

THE ROLE OF COMPLIANCE IN MAMMALIAN RUNNING GAITS

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SUMMARY

The running gaits used by both bipedal and quadrupedal animals are reviewed and contrasted. At high speeds, bipeds use both ordinary running, in which the legs move opposite one another, and hopping. Quadrupeds generally use the trot or its variations at moderate speeds, and first the canter and then the gallop as speed increases. Running in both bipeds and quadrupeds generally involves at least one aerial phase per stride cycle, but certain perturbations to running including running in circles, running under enhanced gravity, running on compliant surfaces and running with increased knee flexion (Groucho running) can reduce the aerial phase, even to zero.

A conceptual model of running based on the idea that an animal rebounds from the ground like a resonant mass-spring system may be used to compare the various gaits. The model makes specific predictions which show that galloping is generally faster than cantering, pronking or trotting, and requires lower peak vertical forces on the legs while also giving a smoother ride. Even so, trotting might be preferred to galloping at low and moderate speeds for the same reason that normal running is preferred to Groucho running – the more compliant gait offers a smoother ride and lower vertical ground-reaction forces on the feet, but this can only be obtained at a high cost of increased metabolic power.

INTRODUCTION

This paper raises questions about certain dynamic features of walking and running, particularly running. The questions concern comparisons between the gaits. What are the relative advantages and penalties of each, and which one is better for a given speed? R. McNeill Alexander and his collaborators have been interested in some of these same questions, and have calculated the power required for running, using mathematical models of the various terrestrial gaits (Alexander, 1977; Alexander, Jayes & Ker, 1980). A different approach is taken here. In deciding which gait is better, the considerations applied in this paper include the running speed, the stiffness of muscles and reflexes, the force applied to the legs and a parameter measuring the smoothness of the ride. A main theme will be the energetic cost of

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maintaining the whole-animal vertical stiffness, which is characteristic of a particular gait at a particular speed. Before beginning these discussions, it will be useful to review some basic facts about the gaits actually used by terrestrial animals, and to examine the results of some experiments in which running performance is changed by altering the effective vertical stiffness of the whole animal.

ANIMAL GAITS

The investigation of terrestrial locomotion has a distinguished history. Most people know that the study of locomotion played a part in the development of motion pictures. In the 1870s, the French physiologist E. J. Marey used an automatic pneumatic recording device to determine the sequence and duration of steps as animals walked and ran. Marey was also interested in the persistence of vision which allowed the zoetrope (invented in the 1830s) to give the viewer the impression of motion as he or she observed a series of drawings through slots in a rotating wheel. In the United States, Eadweard Muybridge photographed horses galloping past a series of cameras, then used a revolving device like the zoetrope to view the pictures in sequence. As Muybridge toured the United States in 1886 giving illustrated lectures, he visited Thomas Edison and showed him his photographs of animals in motion. Edison was intrigued. Five years later, Edison's motion picture camera was a new fact of life.

Muybridge's photographs are still instructive and useful today. Fig. 1, showing a horse with a rider galloping at high speed, is from his *Animals in Motion*, first published in 1887. Six different gaits may be distinguished for quadrupedal animals by specifying two parameters for the motion of each foot (Table 1). The duty factor is defined as the fraction of the total stride cycle during which that foot is in contact with the ground. (A stride cycle is the time from one foot strike until the next strike of the same foot.) The relative phase gives the fraction of a stride cycle by which the foot in question lags the phase of a reference foot. The reference foot is arbitrarily assigned a phase of zero.

The alternate gaits, which are used at low speeds, are the walk, trot and rack. In the *walk*, each leg lags the previously-placed one by a quarter of a stride cycle. In a *trot*, either one or the other pair of diagonal limbs is on the ground at a time, and a short period of flight separates each ground contact period. The *rack*, also called the *pace* or *amble*, is a trot employing both legs on the same side of the body synchronously.

The in-phase gaits are used for moderate and high speeds. These make significant use of bending of the back, whereas the alternate gaits do not. The distinctions between the in-phase gaits are more a matter of degree than a matter of kind. In the *canter*, a forefoot and a diagonal rearfoot strike the ground together. At higher speeds, large animals use either a *transverse gallop* (in which there is a delay between the strike of the last hindfoot and the next forefoot) or a *rotary gallop* (in which the sequence of footfalls orbits in a circle, either clockwise (not shown in the table) or counter-clockwise. In a canter, there is usually no aerial phase or only one aerial phase per stride cycle, and that follows the lifting of the last forefoot to be placed (this leg is



Fig. 1. Horse with rider at a fast gallop. From Muybridge (1887, reprinted 1957).

called the lead leg). In a fast gallop (or what is sometimes called a *full gallop*), there may be an additional aerial phase in the stride cycle which occurs after the last hindfoot has lifted but before the next forefoot strikes. This is called the *stage of extended flight*, since the forelimbs are stretched forward and the hindlimbs are stretched backward at this time. It stands in distinction to the *stage of crossed flight* which occurs after the lead leg (last foreleg) leaves the ground, at which time the forelimbs and hindlimbs are crossed.

At very fast galloping speeds, there may be a short stage of flight after the thrust of each limb, although the longest period of flight, corresponding to the time when the animal is rebounding upward from the ground, occurs during the stage of crossed flight, as with the lower speeds.

There are regular characteristics of the galloping pattern which change with the body size of the animal. Small mammals (including mice) use a mode called the paired gallop or *bound*, in which both forelimbs move together and both hindlimbs move together, and there are two distinct flight phases per stride cycle. In the *half bound*, used by animals the size of hares, the hindlimbs are used in phase as in the bound, but the forelimbs are out of phase, as in a transverse or rotary gallop. Finally, there is the *prong*, a gait in which all four legs are used synchronously to hop forward.

