RUNNING SPRINGS: SPEED AND ANIMAL SIZE

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Summary

Trotting and hopping animals use muscles, tendons and ligaments to store and return elastic energy as they bounce along the ground. We examine how the musculoskeletal spring system operates at different speeds and in animals of different sizes. We model trotting and hopping as a simple spring-mass system which consists of a leg spring and a mass. We find that the stiffness of the leg spring (k_{leg}) is nearly independent of speed in dogs, goats, horses and red kangaroos. As these animals trot or hop faster, the leg spring sweeps a greater angle during the stance phase, and the vertical excursion of the center of mass during the ground contact phase decreases. The combination of these changes to the spring system causes animals to bounce off the ground more quickly at higher speeds.

Analysis of a wide size range of animals (0.1–140kg) at equivalent speeds reveals that larger animals have stiffer leg springs (k_{leg} $M^{0.67}$, where M is body mass), but that the angle swept by the leg spring is nearly independent of body mass. As a result, the resonant period of vertical vibration of the spring-mass system is longer in larger animals. The length of time that the feet are in contact with the ground increases with body mass in nearly the same way as the resonant period of vertical vibration.

Introduction

Running, hopping, trotting and galloping animals bounce along the ground using springs to store and return elastic energy (Cavagna *et al.* 1964, 1977; Heglund *et al.* 1982*b*). These springs include muscles, tendons and ligaments which alternately stretch and recoil, storing and releasing elastic energy, while the feet are on the ground (Alexander, 1988). The long and compliant Achilles tendon is an example of a spring which stores and returns elastic energy during locomotion. In a hopping kangaroo or a running human, the Achilles tendon alone conserves as much as 35% of the mechanical energy required for a stride (Alexander, 1988).

The concept of musculoskeletal springs has been the basis for several simple spring-

mass models for running (Alexander, 1992; Alexander and Vernon, 1975; Blickhan, 1989*a*; Full and Blickhan, 1992; Cavagna *et al.* 1988; He *et al.* 1991; Ito *et al.* 1983; McGeer, 1990; McMahon and Cheng, 1990; McMahon and Greene, 1979; Thompson and Raibert, 1989). These simple models, which employ a single linear leg spring and a mass, accurately predict the mechanics of running gaits. The body's complex system of active muscles, tendons and ligaments therefore behaves much like the single linear spring employed in the models (Farley *et al.* 1991).

In the simplest application of a spring-mass model, the spring-mass system only moves vertically, simulating hopping or running in place. This model makes accurate predictions of the mechanics of a human hopping in place (Farley *et al.* 1991). In this purely vertical model, the stiffness of the leg spring is the most important determinant of the amount of time that the feet are on the ground (ground contact time). Experimental evidence shows that the stiffness of the leg spring changes by more than twofold when humans hop in place at different hopping frequencies (Farley *et al.* 1991). This leg spring stiffness can be adjusted by changing the amount that the knee flexes while the feet are on the ground (Greene and McMahon, 1979). Because of the adjustable leg spring stiffness, humans can hop in a spring-like manner over the large range of ground contact times associated with a twofold range of frequencies (Farley *et al.* 1991).

In forward locomotion, unlike hopping in place, the leg spring is not oriented vertically during the entire time that the feet are on the ground. Because the body moves forward while the feet are on the ground, the leg spring sweeps an arc (Fig. 1). As a result, the vertical motions of the body and the ground contact time depend on a combination of the leg spring's stiffness and the angle through which the leg spring sweeps (McMahon and Cheng, 1990). For example, as a human runs faster, although the time that each foot is on the ground decreases dramatically, the stiffness of the leg spring does not change substantially (He *et al.* 1991). The shorter ground contact times at higher speeds are achieved by having the leg spring sweep a greater angle while the foot is on the ground. The greater angle at higher speeds leads to an increased compression of the leg spring and an increased force in the leg spring. Consequently, the vertical excursion of the center of mass is reduced and the ground contact time decreases at higher speeds (McMahon and Cheng, 1990).

The first goal of this study is to examine how the properties of the spring-mass system change with speed in trotting and hopping animals. We hypothesize that the stiffness of the leg spring will be independent of speed but that the angle swept by the leg spring will be larger at higher speeds.

