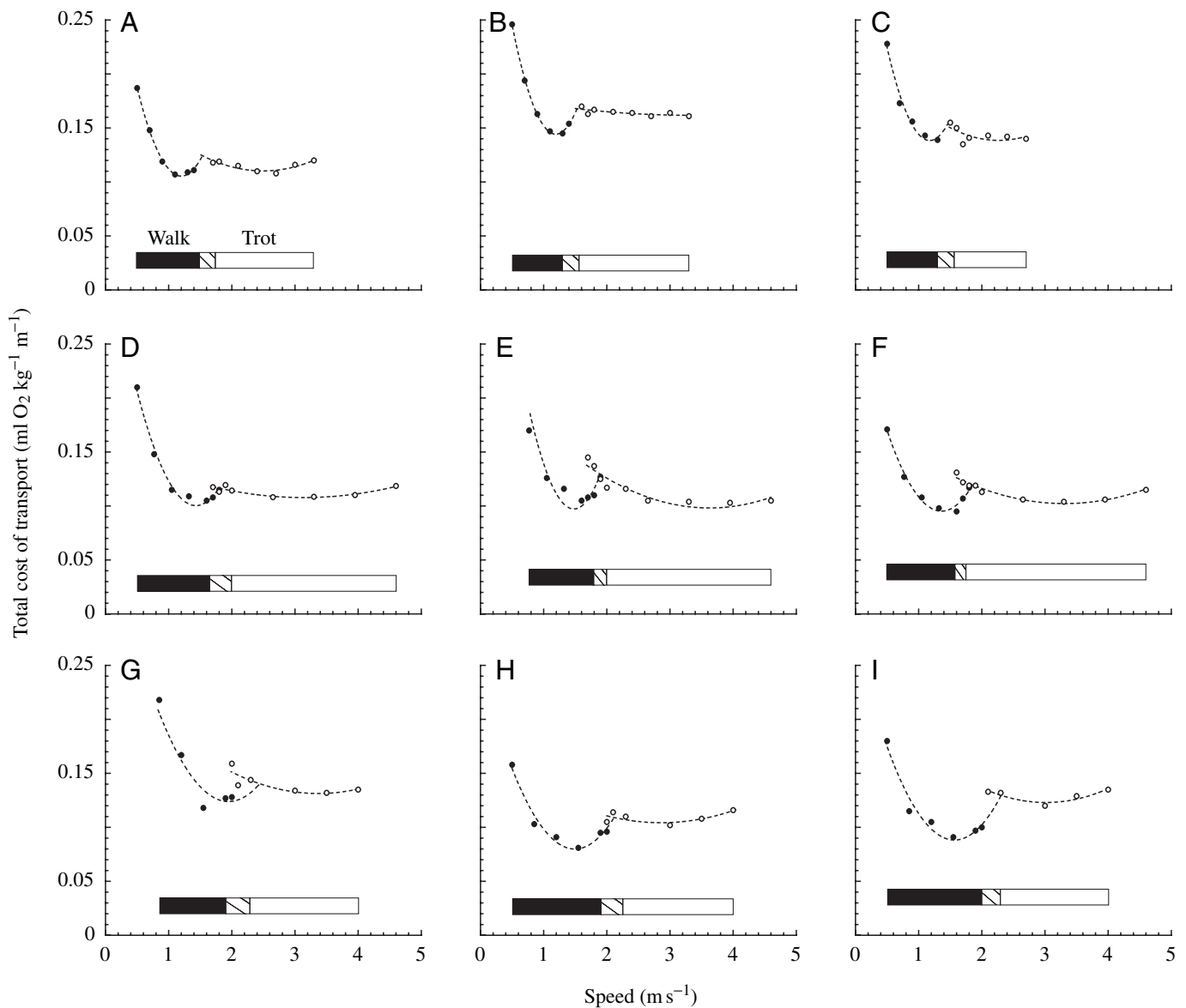


Fig. 2. Cost of transport for a range of walking and trotting speeds (closed and open circles, respectively). Data are shown for the miniature (A–C), Arabian (D–F) and draft (G–I) horses. Dashed lines are least-squares second-order polynomial curve fits. Bars indicate the observed gait used continuously by the horse during the transition speed measurements. Hatched bars indicate speed range where the horses switched gaits at least once during the 1 min observation period. Horses were then trained to use a prescribed gait for oxygen consumption measurements at speeds within the hatched bar region after the transition speed measurements were completed. However, we were not able to obtain walking and trotting \dot{V}_{O_2} data at the same speeds in the transition region for the miniature and draft horses. In these cases, the curve fits were extended beyond the data as shown to calculate the optimal metabolic transition speed.