By comparison with quadrupeds, bipeds have a relative paucity of distinct gaits. They may *walk*, employing alternating periods of support by one or two legs. During periods of single-leg support, the other leg is swinging forward. It has been well established for both bipeds (Cavagna, Thys & Zamboni, 1976) and quadrupeds (Cavagna, Heglund & Taylor, 1977) that in walking, the changes in gravitational potential energy of the body are substantially equal in amplitude and opposite in phase to the changes in the forward kinetic energy of the centre of mass, so that the total mechanical energy changes only a little throughout a walking step. *Running* in bipeds does not make use of a double-support period; in running, there is usually a period of

Table 1. *The gaits of quadrupedal animals*

| Alternate gaits | | Walk | | Trot | | Rack | |
|-----------------|------|---------|------|---------------------|-----|-----------------|-----|
| Duty factor | | > 0.5 | | 0.3-0.5 | | 0.3-0.5 | |
| | | L | R | L | R | L | R |
| Relative phase | fore | 0 | 0.5 | 0 | 0.5 | 0 | 0.5 |
| | hind | 0.75 | 0.25 | 0.5 | 0 | 0 | 0.5 |
| In-phase gaits | | Canter | | Gallop (transverse) | | Gallop (rotary) | |
| Duty factor | | 0.3-0.5 | | < 0.4 | | < 0.4 | |
| | | L | R | L | R | L | R |
| Relative phase | fore | 0 | 0.8 | 0 | 0.8 | 0 | 0.8 |
| | hind | 0.8 | 0.5 | 0.6 | 0.5 | 0.5 | 0.6 |

Duty factor is the fraction of the stride cycle a foot is in contact with the ground. Relative phase is the fraction of a stride cycle a particular foot lags the reference foot. Adapted from Alexander (1977).

flight when both feet are off the ground. In bipedal running, the legs are used in strict alternation; in bipedal *hopping*, the legs may be used together or with a phase delay between foot placements.

RUNNING DOES NOT ALWAYS INVOLVE AN AERIAL PHASE

A usual characteristic of both bipedal and quadrupedal running is at least one period of flight (more often two) during the stride cycle. There are, however, ways of perturbing the running gaits which result in the reduction or elimination of the aerial phase.

First, let us consider what happens when an animal runs around a sharp turn. Recently, we conducted experiments in which human subjects ran at top speed around a series of circular tracks marked on a natural turf surface (McMahon, 1984). The only instructions given to the subjects were that they were to run as fast as possible. The runners' speeds were markedly reduced when they ran around a circle with a radius less than about 20 m. The results showed that the contact time, t_c , for a single step increased and the period of a single aerial phase, t_a , decreased as the radius of the turn was reduced, but the period of half a stride cycle, $T = t_a + t_c$, was about constant at all radii. The experimental results were compared with the predictions of a simple theoretical model assuming that T and the step length (distance the body moves forward during the ground contact) are both fixed. It was also assumed that the force applied by the runner's leg has a constant amplitude but a variable duration. Although agreement between the experimental points and the theoretical lines was only good and not perfect, the theoretical model provides the essential explanation for the reduced speed in a sharp turn. If the force borne by the leg is not to exceed some given maximum, the contact time must be increased to offset the effects of centripetal acceleration during a turn. The aerial phase was predicted to disappear entirely when the radius of the turn was less than about 1 m, but this was not a practical point to check experimentally because the step length was also about 1 m. If gravitational acceleration were increased, as it would be in a large centrifuge or on a planet larger than the Earth, these studies would predict that a runner's speed would be reduced and his contact time increased, just as it is for running in circles on Earth.

If the surface under a runner's feet is soft and compliant, more time is required to reverse the runner's downward velocity as he or she rebounds into the air, by comparison with the time required to rebound from a hard surface. In Fig. 2, stick figures traced from movie films show the contact period in a step on a hard surface and on a surface made of large foam-rubber pillows (McMahon & Greene, 1979). In these experiments, the subjects were attempting to run at top speed, but their speed was slower on the pillow track because the contact phase was markedly increased (even though the step length was also increased).

A result from a closely-related experiment is shown in Fig. 3. Here, a subject is running on a treadmill, and in the top part of the figure he is running normally. In the bottom part of the figure he has deliberately increased his knee flexion in order to rub his elbow lightly, at mid-rebound, on a horizontal bar used as a guide (not shown in

the figure). As a result of this increased knee flexion, his leg is more compliant than in the normal posture for running and the time required for rebound from the ground is increased. In the experiments shown, the total flight time occupied 25.2 % of a stride cycle when the subject was running normally, but only 6.9 % of a stride cycle when the subject was running like Groucho Marx (with increased knee flexion). When the

