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The energetics of the trot–gallop transition

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Summary

Two studies have focused on potential triggers for the trot–gallop transition in the horse. One study concluded that the transition was triggered by metabolic economy. The second study found that it was not metabolic factors but, rather, peak musculoskeletal forces that determine gait transition speeds. In theory, peak musculoskeletal forces should be the same when trotting up an incline as when trotting at the same speed on the level. Assuming this is the case, we hypothesized that if peak forces determine gait transition speeds then horses should switch from a trot to a gallop at the same speed (i.e. the same critical force) regardless of incline. The aim of the present research was to examine the effects of incline on the trot–gallop transition speed in horses and to re-examine the role of metabolism in determining the trot–gallop transition. Horses (*Equus caballus*) were conditioned to run on a high-speed treadmill prior to data collection. Gait changes were recorded for each horse using a standardized testing protocol on the level and when trotting up a 10% incline. Both maximum sustained trotting speeds and minimum sustained galloping speeds, representing the lower and upper limits of the trot–gallop transition, respectively, were significantly slower when trotting up an incline. After completing collection of gait transition data, the horses were trained to extend their gaits beyond the normal transition speeds, and metabolic data were collected. Maximum sustained trotting speeds were not different from the energetically optimal transition speeds, i.e. the speed at which metabolic rates are the same for both gaits.

Key words: equine, horse, *Equus caballus*, oxygen consumption, time of contact, trot–gallop transition, gait.

Introduction

One of the most obvious locomotory behaviors is gait transition (changing from walk to trot/run and changing from trot to gallop). There have been numerous attempts to explain gait transitions. These include considerations of muscle function (Taylor, 1978, 1985) and bone strain (Biewener and Taylor, 1986; Rubin and Lanyon, 1982), theoretical explanations based on mathematical models (Alexander, 1989; Alexander and Jayes, 1983), psychological factors (Diedrich and Warren, 1995) and engineering models (Schoner et al., 1990; Vilensky et al., 1991).

The walk–trot and trot–gallop gait transitions were originally explained on the basis of metabolic economy (Hoyt and Taylor, 1981). In ponies (*Equus caballus*), metabolism increased curvilinearly for walking and trotting, and the gait transitions occurred at the speeds where the metabolism curves intersected. This is referred to as the 'energetically optimal transition speed' (EOTS; Hreljac, 1993) because, when the animals extended their gaits beyond the normal transition speeds, the metabolic rate was higher in the extended gait than in the normal gait. Hoyt and Taylor concluded that ponies changed gaits to minimize energetic costs. However, one limitation of this study was that gait transition speeds were not rigorously determined.

Subsequently, this explanation was challenged by the 'force trigger' hypothesis. Farley and Taylor (1991) showed that the transition from trotting to galloping in ponies is correlated with musculoskeletal forces by demonstrating that the transition occurs at a slower speed when a pony carries a load. Measurements of oxygen consumption (again observed to be a curvilinear function of speed) indicated that the ponies were making the transition to a gallop at speeds where it is energetically more expensive to gallop than to trot – at speeds slower than the EOTS. In some studies, the walk–run transition in humans occurs at the EOTS (Mercier et al., 1994; Diedrich and Warren, 1995) and in others it does not (Hreljac, 1993; Minetti et al., 1994a,b). Hreljac (1993) ruled out muscle stress as the trigger for the walk–run transition in humans and suggested that the trigger is kinematic (Hreljac, 1995).

In a study of horses and preferred speed (Wickler et al., 2000), the energetics of trotting were measured on the level and up a 10% incline. In the preliminary portion of this study, we determined the speeds at which the horses would trot. We noted that, when trotting up an incline, the horses made the transition to a gallop at a slower speed than they would when on the level. Because forces are not expected to be higher when trotting up an incline (Roberts et al., 1997), this observation appeared to be inconsistent with the force trigger hypothesis. In the present study, we revisited the energetics of the trot–gallop transition and, based on the earlier work of Hoyt and Taylor (1981), hypothesized that horses would make the transition at the energetically optimal speed. Our second hypothesis was that, when trotting up an incline, horses would also make the transition at the energetically optimal transition speed. Thirdly, we hypothesized that, when trotting up an incline, the EOTS would be a slower speed than on the level.