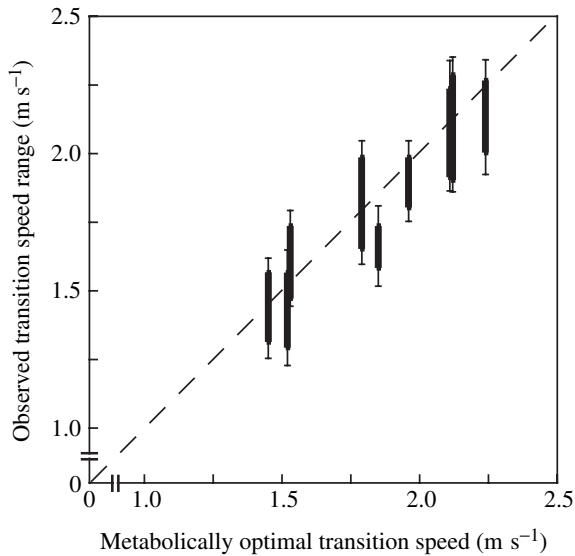


Fig. 3. Observed range of gait-transition speeds plotted against the metabolically optimal transition speed for the different-sized horses. Horses switched from a walk to a trot at speeds corresponding to the optimal metabolic transition speed (i.e. the speed at which the cost of transport for walking intersects that for trotting). The top of the bars are the slowest speeds that the horses trotted at for 1 min, and the bottom of the bars are the fastest speeds that the horses walked at continuously for 1 min. Therefore, the bars represent the observed range of speeds in which the horses spontaneously switched between walking and trotting. Top and bottom error bars are 1 S.D. Our method of extrapolating polynomial curve fits for several of the horses' data produces some error in determining the optimal metabolic transition speed. This error, however, is likely to be only about a quarter the magnitude of the observed transition speed range (i.e. the vertical bar). Dashed line is the line of identity.

slowest speed that the horses trotted at continuously for 1 min was slightly faster than the optimal metabolic transition speed, whereas the fastest speed that the horses walked at continuously for 1 min was slightly slower (Fig. 2). Horses spontaneously alternated between walking and trotting gaits within a small range of speeds ($0.28 \pm 0.07 \text{ m s}^{-1}$; mean \pm S.D. for all horses) – the optimal metabolic transition speed fell within this range (Fig. 3).

Discussion

The results support our hypotheses that mechanical and energetic factors determine the walk–trot transition. Different-sized horses switch from a walk to a trot at different absolute speeds but at the same ratio of inertial to gravitational forces (i.e. the same Froude number). This suggests that horses switch gaits at a speed determined by inverted-pendulum-like movements of the body as it vaults up and over relatively stiff support limbs. We also find that different-sized horses switch from a walk to a trot at the speed that optimizes metabolic economy. Horses spontaneously switch between walking and trotting over a small range of speeds, and the optimal metabolic

transition speed occurred within this speed range. Overall, the results suggest that both inverted-pendulum dynamics and metabolic energy expenditure are strongly coupled at the gait change.

Inverted-pendulum dynamics

Analysis of data from other studies supports the idea that the Froude number is an appropriate means of comparing inverted-pendulum dynamics in different-sized animals walking at different speeds. The traditional method of quantifying inverted-pendulum-like dynamics in walking animals is to calculate the percent of mechanical energy recovered *via* the exchange between kinetic and gravitational potential energies of the center of mass (Cavagna et al., 1977). In humans, percent recovery is similar at a given Froude number over a twofold variation in leg length (same as the horses in our study) and gravity levels (Fig. 4A; see also Saibene and Minetti, 2003). Although humans do not walk in a dynamically similar fashion at equal Froude numbers in simulated reduced gravity (Donelan and Kram, 1997), gravity does affect the speed at which humans prefer to change gaits. Kram et al. (1997) found that at lower levels of gravity, people switch from a walk to a run at progressively slower absolute speeds but at approximately the same Froude number.