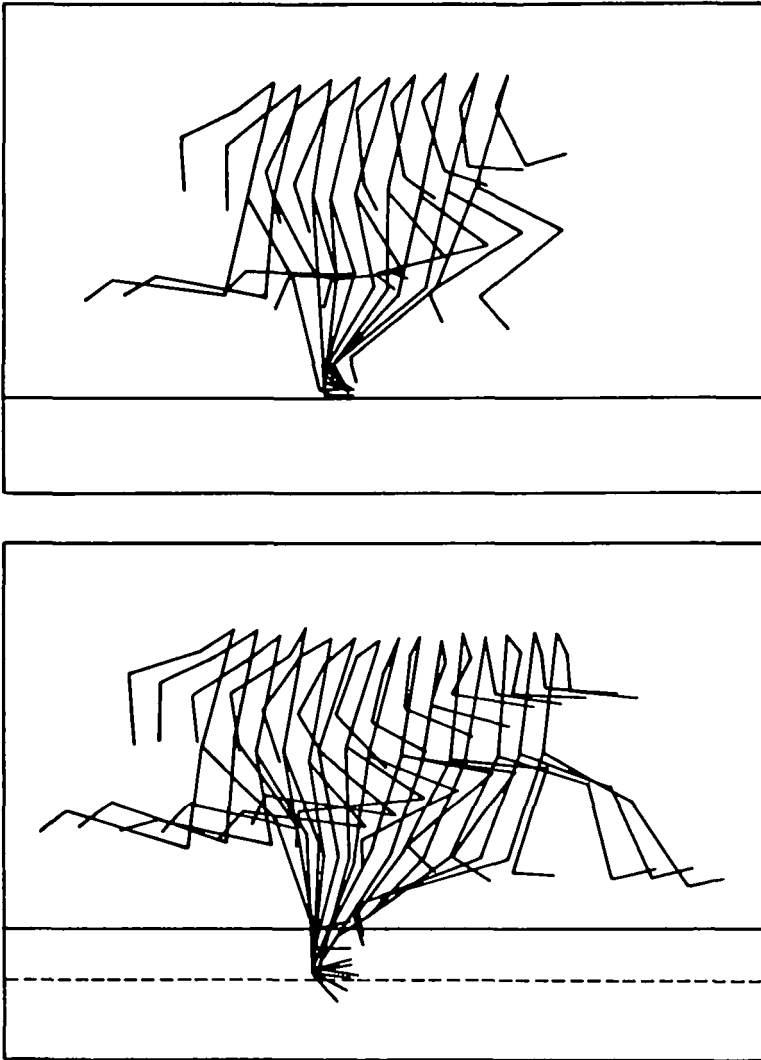


Fig. 2. Stick figures showing a subject running on a hard surface (top) and on foam pillows (bottom). The lines intersect at points marking the runner's right hip, ear, shoulder, elbow, wrist and both knees, ankles and shoe tips. The framing speed of the camera was 59 frames s^{-1} in each case. Only those frames where the foot touches the ground are drawn. The broken line indicates the mean deflection of the pillows over a step cycle. Note that contact time is increased on the soft surface (there are more frames drawn), but step length is also increased (the hip moves a greater distance forward during foot contact). From McMahon & Greene (1979).

subject increased his knee flexion even more, the aerial phase disappeared entirely. This experiment is in many ways analogous to running on a compliant surface, except that in this case, the increased compliance is in the runner's legs rather than under his feet. The broken line in the lower part of the figure shows the trajectory of the runner's

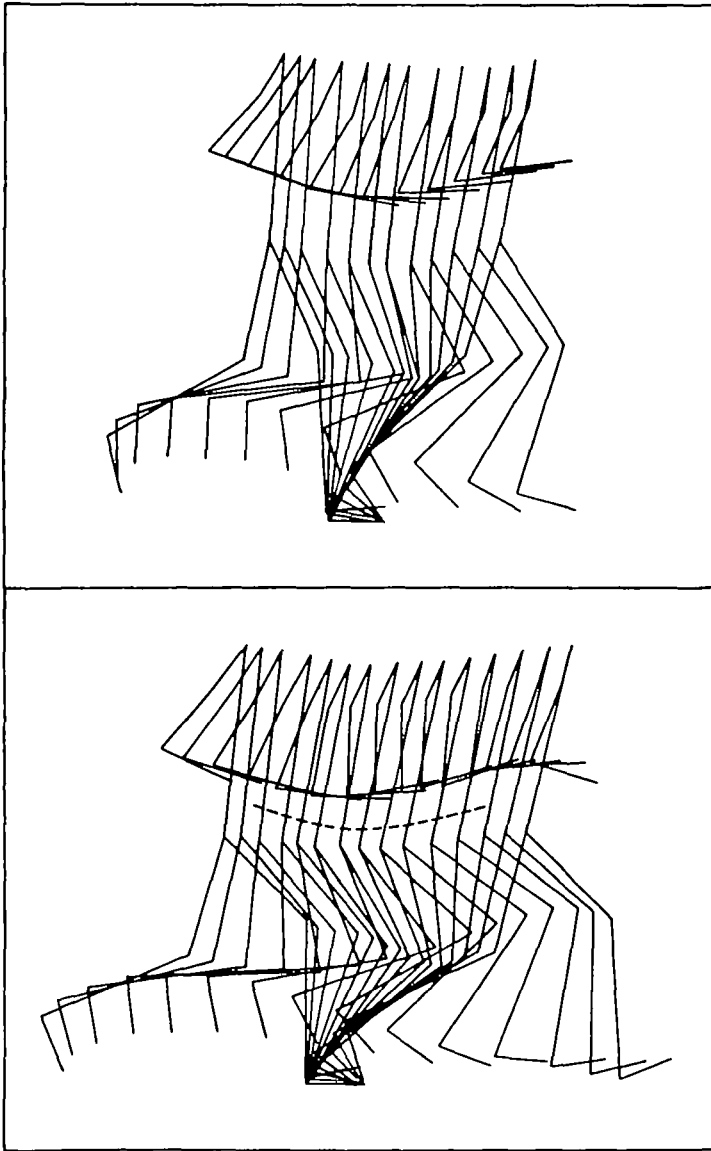


Fig. 3. Groucho running. In the top illustration, the subject ran normally, but in the bottom illustration, the subject ran in such a way as to deliberately increase his knee flexion during the contact period (Groucho running). The broken line shows the hip trajectory in normal running, for comparison. The time interval between adjacent stick figures is $1/40$ s. The vertex points of the stick figures are the same as Fig. 2.

hip in normal running, brought down from the upper part of the figure for comparison. It is clear that the hip follows not only a lower, but a smoother path in Groucho running, by comparison with normal running at the same speed. Force-plate records show that the magnitude of the ground-reaction force at mid-stance is markedly reduced in Groucho running. Thus, Groucho running reduces the bumpiness of the ride.

This bumpiness is a quality of a running gait which depends intimately on the stiffness and phasing of the legs; it will be one important basis for comparison among the various alternative quadrupedal gaits considered later. But before leaving the subject of bipedal running, it is important to point out that although running in tight circles, running under conditions of enhanced gravity, running on very compliant surfaces and Groucho running all represent ways of reducing the aerial time, even to zero, it is not entirely correct to assert that running has been converted to walking when the aerial time reaches zero. This is because force-plate records and film studies show that in each of these altered gaits, the centre of mass reaches its lowest altitude and slowest speed at the middle of the stance phase, just as in normal running. By comparison, in walking, where there is substantial exchange between gravitational and kinetic energy, the centre of mass is at its highest point in the middle of the stance phase.

