of early differentiation of the earth proposed here. Core-mantle differentiation at high temperatures provides a direct mechanism for the incorporation of some highly lithophile elements into the core. Metal-silicate partitioning data for such elements are not available. However, if the dominant lithophile elements in the mantle, Mg, Si, and O, have low-temperature (1500 to 1600 K) metal-silicate K_d's in the range of 10^{-4} to 10^{-6}, as would be consistent with their strongly lithophile nature, core-mantle differentiation at 3000 to 3500 K could have resulted in the incorporation of $\sim$1 to 3% of each of these elements into the core, in addition to S which will enter the core as Fe-S melt (*20*). Thus, a high-temperature differentiation of the earth is consistent with the low density of the core.

The presence of radioactive heat sources in the core has been a much debated topic (*21, 22*). High-temperature differentiation may also lead to the incorporation of significant amounts of radioactive elements into the core. Distribution coefficients for U and Th have not been measured, but the K_d for K of about 10^{-2} (*22*) indicates that $\sim$10% of the earth's inventory of K could be partitioned into the core, in which case it would provide an important energy source in the core. Precise measurements of metal-silicate distribution coefficients for the lithophile and radioactive elements are needed to verify these suggestions of light elements and radioactive energy sources in the core.

In summary, consideration of the effect of temperature on K_d's indicates that the abundances of siderophile elements in the mantle can be satisfactorily accounted for by core-mantle differentiation at high temperatures during the accretional history of the earth. The low density of the core may be a result of this process. This scenario of the early chemical differentiation of the earth is entirely consistent with recent physical models of planetary accretion that postulate that the earth was largely or totally molten during accretion. It appears that the siderophile element abundances in the mantles of terrestrial planets may be useful as geothermometers of initial planetary differentiation.

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A Mechanical Trigger for the Trot-Gallop Transition in Horses

CLAIRE T. FARLEY AND C. RICHARD TAYLOR

It is widely thought that animals switch gaits at speeds that minimize energetic cost. Horses naturally switched from a trot to a gallop at a speed where galloping required more energy than trotting, and thus, the gait transition actually increased the energetic cost of running. However, by galloping at this speed, the peak forces on the muscles, tendons, and bones, and presumably the chance of injury, are reduced. When the horses carried weights, they switched from a trot to a gallop at a lower speed but at the same critical level of force. These findings suggest that the trot-gallop transition is triggered when musculoskeletal forces reach a critical level.

QUADRUPEDS WALK AT LOW SPEEDS, trot at moderate speeds, and gallop at high speeds. Within each gait, they prefer to use a narrow range of speeds where the energetic cost of moving each kilogram of their body mass a meter (cost of transport) is minimizes (*1*). An earlier study from our laboratory showed that at these preferred speeds, horses naturally use the gait that minimizes energetic cost (*1*). It seems reasonable that horses switch from one gait to another at the speeds that minimize energetic cost (*1–3*). However, the earlier study did not include systematic measurements of the gait transition speeds (*1*). It is difficult to imagine how energetic cost could trigger a gait transition as an animal rapidly changes speed. In terms of the available biological transducers, it seems more likely that musculoskeletal forces trigger the transition from trotting to galloping. In dogs, goats, and horses, peak skeletal forces increase with trotting speed and are reduced when they switch to a gallop (*4–7*). By galloping rather than trotting at higher speeds, the peak forces and presumably the chance of injury are reduced. Although even higher forces occur during jumping or falling than during locomotion (*7*), these are rare events. A horse's feet hit the ground

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Harvard University, Museum of Comparative Zoology, Concord Field Station, Old Causeway Road, Bedford, MA 01730.

more than 7000 times during an hour of trotting, and as a result, the bones, muscles, and tendons may be damaged by relatively low levels of force (*8*).