The second goal of this study is to examine how the properties of the body's spring system vary with animal size. The mechanics of bouncing gaits change even more dramatically with body size than with speed. For example, when a horse and a white rat trot at moderate speeds, the horse's feet are on the ground four times longer than the rat's. We will examine whether these dramatic differences in the mechanics of locomotion in small and large animals are the result of differences in the stiffness of the leg spring or in the angle that it sweeps.
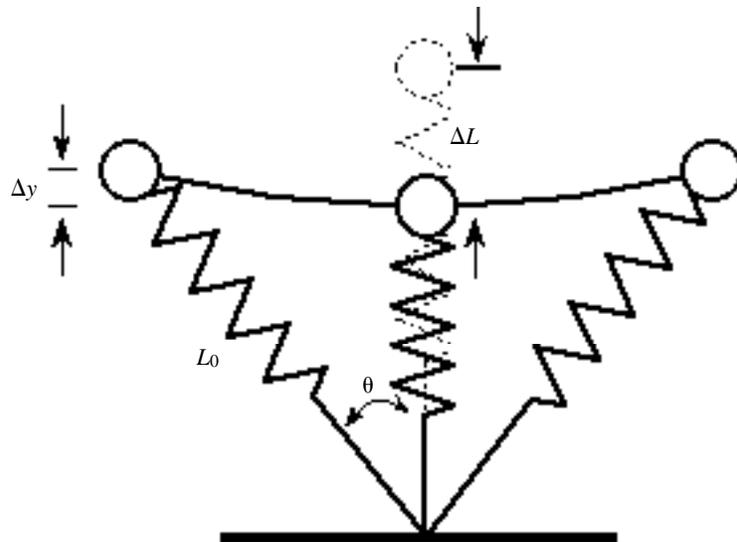
Fig. 1. Trotting and hopping are modeled as simple spring-mass systems bouncing along the ground. The model consists of a mass and a single leg spring (which joins the foot and the center of mass of the animal). This figure depicts (for an animal moving to the right) the model at the beginning of the stance phase (left-most position), at the middle of the stance phase (leg spring is oriented vertically) and at the end of the stance phase (right-most position). The arc shows the movement of the mass during the stance phase. The leg spring has an initial length (L_0) at the beginning of the stance phase, and its maximal compression is represented by ΔL. The dashed spring-mass model shows the length of the uncompressed leg spring. Thus, the difference between the length of the dashed leg spring and the maximally compressed leg spring represents the maximum compression of the leg spring (ΔL). The downward vertical displacement of the mass during the stance phase is represented by Δy and is substantially smaller than ΔL. Half of the angle swept by the leg spring during the ground contact time is denoted by θ.

Materials and methods

Protocol

In the first part of the study, we examined how the properties of the spring system changed with trotting or hopping speed. We focused on trotting and hopping because these are symmetrical gaits which can be modeled as simple spring-mass systems. Our experimental animals were three dogs (*Canis familiaris*), two horses (*Equus caballus*), one African pygmy goat (*Capra hircus*) and one red kangaroo (*Megaleia rufa*) (Table 1). Each animal either ran across a ground-mounted force platform or ran on a treadmill with a force platform mounted in it. We obtained the largest possible range of trotting and hopping speeds for each animal.

In the second part of the study, we examined how the properties of the spring system changed with animal size. The additional animals studied in this part were three white rats (*Rattus norvegicus*), three kangaroo rats (*Dipodomys spectabilis*) and one tammar wallaby (*Macropus eugenii*) (Table 1). Each of the additional animals ran across a

ground-mounted force platform at a speed near the middle of its trotting or hopping speed range. These speeds were considered to be physiologically equivalent because the duty factors (the ratio of the ground contact time of one foot to the stride time) and Froude numbers were similar in all of the animals (Table 1; Alexander and Jayes, 1983; Heglund and Taylor, 1988; Perry *et al.* 1988). On average, the duty factor was 0.411 ± 0.017 (S.E.M.) and the Froude number was 1.5 ± 0.095 for all the animals. Errors, where stated, are standard error of the mean.

Measurements

For the dogs, goat and horses, the vertical ground reaction force was measured as the animal trotted on a treadmill. The treadmill had a force platform equipped with strain gauges (model OR6-5-1, Advanced Mechanical Technology, Newton, MA) mounted under the tread. The natural frequency of vertical vibration of the force platform mounted in the treadmill was 160Hz, and the cross-talk from a horizontal force to the vertical was less than 1%. The signal-to-noise ratio for the measurement of the ground reaction force for a 700N runner was approximately 100:1. The treadmill-mounted force platform is described in greater detail elsewhere (Kram and Powell, 1989). The force signal was sampled at 1000Hz for the dogs and goat, and at 500Hz for the horses. During the treadmill runs, the animals were either filmed (horses, Photosonics 1Pl, 100frames$\,$s^{-1}) or videotaped (dogs and goats, NAC video recorder, 200fields$\,$s^{-1}) in lateral view.