The majority of the cost of running gaits can be explained by the rate that force must be applied during the support phase of the stride cycle (Kram and Taylor, 1990). Kram and Taylor's study reports that the metabolic rate when locomoting is inversely proportional to the time of contact (the length of time the foot is in contact with the ground): the shorter the time of contact, the greater the metabolic cost. Given these observations, we measured time of contact and stride frequency to determine how these change at the trot–gallop transition.

Materials and methods

Animals

Seven horses (*Equus caballus* L.; four Arabians, two Thoroughbreds and one Quarter Horse cross), with a mean (±S.D.) age of 7.8±3.4 years and a mean mass of 467±68 kg were conditioned on a high-speed treadmill (SÄTO I; SÄTO AB, Knivsta, Sweden) for a period of 9–12 months prior to data collection. Two horses were removed from the metabolism portion of the study because of a lameness that occurred after gait transition speeds had been determined.

Gait transition speeds

Horses were warmed up on the treadmill for a minimum of 8 min (3 min of walking and 5 min of trotting at 3.5 m s^{-1}). Speeds were then either increased from 3.75 m s^{-1} or decreased from 6.75 m s^{-1}. The result was that, at the beginning of a transition speed trial, all the horses were either trotting (increasing speed) or galloping (decreasing speed). The speed was then changed in 0.25 m s^{-1} increments and held for 1 min. The gait or number of gait transitions was recorded for each speed. It soon became obvious that there was a range of speeds where the animals switched repeatedly between gaits; below this range of speeds they trotted consistently, and at faster speeds they galloped consistently. Thus, two transition speeds were defined: the maximum sustained trotting speed was the fastest speed at which the horse trotted continuously for 1 min, and the minimum sustained galloping speed was the slowest speed at which the horse galloped continuously for 1 min. It should be emphasized that these terms, maximum sustained trotting speed and minimum sustained galloping speed, are defined as the speeds at which a horse normally exhibits these behaviors because, subsequently, we trained our horses to extend their gaits beyond these speeds (e.g. to gallop for several minutes at speeds below minimum sustained galloping speed). This procedure for determining maximum sustained trotting speed and minimum sustained galloping speed was followed for horses on the treadmill on the level or with the treadmill inclined 10% (inclination calibrated with a transit). The condition (level or incline) and the direction of speed change (increasing or decreasing) were randomized on different days.

Extended gaits

After the data for gait transition speeds had been collected and analyzed, horses were trained to extend their gait: to trot consistently at speeds 0.5 m s^{-1} faster than the minimum sustained galloping speed and to gallop at speeds 1.0 m s^{-1} below the maximum sustained trotting speed. This procedure involved using voice and visual cues or gentle pressure on the animal's halter to either maintain the gait or to switch. Only positive reward was used to train the horses.

Oxygen consumption

After the training to extend the horses' gaits, metabolic measurements were made using techniques described previously (Wickler et al., 2000). Briefly, an open-flow system was used with flow continuously monitored during metabolism trials and calibrated at the end of each day using a nitrogen dilution technique. Tread speed was measured optically using a sensor to detect rotation of the non-drive axle. The tread speed was checked every week by timing a minimum of 10 tread revolutions, with the horse on the treadmill.

Speeds (in 0.25 m s^{-1} increments between 3.75 m s^{-1} and 6.75 m s^{-1}) and conditions (level or incline) were all randomized. A maximum of three speeds were run per day. The initial gait that the horse would maintain was determined at random for each speed, and the rate of oxygen consumption ($\dot{V}_{O_2}$) was measured for 3 min. After 3 min, the horse was instructed to change gaits and metabolic rate was measured for another 3-min period without changing tread speed. Before metabolic measurements were made at the next speed and condition, the horses walked for 5 min. Calculations of oxygen consumption were made from the average of the last minute (a total of 12 points), because 2 min is a sufficient time to reach steady-state rate of oxygen consumption in horses at these speeds (Wickler et al., 2000, 2001).