The purpose of this study was twofold: to investigate whether the transition from a trot to a gallop is triggered when musculoskeletal forces reach a critical level and whether it occurs at the speed that minimizes energetic cost. First, we determined whether peak muscle and tendon forces are reduced when an animal switches from a trot to a gallop. To test whether the gait transition is triggered when musculoskeletal forces reach a critical level, the peak force at each trotting speed was increased by having the horses carry weights. We predicted that when horses carried weights, they would begin to gallop at the same critical level of force but at a lower speed. In the second part of the study, we investigated whether horses normally switch from a trot to a gallop at the speed that minimizes energetic cost.

The preferred trot-gallop transition speed was determined for three horses (adult Shetland ponies, average mass 150 kg) that were trained to run on a motorized treadmill. The transition speed was found by gradually increasing the treadmill speed (0.3 m/s per minute) from 2.5 m/s to the lowest speed where the animal galloped. The speed was then held constant. If the animal switched back to a trot, the speed was increased again. This process was repeated until we found the lowest speed at which the animal galloped continuously for a minute, and we defined that as the trot-gallop transition speed. The transition speed was the same whether it was approached from higher (gallop to trot) or lower speeds (trot to gallop). For half the trials, the horses carried lead weights equal to 23% of their body weight. The weights were carried in a pack firmly attached to the body and positioned so that the fraction of body weight on the fore and hindlimbs was unchanged. The procedure was repeated at least 20 times for each animal, unweighted and weighted.

Table 1. The trot-gallop transition speeds (± SEM) and the peak vertical forces at the transition speeds ($\mathbf{F}_p$, average of all of the limbs). The peak vertical force, $\mathbf{F}_p$, was reduced when the horses switched from a trot to a gallop (P = 0.049). When the horses carried weights, they switched gaits at a lower speed (P = 0.009) but at essentially the same level of force (P = 0.53). Horses 1, 2, and 3 weighed 148 kg, 132 kg, and 170 kg, respectively.

	Unweighted transition			Weighted transition	
	Speed (m/s)	Trot $\mathbf{F}_p$ (body weights)	Gallop $\mathbf{F}_p$ (body weights)	Speed (m/s)	Trot $\mathbf{F}_p$ (body weights)
Horse 1	4.29 ± 0.07	1.16	0.96	3.41 ± 0.06	1.15
Horse 2	4.05 ± 0.05	1.22	1.01	3.33 ± 0.03	1.23
Horse 3	3.87 ± 0.07	1.03	0.94	3.23 ± 0.06	1.05

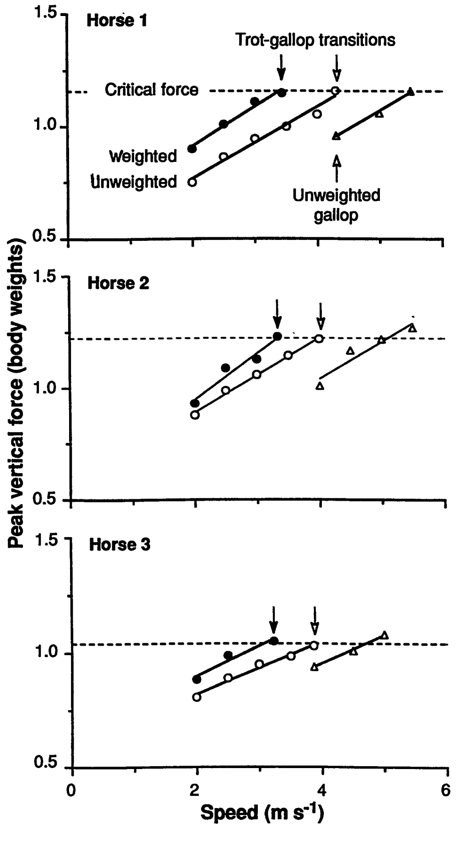

Fig. 1. When the horses carried weights, they switched to a gallop at a lower speed but at essentially the same critical level of force as when they did not carry weights (Table 1) (*12*). By switching to a gallop, the peak ground reaction force was reduced by an average of 14% (*16*). The open circles and triangles denote unweighted trotting and galloping, respectively, and the closed circles denote weighted trotting. The plotted values are the average of the peak forces under each of the four legs. The lines are linear least-squares regressions.