COMPARISON OF GAITS ASSUMING A RESONANT REBOUND

The discussion of animal gaits up to this point has considered separately the sequence of leg placements and the role of the stiffness of the leg (the inverse of its compliance). It is interesting to work out the consequences of these two factors taken together in a single conceptual model of running. The goal is a basis for comparing the various running gaits using physical principles, in an effort to understand why one gait works better than another under stated conditions.

Drawings depicting a mathematical model (hereafter called the mass-spring model) are shown in Fig. 4. The arc-shaped foot contacts the ground at the same moment that the mass M begins to compress the spring. Only vertical motions of the mass lead to a compression of the spring. Under some circumstances, more than one leg may be in contact with the ground at one time, and when this happens each leg contributes its own separate spring stiffness in parallel. An example is the case of the horse trotting in the top part of the figure, where the stiffness of the spring is $2K$ because two legs are on the ground at a time, each contributing a stiffness, K . It is further assumed that once the horizontal motion of the body exceeds a distance L (the step length) in the forward direction, the leg lifts from the ground, transferring reversibly any elastic energy which may be stored at that moment to any other legs that may be on the ground. The galloping horse in the lower part of the figure demonstrates how this works. In a real animal or legged robot, this transfer of stored elastic energy between one leg and another could be facilitated by allowing the energy to go through an intermediate kinetic form, perhaps utilizing the various components of rotational kinetic energy of the trunk. (I am grateful to Marc Raibert for pointing this out.)

Clearly, once the distance moved during a rebound is assumed to be constant (within any particular running gait), the running speed is inversely proportional to the half-period of the mass-spring system. Therefore, for any of the gaits described by this

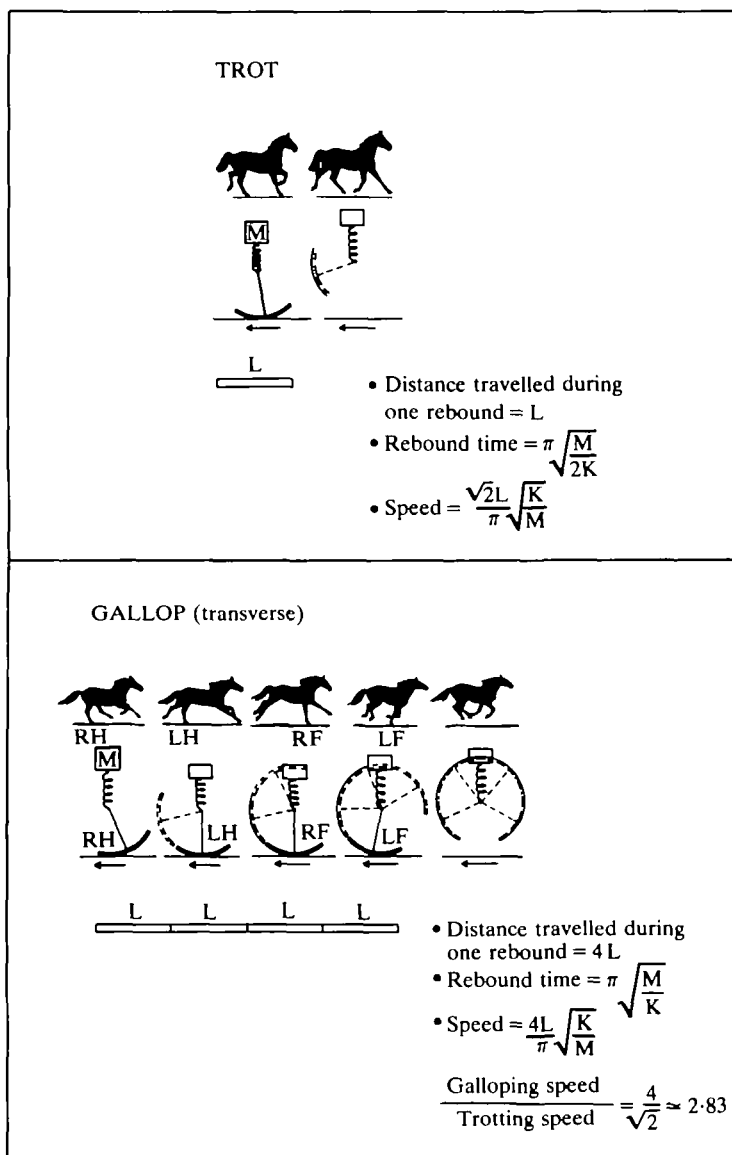


Fig. 4. The mass-spring model used for calculating Tables 2, 3, and 4. The top part of the figure shows a horse trotting and the corresponding position of the mass-spring model just prior to the midpoint of the rebound period. Because two legs are on the ground at once, the stiffness of the spring is $2K$. In the lower part of the figure, a horse galloping illustrates the way several legs may be used in succession during a single rebound. Arrows show the direction of motion of the ground relative to the body. The calculations in the figure show that when the stiffness of an individual leg is assumed to be the same in the two gaits, galloping is nearly three times as fast as trotting.

model, the required whole-animal vertical stiffness increases with the square of the speed. In the comparisons that come later, it will be stated specifically whether the speed, stiffness of an individual leg, or some other parameter of the model is kept the same in the gaits to be compared. The calculations in Fig. 4 show what happens when the stiffness of an individual leg is assumed to be the same in trotting and galloping: in this case, the model predicts that galloping is nearly three times faster than trotting.

Assumptions of the model

The model shown in Fig. 4 requires several specific assumptions. The first is that the distance the body moves forward over the ground while a particular foot is in contact with the ground (step length, L) does not change with running speed. Experimental observations of humans (Cavagna *et al.* 1976; McMahon & Greene, 1979) and both bipedal and quadrupedal animals, including rhea, turkeys, spring hare, kangaroos, dogs, monkeys and rams (Cavagna *et al.* 1977) and dogs and sheep (Jays & Alexander, 1978) show that step length increases with speed in walking, but changes little with speed at moderate to high running speeds within a particular running gait. This observation applies only to normal running on a hard surface; either running on a compliant surface or Groucho running increases the step length by comparison with the step length for a hard surface. Although flexion and extension of the spinal column and pitching motions of the trunk can add to the effective step length of an individual leg in galloping, as opposed to trotting, this effect is not considered in this basic version of the model, since step length is assumed to be the same in all running gaits.