The vertical and horizontal (fore–aft) ground reaction forces were measured as the white rats trotted and the kangaroo rats hopped across a series of five small ground-mounted force platforms equipped with strain gauges. The platforms were $0.25\,\text{m}\times0.25\text{m}$ and had natural frequencies of 180Hz in the vertical direction and 200Hz in the horizontal direction. The cross-talk from a horizontal force to the vertical was less than 3%. The force signal was sampled at 1000Hz and was digitally filtered with a cut-off frequency of 100Hz. The design and specifications of these force platforms have been described in detail elsewhere (Heglund, 1981). The average forward speed of the animals was calculated from the time between breaking two light beams located over the series of

Table 1. *The body masses, leg lengths, speeds, Froude numbers and duty factors of the animals in the study*

Animal	Body mass, M (kg)	Leg length, L_0 (m)	Speed (m s^{-1})	Froude number $u/(gL_0)^{0.5}$	Duty factor
Kangaroo rat	0.112	0.099	1.8	1.8	0.36
White rat	0.144	0.065	1.1	1.4	0.50
Tammar wallaby	6.86	0.33	3.0	1.7	0.44
Dog	23.6	0.50	2.8	1.3	0.39
Goat	25.1	0.48	2.8	1.3	0.44
Red kangaroo	46.1	0.58	3.8	1.6	0.43
Horse	135	0.75	2.9	1.1	0.39

The Froude number represents a normalization of the forward speed (u) for leg length.
Duty factor is calculated from the ratio of the ground contact time to the time for a stride.

force platforms (0.5m apart). The horizontal force was integrated to find the net change in the forward velocity during the stance phase. If this change was greater than 5%, the trial was not accepted. During the trials, the animals were filmed in lateral view at 200frames s^{-1} (Photosonics 1Pl).

The tammar wallaby and the red kangaroo hopped across a ground-mounted Kistler force platform (model 9261). The natural frequency of vertical vibration was greater than 200Hz, and the force signal was sampled at 1000Hz. The forward velocity of the animals was calculated from the time between breaking four light beams placed 1m apart, equally spaced before and after the force platform. To check that a particular stride was at a steady speed, we integrated the horizontal force to find the net change in the forward velocity of the center of mass during the stance phase. If it changed by more than 5%, the trial was not accepted. During the trials, the animals were filmed in lateral view at 200frames s^{-1} (Photosonics 1Pl).

Spring-mass model

The spring-mass model consisted of a mass and a single 'leg spring' (Fig. 1; McMahon and Cheng, 1990). The stiffness of the leg spring (k_{leg}) was defined as the ratio of the peak force in the spring (F) to the peak displacement of the spring (ΔL):

$$k_{leg} = F/\Delta L. \tag{1}$$

The peak force in the leg spring occurred at the middle of the stance phase when the leg spring was oriented vertically, and thus corresponded to the peak vertical ground reaction force. It is important to notice that this method of calculating k_{leg} gives a measurement of the total stiffness during the stance phase and not of the stiffness of an individual limb. In both trotting and hopping, two limbs are in contact with the ground at the same time, and our method of calculating k_{leg} gives the overall stiffness of the two limbs during ground contact. This overall leg spring stiffness is probably about twice as great as the stiffness of an individual limb. However, we have no information about whether the forelimb and the hindlimb are equally stiff in a quadrupedal trotter.

The peak displacement of the leg spring (ΔL) was calculated from the peak displacement of the center of mass (Δy), the length of the leg spring at the instant that it hit the ground (L_0) and half of the angle swept by the leg spring while it was in contact with the ground (θ) (Fig. 1; McMahon and Cheng, 1990):

$$\Delta L = \Delta y + L_0(1 - \cos\theta). \tag{2}$$

The vertical displacement of the center of mass (Δy) was calculated by integrating the vertical acceleration twice, as described in detail by Cavagna (1975). The length of the leg spring in the model is defined as the distance from the point of ground contact to the center of mass. We estimated the length of the leg spring by measuring, from high-speed film or video, the length of the leg at the instant that the foot hit the ground. In the bipedal hoppers, L_0 was defined as the distance between the foot and the hip. In the quadrupedal trotters, L_0 was defined as the average of the forelimb length and the hindlimb length. The forelimb length was measured as the distance from the foot to a point midway between the greater tubercle of the humerus and the dorsal aspect of the scapula, and the hindlimb

length was measured as the distance from the foot to the greater trochanter of the femur. Because the height of the center of mass is similar to the hip height in most mammals, the leg length provided a good estimate of the initial length of the leg spring (L_0).