The muscle and tendon forces depend on the effective mechanical advantage of the limbs and the ground reaction force (*9*). The effective mechanical advantage is defined as the ratio of the moment arm of the extensor muscles (r) to the moment arm of the ground reaction force (R) about a joint. The muscle and tendon force ($\mathbf{F}_{m-t}$) can be calculated from the effective mechanical advantage and the ground reaction force ($\mathbf{F}_g$).

$$\mathbf{F}_g/\mathbf{F}_{m-t} = r/R \qquad (1)$$

We estimated the moment arms of the extensor muscle groups about the joints of the fore- and hindlimbs from external measurements. The moment arm of the ground reaction force about the joints was measured from film (lateral view, Photosonics camera 16mm 1PL, 100 frames per second) for the middle third of the support phase (*10*).

The vertical ground reaction force was measured with a treadmill-mounted force platform (*11*). The horses were positioned on the treadmill so that either just the forelimbs or just the hindlimbs were on the force platform during running. The horses could trot and gallop at moderate speeds in this position. It was possible to resolve the peak force under an individual limb because there was only one foot on the ground from the fore or hindlimb pair at the time of each limb's peak force during trotting and moderate speed unweighted galloping (*12*). The vertical force alone can be used to calculate the peak muscle and tendon forces because the peak vertical force is about ten times greater than the peak horizontal, and the horizontal force is nearly zero at the middle of the support phase when the total force is maximum (*5, 10*). This method of calculating muscle and tendon force from the effective mechanical advantage and the ground reaction force yields almost identical results as tendon buckle measurements (*13*).

The energetically optimal speed for the trot-gallop transition (that is, the speed above which trotting costs more than galloping and below which the opposite is true) was measured in the following manner. After the preferred transition speeds were measured, the horses were trained to trot at higher than normal speeds and gallop at lower than normal speeds on command. Oxygen consumption was measured with an open flow system as described by Fedak *et al.* (*14*). The highest rates of oxygen consumption measured were less than 50% of the maximum rates for these animals, and the contribution of anaerobic metabolism is insignificant at these intensities (*15*). The cost of transport (the mass-specific cost of moving a unit distance) was calculated by dividing the mass-specific oxygen consumption by the speed. The data from this and other parts of the study were analyzed using paired t tests.

The peak ground reaction force (the average of the four limbs) increased from 0.81 to 1.14 body weights over the range of trotting speeds and then fell by an average of 14% when the horses switched to a gallop (Fig. 1 and Table 1). The peak force increased with galloping speed and reached the critical level of force at a moderate galloping speed. The reduction in peak force at the trot-gallop transition was not equal in all limbs and was greatest in the second forelimb (−19%) and first hindlimb (−28%) to hit the ground (*16*). The limb posture during the middle of the support phase was unchanged when the horses switched gaits, and the effective mechanical advantage was similar for trotting (0.59 ± 0.02, SEM) and galloping (0.58 ± 0.04) at the transition speed ($P = 0.85$). This indicates that the peak force on the musculoskeletal system decreased in proportion to the ground reaction force. Quadrupeds can change the footfall pattern by switching lead limbs during galloping, sharing the force reduction among the limbs.

The decrease in peak force at the trot-gallop transition was partially accomplished by an increase in the fraction of the stride that each foot was on the ground (the duty factor) in the gallop. This increased duty factor was due to a 10% increase in stride frequency with no change in the ground contact time. In addition, a moderate speed gallop is a more compliant gait than a trot because the feet are placed on the ground sequentially, thus reducing the peak accelerations of the body (*17*).