A further assumption to be made throughout this paper will be that the vertical force applied to the ground is a fixed fraction of a sine curve. More specifically, it will be assumed that the mass-spring model remains in contact with the ground for a half-period of resonant vibration. In fact, the effects of gravity cause the contact time to be somewhat longer than a half-period, but these effects will not be considered here. Furthermore, in all of the discussions to follow, the mass-spring system will be assumed to be undamped. None of the conclusions would be changed, however, if damping were introduced, provided that the damping ratio were assumed to be constant, because in that case all ground rebound periods, t_r , would be multiplied by the same factor.

In order to facilitate comparisons, another assumption will be that the vertical velocity on landing after any aerial phase is a constant, independent of the gait chosen and the running speed. Force-plate studies (Cavagna *et al.* 1977) show that the vertical excursion of the centre of mass in a stride cycle is larger in galloping than in trotting (and larger in trotting than in walking), and furthermore that this vertical excursion generally decreases somewhat with increasing speed within a gait, although there are exceptions. Thus this assumption of the model does not fit all the observations well, but it will be shown later how modifying this assumption to agree with the observations leads to only modest changes in the conclusions.

When two or more legs are on the ground at one time, the basic model assumes that each leg adds its stiffness in parallel, so that the total vertical stiffness is proportional to

the number of legs supporting weight. In experiments in which human subjects made a small vertical jump and landed on the balls of their feet without bending their knees, the effective vertical stiffness calculated from the damped frequency of the ringing oscillation was 1.53 times greater on two legs as opposed to one (Cavagna, 1970). In another study, when subjects executed small-amplitude vertical bouncing motions while standing in a flexed-knee posture on a springboard, the stiffness calculated from the damped natural frequency was 1.25 times higher for standing on two legs by comparison with standing on one (Greene & McMahon, 1979). Therefore, the assumption of the model that the vertical stiffness is proportional to the number of legs used for support is not in good agreement with experimental measurements. This is another point where the model may be modified to agree with observations, and the results are discussed later.

Finally, the model of Fig. 4 does not take into account the fact that real animals do not have large arc-shaped feet, nor is all the mass of a real animal located at a point above a spring. In real animals, the centre of mass decelerates and reaccelerates in the forward direction as well as the vertical direction on landing and taking off. Part of the spring may be in the animal's trunk as well as in its legs (this would be particularly true of galloping). Furthermore, the legs of real animals have mass as well as stiffness, and this is ignored in the model.

Equal-speed comparison

Keeping in mind all these limitations, we can proceed to use the model to compare various features of five idealized gaits at the same speed (Table 2). Results describing the basic model appear in the centre of each large rectangular block.

A diagram showing the relative phase of the contact period of each foot appears at the top of the table. Time increases from left to right, and any period when no foot is on the ground is an aerial phase.

The first column shows bipedal running, in which there is an aerial phase after each contact period. The second column refers to any gait in which two feet work in synchrony and whenever a foot is lifted, an aerial phase follows. Thus, the second column describes a bipedal hop and a quadrupedal trot, but it also describes a rack, merely by making the limbs on the same side of the body move synchronously.

The last three columns show three simplified patterns representing quadrupedal gaits used at medium and high speeds. The column showing four legs used synchronously describes the pronk and needs little explanation. The next column shows a gait in which pairs of legs are used in succession, so that one rebound period corresponds to a forward movement of the body through a distance $D = 2L$. A glance back at Table 1 will reveal that no gait spontaneously chosen by animals corresponds identically to this pattern, but the canter is the most similar, since it features only one aerial phase per stride cycle and a nearly synchronous use of a pair of legs (RF and LH in the example shown in Table 1). Therefore, this gait will be called a pseudo-canter.

The last column in Table 2 describes a gait in which all four legs are placed in quick succession, so that the body moves forward a distance $D = 4L$ during one rebound

Table 2. *Equal-speed comparison*

| | One foot at a time (bipedal running) | Two synchronous (bipedal hop; quadrupedal trot) | Four synchronous (pronk) | Pairs in succession (pseudo-canter) | Four in succession (gallop) |
|---|---|---|-----------------------------|--|--------------------------------|
| Number of flights = number of rebound periods per stride cycle | 2 | 2 | 1 | 1 | 1 |
| Number of legs on the ground at once = N | 1 | 2 | 4 | 2 | 1 |
| Stiffness of an individual leg | K | K/2 | K/4 | K/8 | K/16 |
| Whole-animal vertical stiffness | K | K | K | K/4 | K/16 |
| Step length per leg | L | L | L | L | L |
| Distance covered in one rebound time = D | L | L | L | 2L | 4L |
| Dimensionless rebound time = $\frac{t_r}{\pi} \sqrt{M/K}$ | 1 | 1 | 1 | 2 | 4 |
| Dimensionless speed = $\frac{D}{t_r} \sqrt{K/M}$ | 1 | 1 | 1 | 1 | 1 |
| Bumpiness: measure of vertical force on centre of gravity = $\frac{A\pi}{t_r} \sqrt{\frac{M}{K}}$ | 1 | 1 | 1 | 1/2 | 1/4 |
| Vertical force measure per leg relative to bipedal run = $\frac{A\pi}{N t_r} \sqrt{\frac{M}{K}}$ | 1 | 1/2 | 1/4 | 1/4 | 1/4 |

The quantity in the centre of each block refers to the basic model for resonant rebound (Fig. 4). The equivalent result for the modified model is given in the lower right-hand corner of each block; when that corner is blank, the modified result is the same as the result for the basic model. In the second column, the result for the bound (modified model) is indicated by the letter B and given at the lower left of each block.