Bipeds (i.e. humans and birds) transition from a walk to a run at a Froude number of about 0.5 (Alexander and Jayes, 1983; Gatesy, 1999; Hreljac, 1995b; Kram et al., 1997; Rubenson et al., 2004). Our results, as well as those from prior studies (Heglund and Taylor, 1988; Pennycuick, 1975), indicate that horses and other quadrupeds switch from a walk to a trot at lower Froude numbers than bipeds (~ 0.35). This difference in the relative gait-transition speeds between bipeds and quadrupeds may correspond to differences in inverted-pendulum dynamics (Griffin et al., 2004). In quadrupeds, percent recovery of mechanical energy decreases more precipitously at faster speeds (i.e. increasing Froude numbers) compared with bipeds (Fig. 4B). The traditional measure of percent recovery does not take into account the mechanical energy lost to the foot–ground collisions (Donelan et al., 2002). However, no alternative global measure of inverted-pendulum-like behavior has been proposed.

Intra- versus inter-specific size comparisons

We chose to use an intra-specific size comparison to control for potential phylogenetic and morphological differences associated with inter-specific comparisons. Although different sized species only deviate slightly from geometric similarity in terms of limb segment lengths (Alexander and Jayes, 1983), limb posture changes dramatically across size, with larger species using more upright limb postures (Biewener, 1989). However, by restricting our study to horses, we minimized body shape and limb posture differences across an eightfold range in body mass. This approach allowed us to better isolate the effects of leg length on the walk–trot transition speed.

Our intra-specific approach may also provide unique insight into the determinants of the metabolic cost of locomotion. In

different species, the metabolic energy required to move a unit body mass a unit distance decreases in larger animals (Full and Tu, 1991; Taylor et al., 1982). For example, an elephant uses ~1/40 the energy to carry 1 g of its body weight for 1 m compared with that of a mouse (Langman et al., 1995). This difference in metabolic economy across size can be explained