Assuming that the forward speed (u) is almost constant during the time of foot contact (t_c), the relationship between half the angle swept by the leg spring (θ; Fig. 1) and the leg length L_0 is:

$$\theta = \sin^{-1}(ut_c/2L_0). \tag{3}$$

Half of the angle swept by the leg spring (θ) is not exactly the same as half of the angle swept by an animal's actual leg because, in the model, the leg spring is defined as connecting the foot to the center of mass rather than to the hip.

The vertical motions of the system during the ground contact phase can be described in terms of an 'effective vertical stiffness' (k_{vert}). The effective vertical stiffness was calculated from the ratio of the peak vertical force (F) to the peak vertical displacement of the center of mass during the stance phase (Δy):

$$k_{vert} = F/\Delta y. \tag{4}$$

The effective vertical stiffness (k_{vert}) does not correspond to any physical spring in the model. Rather, k_{vert} describes the vertical motions of the center of mass during the ground contact time and is determined by a combination of the stiffness of the leg spring (k_{leg}), half the angle swept by the leg spring (θ) and the compression of the leg spring (ΔL, McMahon and Cheng, 1990). Equation 4 can be rewritten to show the relationship between k_{vert}, k_{leg} and θ by defining F in terms of k_{leg} and ΔL (equation 1) and defining Δy in terms of L_0, ΔL and θ (equation 2):

$$k_{vert} = k_{leg}\Delta L/[\Delta L - L_0(1 - \cos\theta)]. \tag{5}$$

Equation 5 shows that when the leg spring is oriented vertically ($\theta=0°$) during the entire time that it is in contact with the ground (e.g. during hopping or running on the spot), $k_{vert}=k_{leg}$. As θ increases above zero (e.g. during forward locomotion), k_{vert} increases relative to k_{leg}. A detailed discussion of the concept of the effective vertical stiffness is included in McMahon and Cheng (1990).

In the spring-mass model, the length of time that the system remains on the ground is determined by the vertical motions of the center of mass and thus depends on k_{vert}. If the spring-mass system has a large downward velocity as it hits the ground, the gravitational forces acting on the mass are small compared with the inertial reaction forces, and the system will remain in contact with the ground for half of a resonant period of vertical vibration ($T/2$). Half of a resonant period of vibration can be calculated from k_{vert} and the body mass of the animal (M):

$$T/2 = \pi(M/k_{vert})^{0.5}. \tag{6}$$

It is important to remember that k_{vert} is determined by a combination of k_{leg}, ΔL and θ. As a result, $T/2$ depends on a combination of the vertical and horizontal motions of the spring-mass system. We compared $T/2$ with the measured ground contact times (t_c) of trotting and hopping animals to examine the importance of the stiffness of the spring

system in determining how long an animal keeps its feet on the ground during locomotion.

In the final part of the study, we tested whether the leg spring behaves as a simple linear spring throughout the range of forces and displacements that occurs during locomotion. In the spring-mass model described above, all of the mechanical energy fluctuations of the center of mass must be conserved by the leg spring. To test the linearity of the spring, we calculated the rate of elastic energy storage (work rate) in the leg spring based on the assumption of a simple linear spring. If the assumption is correct and the leg spring behaves as a simple linear spring, the work rate of the spring will be similar to the mechanical work rate of the center of mass during locomotion. However, if the assumption is incorrect and the leg spring does not behave as a simple linear spring, the work rate of the spring will be calculated incorrectly and will not match the work rate of the center of mass. For a simple linear leg spring, the mass-specific work rate of the spring (P_{spring}) can be calculated from the stiffness of the leg spring (k_{leg}), the peak force in the spring (F), the step frequency (f) and body mass (M) by the following equation:

$$P_{spring} = (0.5F^2f)/(k_{leg}M). \qquad (7)$$

We calculated the mechanical work rate of the center of mass using allometric equations from an earlier study which included mammalian species similar to those in our study (Heglund *et al.* 1982a). Over the whole size range of animals, we compared the mass-specific work rate of the center of mass and the mass-specific work rate of the leg spring at equivalent speeds. This comparison was designed as a first test of whether the leg spring approximates the behavior of a linear spring in the variety of mammals in this study. However, this comparison was not designed to resolve small deviations from the behavior of a linear spring.