* A = $\sqrt{2}$ for modified model: bound, pronk, canter, gallop. A = 1 otherwise.

from the ground. It is reasonable to call this pattern a slow gallop, because there is only one aerial phase per stride cycle. Nevertheless, it will be assumed that this same pattern is also used at high galloping speeds. Notice that when this pattern is in use, the RH and RF legs must bear higher vertical loads than the other two legs since RH and RF are on the ground during the middle part of the rebound when the vertical ground reaction force is highest. Just which two legs bear the high forces depends on whether the galloping pattern is rotary (as illustrated), or transverse. Measurements on cantering horses whose forelimb bones (metacarpus and radius) were instrumented with strain gauges showed that the peak bone stress was about 20 % less in the non-lead leg as opposed to the lead leg (Biewener, Thomason, Goodship & Lanyon, 1983). In cantering, the non-lead leg shares part of its load.

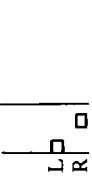
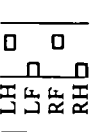

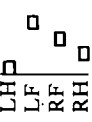
Several comparisons are worthy of comment. At the outset, one would guess that an important measure of the muscular effort required would be given by the vertical force per leg. The bottom row shows that this parameter is the same in the pronk, pseudo-canter and gallop at the same speed, but rises by a factor of 2 in the quadrupedal trot. Thus, the force per leg at a given speed may be reduced substantially by making a transition from trotting to one of the high-speed gaits, but this parameter does not say which of the several high-speed gaits is better. A plausible reason for preferring galloping among the high-speed gaits, particularly if you happen to be riding this animal, is given in the second row from the bottom in Table 2. This column gives a measure of the average vertical force acting on the centre of mass during the rebound. It therefore gives an indication of the vertical acceleration during ground contact, or what may be called the bumpiness of the ride. According to this line, cantering is better than trotting, but galloping gives the least bumpy ride of all.

This is a reasonable place to admit that the model presented in this paper is unable to accommodate some very important features of quadrupedal gaits. The most serious shortcoming is that it is not possible to consider more realistic canters and gallops in which a single rebound period includes portions with one leg on the ground and other portions when two or more legs are in contact. This is because the relative phases of the vertical and horizontal motions of the model are coupled, which means that the phase velocities of those motions must also be coupled. The horizontal velocity of the body cannot suffer instantaneous changes because it has inertial mass, and this means that instantaneous changes of the phase velocity of the vertical motion (which would take place if the spring stiffness suddenly changed as a second or third leg was added) are not permitted. It is for this reason that the whole-animal vertical stiffness must be made constant (or, at least, continuous) during an entire rebound period, although that stiffness may be produced by different legs at different times.

Equal-force-per-leg comparison

When the various gaits are compared under conditions which give rise to the same maximum vertical force in any leg during a rebound (specifying the mid-rebound legs RH and RF in the rotary gallop), the situation is as shown in Table 3. Each of the three high-speed gaits is twice as fast as trotting. The stiffness required of an individual leg is higher for the pronk than the trot, but equal to the trot for the canter

Table 3. Equal-force-per-leg comparison

| | Two synchronous | | | | Four synchronous (pronk) | Pairs in succession (pseudo-canter) | Four in succession (gallop) |
|--|---|--|-----|--------------------|--------------------------|---|---|
| | One foot at a time (bipedal running) | (bipedal hop; quadrupedal trot) | | | | | |
| Number of flights = number of rebound periods per stride cycle |  |  | 2 | | 1 |  |  |
| Number of legs on the ground at once = N | 1 | 2 | 2 | 4 | 2 | 1 | 1 |
| Stiffness of an individual leg | K | $\frac{B}{1.33K}$ | 2K | $\frac{2.66K}{4K}$ | 4K | 2K | K |
| Whole-animal vertical stiffness | K | $\frac{B}{2K}$ | 4K | $\frac{8K}{16K}$ | 16K | 4K | K |
| Step length per leg | L | $\frac{B}{1.2L}$ | L | L | L | L | L |
| Distance covered in one rebound time = D | L | $\frac{B}{1.2L}$ | L | L | L | 2L | 4L |
| Dimensionless rebound time = $\frac{t_r}{\sqrt{M/K}}$ | 1 | $\frac{B}{\sqrt{2/2}}$ | 1/2 | 1/4 | $\frac{\sqrt{2/4}}{1/4}$ | 1/2 | 1 |
| Dimensionless speed = $\frac{D/t_r}{\sqrt{K/M}}$ | 1 | 1.7 | 2 | 4 | 2.83 | 4 | 4 |
| Bumpiness: measure of vertical force on centre of gravity* = $A \frac{\sqrt{M}}{t_r \sqrt{K}}$ | 1 | $\frac{B}{2}$ | 2 | 4 | 2 | 4 | 1 |
| Vertical force measure per leg, relative to bipedal run* = $\frac{A\pi}{N t_r} \sqrt{\frac{M}{K}}$ | 1 | $\frac{B}{1}$ | 1 | 1 | 1 | 1 | 1 |

* The vertical ground reaction force per individual leg at mid-rebound is assumed the same in each gait. * A = $\sqrt{2}$ for modified model: bound, pronk, canter, gallop. A = 1 otherwise.

and lower for the gallop. The bumpiness of the ride follows the same pattern: it is greater for the pronk, equal for the canter and lower for the gallop, by comparison with the trot.

Equal-leg-stiffness comparison

Table 4 shows how the results change when the stiffness of an individual leg is assumed to have a particular value K , no matter which gait is chosen. The speed comparison now puts the gallop clearly first, followed by the canter, pronk and trot, respectively. Within the quadrupedal gaits, the force per leg is highest in the gallop, approximately 1.4 times that of the canter and trot, while the speed is about 1.4 and 2.8 times that of the canter and trot, respectively. Although the gallop is the fastest quadrupedal gait, it has the lowest measure of bumpiness.