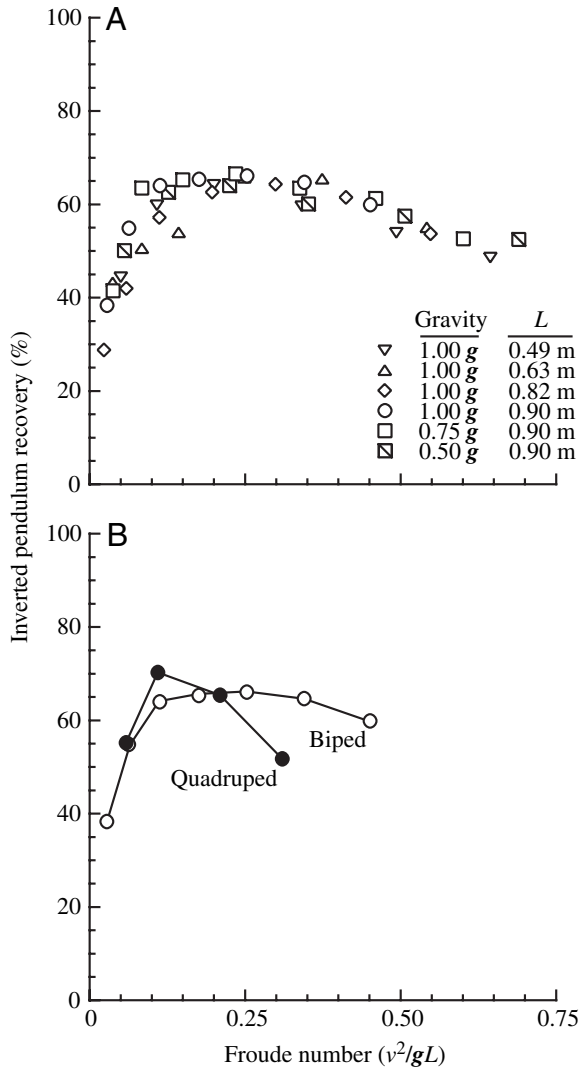


Fig. 4. (A) Percent recovery of mechanical energy via the inverted-pendulum-like mechanism in walking as a function of the dimensionless Froude number. Data from the literature are presented for children and adults walking at a range of speeds in normal gravity, and for adults walking at a range of speeds in simulated reduced gravity. Percent recovery is similar at equal Froude numbers, suggesting that at equal Froude numbers the inverted-pendulum dynamics are mechanically equivalent. Child data from Cavagna et al. (1983) for 3–4, 7–8 and 11–12-year olds. Adult and reduced gravity data from Griffin et al. (1999). (B) Percent recovery for a biped (humans) and quadruped (dogs) versus Froude number for a range of walking speeds. Percent recovery decreases more precipitously at faster speeds for the quadruped compared with the biped at similar Froude numbers. Quadruped data are from Griffin et al. (2004), and biped data are for adults walking in normal gravity from Griffin et al. (1999).

by the volume of active muscle required to support body weight and the rate of activating this volume (Kram and Taylor, 1990; Roberts et al., 1998; Taylor, 1994). The volume of active muscle required to support a unit of body weight appears to be similar across size (Biewener, 1989). Therefore, the primary reason that larger animals are more economical is because their longer legs allow them to generate muscular force more slowly, which uses slower, less expensive muscle fibers (Kram and Taylor, 1990).

We find, however, that across an eightfold size range in horses, metabolic economy remains unchanged (Fig. 5). This finding may be due to the consistent limb posture among different-sized horses. If the muscular dimensions of horses are geometrically similar like their body dimensions, then muscle stress would increase with size ($\propto M_b^{0.33}$), where muscle stress = force ($\propto M_b^{1.00}$) / area ($\propto M_b^{0.67}$), and larger horses would require a larger volume of active muscle to support a unit of body weight compared with smaller horses. This differs from the inter-specific case in which muscle stress is nearly independent of body size because the more upright limb posture of larger animals decreases the muscle force required to support a unit of body weight. Therefore, within horses, the metabolic savings associated with longer leg lengths and slower rates of generating force may simply act to offset the relatively greater volume of active muscle in larger horses.

We recognize that the large size range of horses obtained in this study is the result of selective breeding rather than natural variation. However, the ancestors of modern horses exhibited

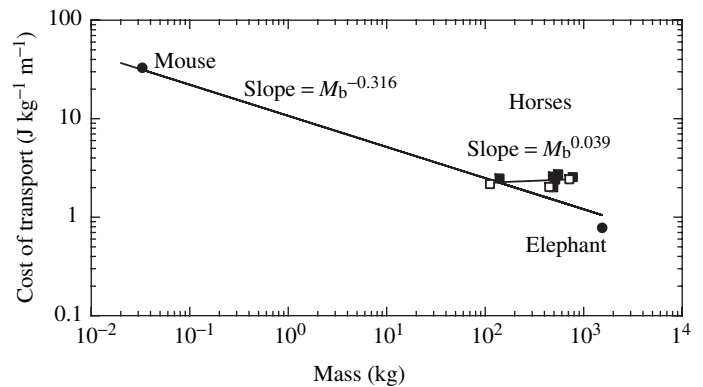


Fig. 5. Cost of transport ($J kg^{-1} m^{-1}$) decreases with body mass among >90 different species of birds and mammals (Langman et al., 1995; Taylor et al., 1982) but does not change with body mass within horses. For clarity, only the mouse and elephant data points are shown for the inter-specific relationship, although the line is derived from data representing >90 species. Open squares are mean values for each size range of horses from the present study and closed squares are mean values from the literature ($N=3$, Hoyt and Taylor, 1981; $N=5$, Eaton et al., 1995; $N=4$, Minetti et al., 1999; $N=4$, Pagan and Hintz, 1986; $N=7$, Potard et al., 1998). The cost of transport was calculated as the linear slope of the rate of oxygen consumption versus trotting speed for horses. We assumed an energetic equivalent of $20.1 J ml^{-1} O_2$. The scaling relationship for the horse data was calculated using a least-squares linear regression, following Taylor et al. (1982). The 95% confidence limits of the exponent for the horse line are ± 0.138 .