Stride parameters

In a separate series of experiments, accelerometers (model # CXL25M1; Crossbow Technology, San Jose, CA, USA; ±25 ***g***) were taped to the lateral aspect of each hoof, and horses were run on the treadmill at speeds around the transition speeds to determine how stride frequency and time of contact changed with gait transition. To facilitate statistical analysis of these data, the speeds studied were defined relative to the minimum sustained galloping speed because this was the speed defined as the trot–gallop transition speed by Farley and Taylor (1991). This was necessary because the transition speeds varied by almost 1 m s^{-1} among animals. Accelerometry trials (Hoyt et al., 2000) were run at the minimum sustained galloping speed,

Table 1. *Speed data for horses on the level and up a 10% incline*

	Level			Incline		
Horse	EOTS	T_{max}	G_{min}	EOTS	T_{max}	G_{min}
Anakin	4.96	5.24±0.49 (7)	5.81±0.38 (7)	NA	4.75±0.14 (7)	5.25±0.14 (8)
Austin	5.47	5.17±0.33 (13)	6.30±0.32 (17)	4.72	4.47±0.33 (11)	5.27±0.43 (17)
GT	5.48	5.56±0.35 (15)	6.10±0.42 (12)	4.39	5.14±0.40 (13)	5.62±0.42 (12)
Red	5.12	4.92±0.39 (26)	5.32±0.41 (28)	4.45	4.03±0.39 (32)	4.55±0.35 (30)
Reign	4.50	4.50±0.20 (13)	5.34±0.39 (18)	4.17	3.94±0.26 (14)	4.67±0.40 (14)
Charlie	NA	4.56±0.37 (16)	4.97±0.41 (16)	NA	3.94±0.29 (15)	4.31±0.33 (15)
Mikey	NA	5.69±0.39 (16)	6.16±0.37 (16)	NA	4.78±0.41 (19)	5.16±0.34 (21)
Mean	5.11±0.41[a]	5.09±0.46[a]	5.71±0.51[b]	4.43±0.23[c]	4.44±0.48[c]	4.98±0.47[d]

Speed data (m s^{-1}) are expressed as means ± S.D. *N* is given in parentheses after each value.

The speed at which the metabolic rate for trotting was equal to galloping [the energetically optimal transition speed (EOTS)] was not different to the fastest speed at which the horse would trot continuously for 1 min without switching to a gallop [maximum sustained trotting speed (T_{max})]. The EOTS was less (P<0.05; indicated by different superscript letters) than the lowest speed at which the horse would gallop continuously for 1 min without switching to the trot [minimum sustained galloping speed (G_{min})]. On an incline, the speed at the EOTS decreased when compared with the speed on the level (P<0.05; indicated by different superscript letters) as did both the T_{max} and the G_{min}. The EOTS on the incline was lower than the G_{min}. 'NA' means not available. For the EOTS of Anakin on the incline, the regression lines for trotting and galloping did not cross, hence there is no speed for which metabolism at the trot equals that at the gallop. Both Mikey and Charlie became lame before metabolic measurements could be made.

0.5 m s^{-1} faster and slower than this speed, and 1.0 m s^{-1} below this speed for each individual horse. For each trial, the horse was brought to speed for 45 s, and then a 15-s recording was made (Labview®; National Instruments, Austin, TX, USA; sampling at 4000 Hz). The horse was then instructed to change gaits and another 15-s recording was made after 45 s at the new gait. Speeds, conditions (level or incline) and the sequence of gaits were randomized. Stride frequencies and contact times for each speed and condition were averaged over 10 strides. Time of contact of each individual limb was determined from the accelerometer record. Because the time of contact of the fore and hindlimbs in trotting horses differ (S. J. Wickler, D. F. Hoyt, E. A. Cogger and G. Myers, unpublished data), we calculated the mean of one pair of contralateral fore and hindlimbs. In galloping horses, the time of contact of all four limbs differed (S. J. Wickler, D. F. Hoyt, E. A. Cogger and G. Myers, unpublished data), so we calculated the mean time of contact for all four limbs. These are the same methods used by Kram and Taylor (1990). The points from the accelerometry records chosen for contact and heel lift were validated using a force plate (9287BA; Kistler, Winterhur, Switzerland; 600 mm×900 mm). For these validation trials, a portable computer (MS-4002; Maxwell Microsystems, Inc., Denver, CO, USA) mounted on a pack frame (total mass, approximately 28 kg) carried by the horse sampled accelerometry data while the horses were trotted over the force plate. Accelerometer records for both the fore and hindlimbs were validated.

Data analysis

Gait transition speeds, maximum sustained trotting speed and minimum sustained galloping speed, on the level and on the incline, were analyzed using a repeated-measures analysis of variance (ANOVA) of mean values from each horse to determine the effects of three variables: gait (trot or gallop), direction of speed change on the treadmill (increasing or decreasing) and slope of the treadmill (level or inclined 10%).