The two bipedal gaits show an interesting and unexpected comparison. (Ivan Sutherland brought this point to my attention during the preparation of this paper.) According to Table 4, the speed of a biped hopping on both feet is about 1.4 times faster than the same animal with the same leg stiffness running by using the feet alternately. The force per leg is also lower for bipedal hopping, by comparison with running, although the bumpiness of the ride is worse in hopping. Looking at Table 3, we see that hopping is twice as fast as running when the vertical force per leg is kept the same in the comparison. There are bipeds of both small and large size (small birds, jerboas and kangaroos) which prefer hopping to running, and the considerations of Tables 2–4 may play a role in their choice. On the other hand, humans can run much faster than they can hop, and this fact leads us to wonder what is wrong with the model of Fig. 4 as a description of human high-speed locomotion.

At least one significant matter concerns the maintenance of balance during the flight phase. In hopping, the schematic animal of Fig. 4 must apply a torque to both legs during flight to swing the legs forward so that they will be in the correct position for the next landing. This torque can only be obtained by applying an equal and opposite torque to the trunk, with the result that the trunk pitches nose-down during flight. This is a problem for bipedal hopping but not for running, where the motion of the legs is in opposite directions. The neglect of these considerations is made less important if the legs (particularly their distal portions) are very light by comparison with the body (and tail, if any). Thus the omission of considerations of balance during the flight phase may not be important in describing some specialized hoppers, but is more likely to be a problem in describing the gaits of humans, whose legs make up about half of their body mass.

Modifications to improve realism

It was mentioned earlier that some assumptions of the model agree well with observations and others do not. Suppose that the model is modified to agree better with the observations by changing the assumptions in the following ways.

First, the step length in the canter and gallop are taken to be $1.2L$, rather than L . This permits the flexion-extension motions of the back and the pitching motions of the

Table 4. *Equal-leg-stiffness comparison*

| | One foot at a time (bipedal running) | Two synchronous (bipedal hop; quadrapedal trot) | Four synchronous (pronk) | Pairs in succession (pseudo-canter) | Four in succession (gallop) |
|---|---|---|-----------------------------|--|--------------------------------|
| | | | | | |
| Number of flights = number of rebound periods per stride cycle | 2 | 2 | 1 | 1 | 1 |
| Number of legs on the ground at once = N | 1 | 2 | 4 | 2 | 1 |
| Stiffness of an individual leg | K | K | K | K | K |
| Whole-animal vertical stiffness | K | 2K | 4K | 2K | K |
| Step length per leg | L | L | L | L | L |
| Distance covered in one rebound time = D | L | L | L | 2L | 4L |
| Dimensionless rebound time = $\frac{t_r}{\pi\sqrt{M/K}}$ | 1 | $1/\sqrt{2}$ | 1/2 | $1/\sqrt{2}$ | 1 |
| Dimensionless speed = $\frac{D/L_t}{\pi\sqrt{K/M}}$ | 1 | $\sqrt{2} = 1.41$ | 2 | $2\sqrt{2} = 2.83$ | 4 |
| Bumpiness: measure of vertical force on centre of gravity = $\frac{\pi}{L_t}\sqrt{\frac{M}{K}}$ | 1 | $\sqrt{2} = 1.41$ | 2 | $\sqrt{2}$ | 1 |
| Vertical force measure per leg, relative to bipedal run = $\frac{A\pi}{Nt_r}\sqrt{\frac{M}{K}}$ | 1 | $1/\sqrt{2} = 0.707$ | 1/2 | $1/\sqrt{2} = 0.707$ | 1 |

The vertical stiffness of each individual leg is assumed the same in each gait.
 * A = $\sqrt{2}$ for modified model: bound, pronk, canter, gallop. A = 1 otherwise.

trunk to augment the distance the body moves forward when a particular foot is on the ground.

Second, the whole-animal vertical stiffness is taken to be 1.5 times greater when two legs are on the ground than when one leg is in ground contact, not 2 times greater as was assumed previously. This agrees better with the results of the one-legged and two-legged vertical bouncing experiments mentioned earlier (Cavagna, 1970; Greene & McMahon, 1979) and recognizes the existence of a spring element in the trunk as well as the legs.

Finally, the vertical velocity on landing will be taken as a factor 1.414 higher in the pronk, canter and gallop, as opposed to the trot. This means that the flight phase in these high-speed quadrupedal gaits raises the centre of mass twice as high as the flight phase of the trot, in agreement with observations on dogs and other quadrupedal animals (see Fig. 9 of Cavagna *et al.* 1977).

When each of the tables has been re-computed to include these three modifications, the results (shown at the lower right-hand corner of each box) change the conclusions very little. In Table 2, the equal-speed comparison, the canter and gallop now have a somewhat lower vertical force per leg than the pronk, but all are still lower than the trot. The bumpiness index continues to be the lowest in a gallop. In Table 3, the canter and gallop are now faster than the pronk, but all are still faster than the trot. In Table 4, the modifications have slowed down the pronk and speeded up the gallop, but the order of gaits according to speed has not changed and the order with respect to bumpiness is only slightly altered.

Entries labelled 'B' have been added in the lower left-hand corner of the blocks of the second column in each table. These represent calculations for the bound, a gait with two aerial phases per cycle in which the body rebounds from the ground using the two forelimbs and then the two hindlimbs in unison, as explained earlier. The modified model is used for calculations of the bound because bounding is generally considered to be a special case of galloping. The tables show that the bound is predicted to be a relatively slow gait, having a speed marginally faster than trotting under the equal-leg-stiffness comparison (Table 4) but somewhat slower than trotting under the equal-force-per-leg comparison (Table 3). At low speeds, where the equal-speed comparison is useful for comparing the relative advantages of the gaits, the bound requires a little more force per leg than the trot, but much more than the pronk, canter or gallop.

WHICH GAIT IS BEST FOR A GIVEN SPEED?

A few general conclusions emerge. The first is that a galloping pattern in which the body goes a long distance on each ground rebound by placing the feet in quick non-overlapping succession is generally superior to other quadrupedal gaits both in speed and smoothness of ride. Furthermore, this gait often results in a lower maximum vertical ground-reaction force required of each individual leg, by comparison with the other gaits. For these reasons, the model under both the basic and modified assumptions predicts that galloping is the most suitable gait for use at high speeds.