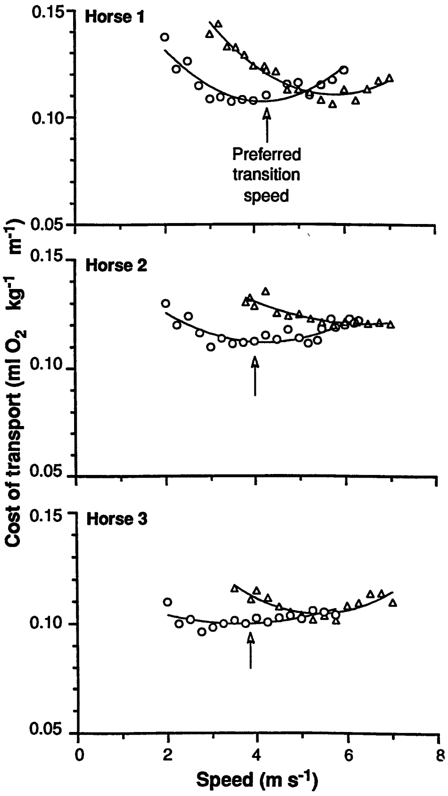

Fig. 2. The horses preferred to switch from a trot to a gallop at a speed that was not energetically optimal. The cost of transport (the mass-specific metabolic cost of moving a unit distance) was 13% greater for galloping than for trotting at the preferred transition speed. The energetically optimal speed for the gait transition was higher than the preferred transition speed for all of the horses. The open circles and the open triangles denote trotting and galloping, respectively. The horses did not carry weights for these trials.

The horses switched from a trot to a gallop at essentially the same level of force whether or not they carried weights (Fig. 1 and Table 1). However, this level of force was reached at a lower speed when the horses carried weights (3.3 ± 0.05 m/s versus 4.1 ± 0.01 m/s). The limb posture and the effective mechanical advantage were the same at the weighted (0.59 ± 0.02) and unweighted (0.59 ± 0.02) transition speeds ($P = 0.93$) indicating that the forces on the musculoskeletal system were similar.

The horses did not switch from a trot to a gallop at the speed that would have minimized energetic cost (Fig. 2). The horses preferred to switch to a gallop at a speed (4.1 m/s) where the cost of transport for galloping was 13% (± 1.9%, SEM) higher than for trotting ($P = 0.008$). The energetically optimal speed for the gait transition (5.3 ± 0.3 m/s) was higher than the preferred transition speed for all of the horses.

We conclude that horses switch from a trot to a gallop when the musculoskeletal forces reach a critical level. Furthermore, we find that this gait transition does not occur at the speed that would minimize energetic cost. Pennycuick observed that ungulates migrating across the African plains only use a narrow range of speeds within each gait (*18*). At these speeds, animals use the gait that requires the least energy and the cost of transport is minimized (*1*). Because the speeds near the gait transitions are only used transiently as an animal accelerates or decelerates, switching gaits at the speeds that minimize energetic cost may not be important in nature.

In terms of avoiding injuries that result from high forces, it seems reasonable that musculoskeletal forces trigger the trot-gallop transition. Peak forces drop when horses switch from a trot to a gallop and increase to the critical level in the range of the preferred galloping speeds (5.00 to 5.75 m/s) (*1*). Presumably, higher levels of force are reached if a horse trots faster than the normal transition speed or gallops faster than the preferred galloping speed. The avoidance of higher levels of force during sustained locomotion suggests that there may be a biomechanical constraint to maintain a certain safety factor for avoiding injuries. We cannot calculate safety factors from our measurements, but it seems likely that the critical level of force for each horse is matched to the structure of the musculoskeletal system. Measurements of bone strain in horses, dogs, and goats all show a similar reduction at the trot-gallop transition (*4*–*7*). Extrapolating from these data, the critical level of force corresponds to a safety factor of about three for bone when compared to the yield stress for a single event (*6*, *7*). The yield stress decreases with repetitive loading, and thus, the actual safety factor during running may be lower than three (*8*). A safety factor of this magnitude seems reasonable for avoiding injury especially under natural conditions where animals must run on uneven surfaces and avoid obstacles.

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