Data for $\dot{V}_{O_2}$ *versus* speed were also analyzed using an analysis of covariance (ANCOVA; with speed as the covariate) to test if there was an effect of gait (Statview® v.5.0; SAS Institute, Cary, NC, USA). In each instance in which there was a difference with gait, the relationship between $\dot{V}_{O_2}$ and speed was tested with step-wise regression analysis (Statview®) to determine the best-fit relationship. For each animal and condition, the energetically optimal transition speed (EOTS), the speed where metabolism at a trot equaled that at a gallop, was determined from the intersection of the regression equations. The EOTSs were compared with the maximum sustained trotting speed and the minimum sustained galloping speed using paired *t*-tests. When no difference was found between the EOTS and the maximum sustained trotting speed, a simple, linear regression analysis between them was performed to see if they were correlated.

Stride frequency and time of contact data were analyzed by a two-way, repeated-measures ANOVA with gait, condition (level and incline) and speed as the independent variables. A means separation comparison test was used to test for the effect of gait at different speeds. Significance was set at P<0.05 for all analyses.

Results

There was no significant effect of increasing or decreasing speed on the transition speeds (P=0.897; power=0.055), so values for increasing and decreasing speeds were combined. On the level (Table 1), the mean minimum sustained galloping

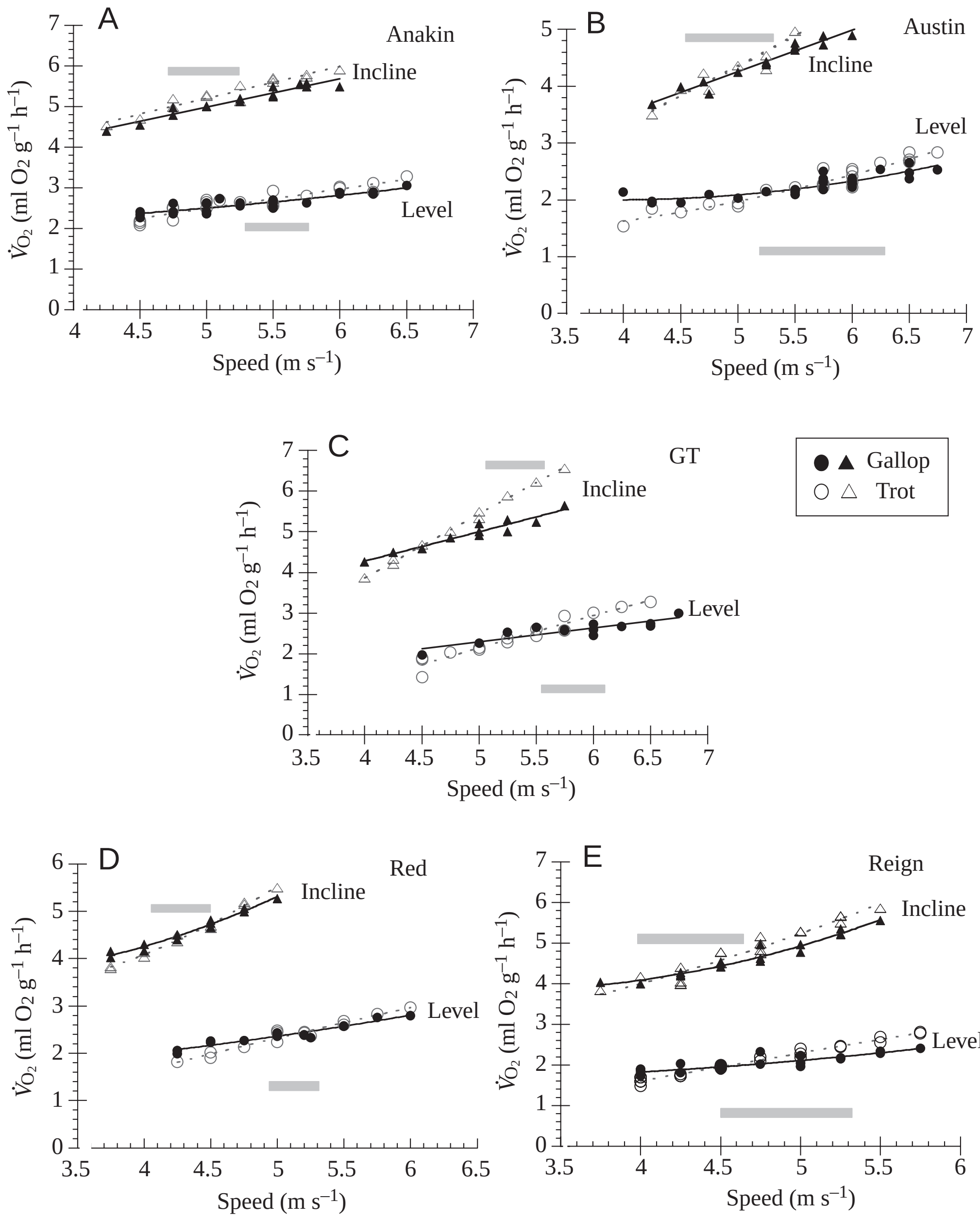

Fig. 1. Metabolism *versus* speed plots for individual horses. Trotting values (open symbols) and galloping values (filled symbols) on the level (circles) and up a 10% incline (triangles). The horizontal gray bars represent the range of transition speeds from the maximum sustained trotting speed (left end of the bars) to the minimum sustained galloping speed (right end) on the level and on the incline. The energetically optimal transition speed (EOTS) occurs where the lines for trotting and galloping intersect. In all cases, the minimum sustained galloping speed was faster than the EOTS.