significant natural plasticity in body size. Throughout the ~57 million year history of horses, the body size of fossil equids ranged from approximately 25–500 kg, with a number of species lineages evolving dwarfism (MacFadden, 1986). This suggests that the size range of horses used in our study is not unnatural. Given that the cost of transport does not change across body size within modern horses, locomotor economy seems unlikely to have driven the selection for greater or smaller body size in the ancestral lineage of modern horses. However, other factors could have influenced the metabolic cost of locomotion. For example, ~12 million years ago, the first equid clade developed a medial trochlear ridge of the femur (Hermanson and MacFadden, 1996). This ridge, which was retained in all subsequent clades, facilitates passive locking of the knee joint while standing (Hermanson and MacFadden, 1996) and may also provide greater mechanical advantage for the knee extensor muscles during locomotion (Kappelman, 1988).

Determinants of gait transitions

Seminal studies by Margaria (1938), and Hoyt and Taylor (1981), showed that humans and horses naturally use gaits that require the least amount of metabolic energy to travel a given distance. These findings suggested that animals switch gaits at speeds that minimize the metabolic cost of locomotion. Yet it is difficult to imagine how the body senses these metabolic measures over a time course that is as rapid as the observed gait transitions; rather, biomechanical factors may provide cues that are more rapidly sensed. Farley and Taylor (1991) found that musculoskeletal force level, not metabolic energy minimization, triggered the trot–gallop transition in ponies. Recent data, however, indicate that the maximum sustained trotting speed is not statistically different from the metabolically optimal transition speed in Arabian horses (Wickler et al., 2003). Within humans, studies provide conflicting reports as to the role of metabolic and mechanical factors in determining the walk–run transition (Hreljac, 1993b; Kram et al., 1997; Mercier et al., 1994; Minetti et al., 1994; Raynor et al., 2002). Some of these differences appear to be due to different methods of determining the gait transition.

Most gait transition studies search for a specific trigger, often metabolic or biomechanical in nature, that controls gait choice. Diedrich and Warren (1995, 1998a, 1998b) proposed an alternative theoretical approach to analyze gait transitions based on dynamic systems analysis. This approach views gaits as complex systems that self-organize around the system's natural dynamics. Gait transitions occur when the stability of the current system dynamics decreases so much that switching to a new system (i.e. gait) improves stability. In this approach, metabolic energy is used as a surrogate for the stability of the underlying dynamics, but it is not considered a trigger *per se*.

Our results are consistent both with traditional 'trigger' and with dynamic systems approaches. The different-sized horses switched gaits at different absolute speeds but at the same Froude number. This suggests that horses switched gaits at

speeds that produced similar pendular dynamics. Because horses switched gaits at a Froude number less than that observed in bipeds (0.35 *versus* 0.5) suggests that the Froude number is adjusted to the particular system rather than being a preset critical value. Furthermore, the walk–trot and walk–run transitions represent a critical transition between the stability of pendular *versus* spring-based systems (Diedrich and Warren, 1998b). Dynamic systems theory predicts that spending extended periods of time at speeds in the transition region will decrease strong hysteresis effects and result in spontaneous shifts between gaits. Our findings are consistent with these predictions: the hysteresis for the walk–trot and trot–walk transition speed is minor, and horses spontaneously switch between gaits around the metabolically optimal transition speed.

Conclusions

We examined the walk–trot transition in horses spanning a twofold range in leg length and eightfold range in body mass to test the hypotheses that quadrupeds switch gaits at similar inverted-pendulum dynamics, and at the speed that maximizes metabolic economy. Larger horses switched from a walk to a trot at faster absolute speeds but at the same mechanically equivalent speed (i.e. a Froude number of 0.35). In addition, horses spontaneously switched between gaits in a small region of speeds that corresponded to the metabolically optimal transition speed. These results indicate that biomechanical and metabolic factors are tightly coupled at the walk–trot transition. These findings are consistent with the interpretation that the walk–trot transition is triggered by the dynamics of an inverted-pendulum system. However, an alternative interpretation, that horses switch gaits at a critical transition between inverted-pendulum- and spring-based system dynamics, may better explain why horses switch gaits at a particular dimensionless speed well below the theoretical limit of 1.0.

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