If galloping is best at high speeds, why is it not also best at the lower running speeds? An answer to this question is suggested by Table 2, which shows that both the whole-animal vertical stiffness and the vertical stiffness of an individual leg in galloping are much lower than that required for trotting or even for cantering. Here it is useful to recall Groucho running, where the runner deliberately decreased the stiffness of his legs (increased the compliance) by running with increased knee flexion. A consequence of the increased compliance was a much increased rate of oxygen consumption, by comparison with normal running at the same speed – in some subjects, the increase was greater than 50%. The increased rate of oxygen consumption in Groucho running almost certainly was due to increased forces in the anti-gravity muscles of the legs caused by the changed mechanical advantage of the muscles. As knee flexion increases, whole-body vertical stiffness decreases, causing the vertical ground reaction force at mid-stance also to decrease, but the peak and average forces borne by the muscles increases.

The increased compliance required for galloping, by comparison with trotting at the same speed, is probably associated with the recruitment of various muscles of the back and abdomen into the locomotory enterprise. Roughly speaking, galloping is to trotting as Groucho running is to normal bipedal running, when the two gaits of a pair are compared at the same (moderate) speed. In both comparisons, the gait with the greater compliance gives lower peak and average vertical forces on the foot, a smoother ride, a longer step length, and requires a greater rate of oxygen consumption. The lower energy requirement for trotting may be a sufficient reason for an animal to prefer trotting to galloping when both are options. Note that this statement applies only to the low and moderate speeds where trotting ordinarily takes place. As speed increases in trotting, both the leg forces and the stiffness required of the legs rises rapidly, perhaps approaching a physiological limit. At this point, the gallop becomes the more attractive gait.

Donald Hoyt and C. R. Taylor have provided valuable evidence concerning the relative energy costs of quadrupedal gaits (Hoyt & Taylor, 1981). Horses were trained to trot on a treadmill at high speeds where they would ordinarily gallop, and to gallop at low speeds where they would ordinarily trot. Thus, the rate of oxygen consumption for trotting and galloping could be compared over a wide range of speeds. The rate of oxygen consumption increased in a curvilinear fashion with speed for each gait. Above the speed where the curves intersected, galloping provided the lower rate of oxygen consumption; below that speed, trotting required less metabolic power.

A particularly interesting finding concerned the cost of transport, defined as the energy required to move a unit weight through a unit horizontal distance. Curves showing the cost of transport for both galloping and trotting were presented as a function of speed. When a horse was allowed to select its own speed while running over the ground (as opposed to running on the treadmill), the animal most often selected a speed near the minimum of the trotting cost-of-transport curve ($3\text{--}3.5\text{ m s}^{-1}$) when it was trotting and near the minimum of the galloping cost-of-transport curve ($5\text{--}5.75\text{ m s}^{-1}$) when it was galloping. At the speed corresponding to the minimum of the trotting cost-of-transport curve, measurements showed that

galloping was about 1.35 times as costly in energy as trotting. An interpretation of this result based on Groucho running would say that the higher rate of oxygen consumption in galloping as opposed to trotting at this speed was due to the greater requirement for vertical compliance in galloping.

COST OF TRANSPORT AND FRICTION

Hoyt & Taylor found that the minimum cost of transport for trotting (at $3\text{--}3.5\text{ m s}^{-1}$) was about the same as the minimum cost of transport for galloping (at $5\text{--}5.75\text{ m s}^{-1}$). In general, when terrestrial animals are not required to keep to one gait, but may change gaits at will, a straight-line relationship is usually found for the metabolic power required as a function of the speed. As a consequence, the cost of transport is almost independent of speed.

This situation puts one in mind of a simple physical interpretation of the cost of transport. (Ivan Sutherland brought this point to my attention during the preparation of this paper.) Suppose a block is sliding at constant speed along a horizontal surface. In pulling the block a unit distance, an outside agency does an amount of work equal to F on the block, where F is equal to the coefficient of sliding friction, μ , multiplied by the weight of the block. In getting a feeling for μ , it is helpful to think of familiar situations: the μ for a hickory ski sliding on dry snow is about 0.03; a rubber tyre sliding on a bitumenous concrete road has a μ near 1.15. The cost of transport is defined as this work divided by the weight, so the cost of transport is equal to μ . A large ship has a cost of transport defined this way of about 0.005; a large truck works out at about 0.1, and an automobile at about 0.5 (Gabrielli & von Karman, 1950; Greenewalt, 1977). In general, the μ for animal locomotion is higher than that for man-made machinery: for humans and dogs running at moderate speeds it is about 1.0, for a rat running it is approximately 5.0, and for a mouse running it is about 15.0 (Greenewalt, 1977). For animals of a particular body size, terrestrial runners have a higher μ than birds, and fish swimming have a lower μ than either.

The important comparison of μ for the purposes of this paper is the one given by Hoyt & Taylor (1981), of a particular animal using two different gaits at a particular speed. At the speed freely chosen for trotting, trotting was found to be more economical than galloping, even though the models of this paper predicted that trotting would give higher foot forces and a bumpier ride. The comparison between trotting and galloping at this low speed is very much like the comparison between riding a balloon-tyred bicycle with firm as opposed to soft tyres. Soft tyres with their low vertical stiffness give a smoother ride, but at the cost of a higher rolling friction.

At high speeds, Hoyt & Taylor (1981) found that galloping required less energy than trotting. Here it is important to recall that whole-animal stiffness increases with the square of the speed in the models presented in this paper. Perhaps the correct comparison to have in mind when comparing trotting and galloping at high speed is a bicycle with steel tyres as opposed to one with high-pressure pneumatic tyres. In the steel-tyred bicycle (representing high-speed trotting), the shocks due to riding on

even a moderately rough road lead to rapid fatigue of the rider and perhaps even breakage of the spokes or other parts. The bicycle with high-pressure tyres (representing galloping) gives, by comparison, a much more controllable and comfortable ride, since the stiffness of the tyres is now correct for the purpose.

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