speed was 0.62 $m\,s^{-1}$ faster than the mean maximum sustained trotting speed ($P<0.001$, $N=7$). On the incline, there was a similar difference between the mean minimum sustained galloping speed and the mean maximum sustained trotting speed (difference=0.54 $m\,s^{-1}$; $P<0.001$, $N=7$). Both the minimum sustained galloping speed and the maximum sustained trotting speed were decreased on the incline [minimum sustained galloping speed decreased by 0.73 $m\,s^{-1}$ ($P<0.0001$), and maximum sustained galloping speed decreased by 0.65 $m\,s^{-1}$ ($P<0.0001$)].

For each horse at each condition (level and incline), the relationship between metabolic rate and speed was different for trotting and galloping. The slope for the regression line (Fig. 1) for trotting was larger than for galloping (with the exception of the horse Anakin on the incline).

In the group of five horses for which all the necessary data have been determined on the level, the mean minimum sustained galloping speed was 0.63 $m\,s^{-1}$ greater ($P=0.010$) than the EOTS. Similarly, an unpaired *t*-test of the data on an incline (required because EOTS was not determined on an incline for one of the five horses) showed that the minimum sustained galloping speed was also 0.63 $m\,s^{-1}$ greater ($P=0.032$) than the EOTS. Therefore, under both conditions, at the minimum sustained galloping speed on the level (the speed used by Farley and Taylor, 1991) the metabolic rate when galloping was lower than when trotting. There was no difference in the EOTS and the maximum sustained trotting speed on the level (difference = 0.07; $P=0.597$) or on the incline (difference = –0.03; $P=0.912$). A regression analysis of maximum sustained trotting speed *versus* EOTS indicated that

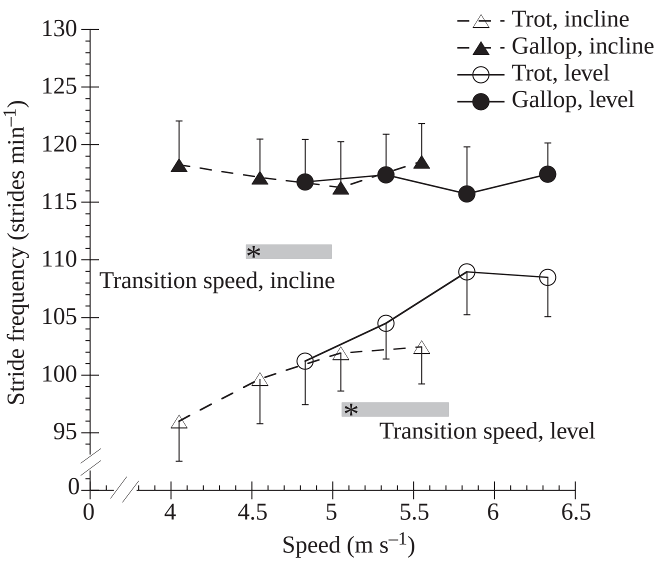

Fig. 2. Stride frequency increased with speed at the trot (open symbols and solid line) on both the level (circle) and incline (triangle and broken line) but was independent of speed at the gallop (solid symbols) on the level (circle) and incline (triangle and broken line). The transition speeds are denoted for incline and level running by a gray bar. The left side of the bar represents the fastest speed at which the horses would trot (the maximum sustained trotting speed) for a 1-min period, and the right side of the bar represents the lowest speed at which the horses would gallop for a 1-min period (the minimum sustained galloping speed). The energetically optimal transition speed (EOTS) is denoted by an asterisk with the gray bar. Values are means ± 1 S.D.