Results

Spring properties as a function of speed

The stiffness of the leg spring (k_{leg}) changed only slightly with speed in all of the animals (Fig. 2A–D). Over a threefold range of trotting speeds in the dog, k_{leg} increased by 16% from 4.24 to 4.92 kN m^{-1}. In the goat and the horse, k_{leg} increased by 25% and 29% respectively, and in the kangaroo, k_{leg} decreased by 21% over the range of speeds measured. The stiffness of the leg spring (k_{leg}) was calculated from the ratio of the peak force (F) to the peak displacement of the leg spring (ΔL, equation 1). On average for all the animals, F increased by 35%, ΔL increased by 20% and k_{leg} increased by 12% between the lowest and highest speeds.

The effective vertical stiffness (k_{vert}) increased dramatically at higher speeds in spite of the relatively slight changes in k_{leg} (Fig. 2A–D). The effective vertical stiffness increased at higher speeds because half the angle swept by the leg spring while it was in contact with the ground (θ) increased (Fig. 2E–H). When θ was greater, the vertical excursion of the center of mass during the ground contact phase (Δy) decreased, and k_{vert} increased (equation 4). On average for all of the animals, θ increased by 31%, Δy decreased by
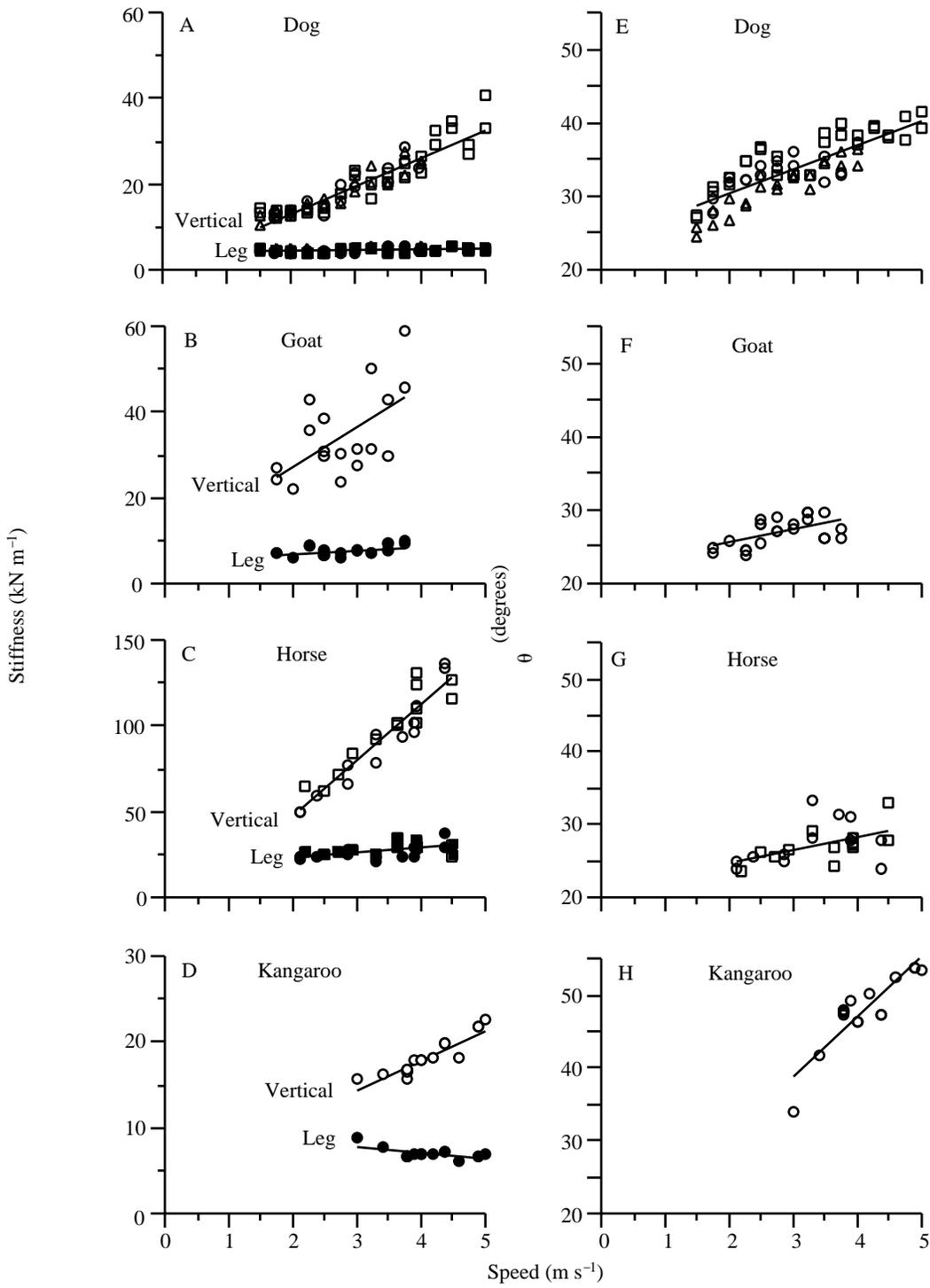
Fig. 2