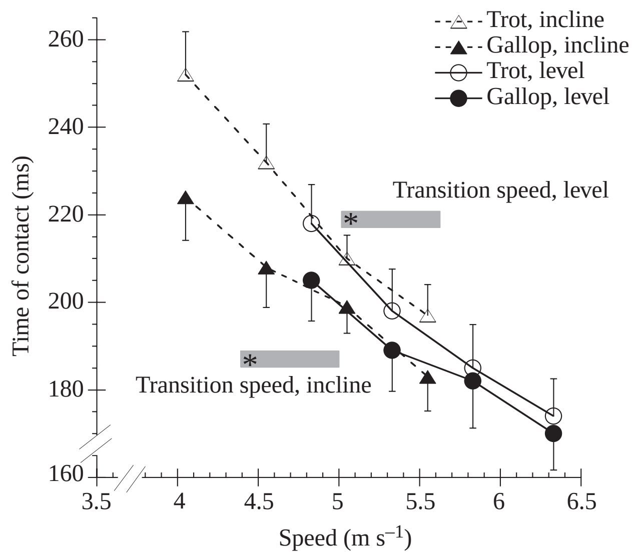

Fig. 3. Time of contact (in ms) decreased with speed at the trot (open symbols) for both the level (circle) and incline (triangle and broken lines). The transition speeds are denoted for incline and level running by a gray bar. The left side of the bar represents the fastest speed at which the horses would trot for a 1-min period, and the right side of the bar represents the lowest speed at which the horses would gallop for a 1-min period. The energetically optimal transition speed (EOTS) is denoted by an asterisk with the gray bar. Values are means ± 1 S.D.

there was a strong correlation (r^2=0.60, P=0.014) and that the slope (0.93) was not different from 1.

On the level, stride frequency (Fig. 2) increased linearly with speed in trotting horses up to the minimum sustained galloping speed. At faster speeds, there was no further increase in stride frequency (P=0.950; power = 0.0531). When a horse made a transition to the gallop, stride frequencies increased by approximately 7% (P=0.0008). Over the limited range of speeds measured in this study, galloping stride frequency was independent of speed (P=0.816; power = 0.0502). The striking difference on the incline was that trotting stride frequencies became constant at a slower speed and frequency than on the level. As on the level, when horses made a transition to the gallop on the incline, stride frequencies increased (approximately 14%). Because the transition occurred at a slower speed on the incline, the increase in stride frequency between trotting and galloping was greater than on the level (14% *versus* 7%).

The time that the hoof is in contact with the ground (t_c; Fig. 3) decreased with increasing speed. On the level, there were no differences in the t_c between trotting and galloping for the limited range of overlapping speeds (P=0.69 and power = 0.2134 for the lowest speed, and P=0.53 and power = 0.1356 for the next higher speed). On the incline, t_c was also not different from that on the level over the range of speeds measured. However, t_c was shorter at a gallop than at a trot on the incline (P=0.0095 for 4.5 m s^{-1} and P=0.003 for 4.0 m s^{-1}).

Discussion

During the initial portion of the study, it became evident that there was not a single transition speed. For each animal, there was a range of speeds where it would switch back and forth between gaits. As a consequence, we have identified two transition speeds: (1) the fastest speed at which they would continuously trot for one minute (maximum sustained trotting speed) and (2) the lowest speed at which they would continuously gallop for one minute (minimum sustained galloping speed).

The results of the present study are consistent with those of Hoyt and Taylor (1981) but lead to the opposite conclusion to those of Farley and Taylor (1991) regarding the metabolic consequences of the trot–gallop transition. The energetically optimal transition speed (EOTS), the speed where metabolic costs were identical for the trot and gallop, always occurred near the range of speeds at which the horses switched back and forth between gaits. The maximum sustained trotting speed was not different from the EOTS (Table 1) and, in fact, was correlated. The minimum sustained galloping speed was always faster than the EOTS. Farley and Taylor (1991) defined the trot–gallop transition as the lowest speed at which their ponies would gallop for one minute (equivalent to our minimum sustained galloping speed) and reported that this speed was slower than the EOTS. This led them to conclude that the animals made the transition from trot to gallop in spite of the fact that the gallop was less economical than the trot. At the minimum sustained galloping speed in our study, the gallop was more economical than the trot.

When the treadmill was inclined 10%, there was a 13% decrease in transition speed. This was true for both maximum sustained trotting speed and minimum sustained galloping speed. Metabolism increased substantially on the incline as expected (Eaton et al., 1995; Wickler et al., 2000); however, the EOTS decreased on the incline. As on the level, the EOTS was significantly slower than the minimum sustained galloping speed and not different from the maximum sustained trotting speed. Hence, when moving up an incline, the horses chose the gait that was metabolically the most economical.

The discrepancy between the present study and Farley and Taylor's is puzzling. One difference was in the breed studied and the correlated substantial differences in mass (140 kg for the ponies) and perhaps differences in behavior that may have influenced the gait transition trigger. Another difference in the methodology was the paradigm for changing treadmill speed. In the study by Farley and Taylor, treadmill speed was changed continuously at 0.33 m s^{-1} every minute and then held constant for one minute after the pony changed gait. If the animal switched gait again, treadmill speed was again continuously increased until another gait change occurred. In our study, we rapidly changed speed in 0.25 m s^{-1} increments and then held it constant for one minute and recorded what gait(s) the horses used. These small differences in our methods were ones we could identify, but it seems unlikely that they can account for the very different results.

There are also conflicting conclusions about the metabolic consequences of the walk–run transition, although walking is fundamentally different from either trotting or galloping. Mercier et al. (1994) found that humans made the transition from the walk to the run at the EOTS. However, in other human studies, the trigger to switch from the walk to the run does not appear to be metabolic minimization (Brisswalter and Mottet, 1996; Hreljac, 1993; Minetti et al., 1994a,b). These studies identified other possible triggers: the maximal angle in the limbs (Grillner et al., 1979), increases in internal work (Minetti et al., 1994b) or the maximal angular velocity of the ankle (Hreljac, 1995). It has also been suggested that the trigger is a function of the dynamics of an inverted-pendulum system that characterizes the walk (Kram et al., 1997).

Forces acting on the bones have been identified as a potential trigger for the trot–gallop transition in several studies. *In vivo* recordings of bone strain from the radius and tibia of goats showed a marked decrease when the animals made a transition from the trot to the gallop (Biewener and Taylor, 1986). These results were consistent with similar observations made in the dog (Rubin and Lanyon, 1982) and the horse (Biewener et al., 1983). In the Farley and Taylor (1991) study, when the ponies made the transition from the trot to the gallop, peak forces on the limbs decreased. When the ponies carried additional weight, the transition speed was reduced but occurred at the same 'critical level of force'. They concluded that musculoskeletal forces trigger the trot–gallop transition.

Our observation that the trot–gallop transition occurs at a slower speed on the incline than on the level appears to be inconsistent with the force trigger hypothesis; however, this depends on the assumption that forces are not elevated on an incline. This assumption is based on the physical fact that total vertical impulse per stride is determined by body mass (which is not elevated on the incline) and the observation that forces in the tendon of the lateral gastrocnemius are not elevated when a turkey runs up an incline (Roberts et al., 1997). The fact that stride frequency and time of contact are not changed when a horse trots up an incline (Figs 2, 3) suggests that impulse and peak forces are the same on the level and on the incline.

Even though total forces are expected to be the same on the level and on the incline, there is evidence that the forces under the fore and hindlimbs of a quadruped may not change in the same way with speed or incline, and this has some interesting implications for the trigger. One kinematic analysis (Sloet van Oldruitenborgh-Oosterbaan et al., 1997) shows that, when trotting up an incline, there is increased hyperextension of the metacarpophalangeal joint (MCP) on the hindlimb and decreased hyperextension of the MCP joint on the forelimb when compared with level locomotion. Because the MCP joint is primarily controlled by ligaments, these changes in the kinematics suggest that smaller forces act on the forelimb and larger forces act on the hindlimb when going up an incline. This observation, combined with a lower transition speed on an incline, suggests that the trigger on the incline might be elevated hindlimb forces. However, this is probably not the case on the level – based on the observation that the tendon strain does not increase with speed in the hindlimb on the level but does increase in the forelimb (Biewener, 1998). This suggests that forces on the hindlimb do not increase with speed on the level, indicating that the trigger on the level cannot be hindlimb forces but might be forelimb forces. Thus, if forces are the trigger for the trot–gallop transition, it is possible that forelimb forces are the trigger on the level and hindlimb forces are the trigger when going up an incline.

As complex as these conclusions are, our results indicate that there may be another signal that indicates to the animal that gait should be changed. In the range of speeds between the maximum sustained trotting speed and the minimum sustained galloping speed, the animal switches gait repeatedly. One possible interpretation of this behavior is that the animal is detecting conflicting signals – one indicating that trotting is the preferred gait and another indicating that galloping is the preferred gait. However, neither of the triggers previously suggested (metabolism and force) can explain this behavior because, in this range of speeds, forces and metabolic rate are both lower when galloping. Thus, it seems likely that some other signal causes the animal to switch from galloping to trotting. The only stride parameter we studied that might be implicated is the duration of the swing phase, which is 10% shorter when galloping at the same speed.

Additionally, different triggers may be required to explain the transition from trotting to galloping when speed is increasing and the transition from galloping to trotting when speed is decreasing (Kram et al., 1997). The fact that forces decrease when a horse changes from trotting to galloping means that forces increase when making the transition from galloping to trotting. It seems unlikely that the change from the gallop to the trot is triggered by increasing strain and forces. However, it is also difficult to provide a link between metabolism and a trigger for the gait transition. The maximum sustained trotting speed was not different to the EOTS, but, at speeds between the maximum sustained trotting speed and the minimum sustained galloping speed, where the horses were making a transition after only a couple of strides, it seems unlikely that the animals could detect very small differences in metabolic rate, and at the minimum sustained galloping speed, metabolic rate is usually higher when trotting. Again, the only parameter that decreases when a horse switches from galloping to trotting is stride frequency, resulting in a longer swing phase. Similar conclusions have come from studies of the walk–run transition in humans (Prilutsky and Gregor, 2001); the transition from the walk to the run was correlated with increased activity of muscles to swing the leg, whereas the run–walk transition was correlated with increased activity of muscles used in supporting the body.

The present study expands our understanding of the relationship between stride frequency and speed. Stride frequency increased as a linear function of speed at the trot up to the minimum sustained galloping speed. At speeds faster than the minimum sustained galloping speed, stride frequency in the extended trot did not change. When the horses made a transition to the gallop, there was a sudden increase in frequency, and stride frequency was independent of speed at all galloping speeds. Using allometric equations from Heglund and Taylor (1988), the stride frequency and speed at the trot–gallop transition (on the level) were calculated to be 100 strides $\min^{-1}$ and 5.8 m s^{-1}, respectively (using a mean mass of 467 kg). Stride frequency at the minimum sustained galloping speed in the present study was 109 strides $\min^{-1}$, and the transition speed was 5.7 m s^{-1}. The calculation of transition speeds in the Heglund and Taylor (1988) study was based on the assumption that this speed occurred at the intersection of separate regression lines fitted to stride frequency *versus* speed for trotting and for galloping; they did not note the sudden increase in stride frequency that occurs when trotting and galloping at the same speed. This phenomenon occurs in horses but it is not known if it occurs in other quadrupeds. In the present study (Fig. 2), this intersection would occur at a speed of approximately 6.7 m s^{-1} and a stride frequency of 118 strides $\min^{-1}$.

The present analysis is the first examination of time of contact at speeds near the transition speed. In a seminal paper, Kram and Taylor (1990) compared metabolic costs and time of contact as a function of speed in a group of mammals with body masses ranging from 30 g to 140 kg. They concluded that the majority of the cost of transport is determined by the cost of supporting the animal's mass and the time course of the application of force during contact. A shorter time of contact would result in the requirement for a faster application of force that would, in turn, increase metabolic costs. In the horses, time of contact was shorter during galloping than trotting on the level at speeds slower than the EOTS, and that is consistent (based on Kram and Taylor, 1990) with the higher metabolic costs of galloping at those speeds. At the EOTS, the time of contact was not different between trotting and galloping; again, an observation consistent with Kram and Taylor (1990). On an incline, the time of contact at the maximum sustained trotting speed is not the same when trotting and galloping in spite of the fact that this is the EOTS on an incline. We do not consider this to be inconsistent with Kram and Taylor (1990) because their hypothesis did not address the cost of locomotion on an incline.

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