35% and k_{vert} more than doubled between the lowest and highest speeds. In the trotting dog, θ increased from 28.6° to 40.4° and k_{vert} increased by 228% (Fig. 2). In the goat, θ increased from 25.1° to 28.5° and k_{vert} increased by 76% over the range of trotting speeds. In the horse, θ increased from 24.7° to 29.2° and k_{vert} increased by 170%. Finally, in the kangaroo, θ increased from 38.7° to 55.3° and k_{vert} increased by 48%. It is important to notice that for a given k_{leg}, k_{vert} depends on $\cos\theta$, a function that is sensitive to small changes in θ in the range used for trotting and hopping (equation 5).

Spring properties as a function of body size

The stiffness of the leg spring increased dramatically with body mass (k_{leg} $M^{0.67}$, Fig. 3C). For a 1000-fold increase in body mass (e.g. horse *versus* white rat), the stiffness of the leg spring increased by approximately a 100-fold. This finding is similar to that of Full and Blickhan (1992), who used the mechanical work rate of the center of mass to calculate the stiffness of the leg spring in a variety of animals. In this study, we calculated the stiffness of the leg spring from the ratio of the peak force (F) to the peak displacement (ΔL) of the leg spring. The peak force increased in direct proportion to body mass (F $M^{0.97}$, Fig. 3A), and ΔL also increased with body mass (ΔL $M^{0.30}$, Fig. 3B).

Half the angle swept by the leg spring during the ground contact phase (θ; Fig. 1) was nearly the same in large and small animals (θ $M^{-0.034}$; Fig. 4A). For example, θ was 29° for the kangaroo rat and 26° for the horse. Because of the similar geometry of the leg spring during the ground contact phase in animals of different sizes, the effective vertical stiffness (k_{vert}) increased nearly in parallel with k_{leg} across the range of body masses (Fig. 4B, k_{vert} $M^{0.61}$). The effective vertical stiffness was about 70-fold greater for a horse than for a white rat.

The ground contact time (t_c) increased with body mass in nearly the same way as half of a resonant period of vertical vibration ($T/2$) (Fig. 5; $t_c=0.0994M^{0.19}$, $r^2=0.927$; $T/2=0.0611M^{0.19}$, $r^2=0.911$). Half of a resonant period of vertical vibration is the amount of time that the spring-mass system would remain on the ground if the landing velocity (the vertical velocity at the instant before the system touches the ground) were large enough for the vertical inertial acceleration to be much greater than the gravitational acceleration. The scaling exponents for t_c and $T/2$ were virtually identical but the coefficient was 38% higher for t_c than for $T/2$. On average, t_c was 38% longer than $T/2$ for the animals in this study.

The work rate of the leg spring was similar to the mechanical work rate of the center of mass for all of the animals regardless of body size (Fig. 6). The mass-specific work rate of the leg spring was nearly independent of body size (P_{spring} $M^{0.11}$, Fig. 6), and the

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Fig. 2. (A–D) In all of the animals, the stiffness of the leg spring (k_{leg}) only changed slightly with speed. In contrast, the effective vertical stiffness (k_{vert}) increased dramatically at higher speeds. The filled symbols represent k_{leg}, and the open symbols represent k_{vert}. (E–H) As speed increased, θ (half of the angle swept by the leg spring) increased in all of the animals. As a result, the effective vertical stiffness (k_{vert}) increased dramatically with speed in spite of the relatively small changes in the stiffness of the leg spring. In the graphs for the dogs and horses, data from more than one animal are included, and each individual animal's data are represented with a different symbol. The lines are the linear least-squares regressions.
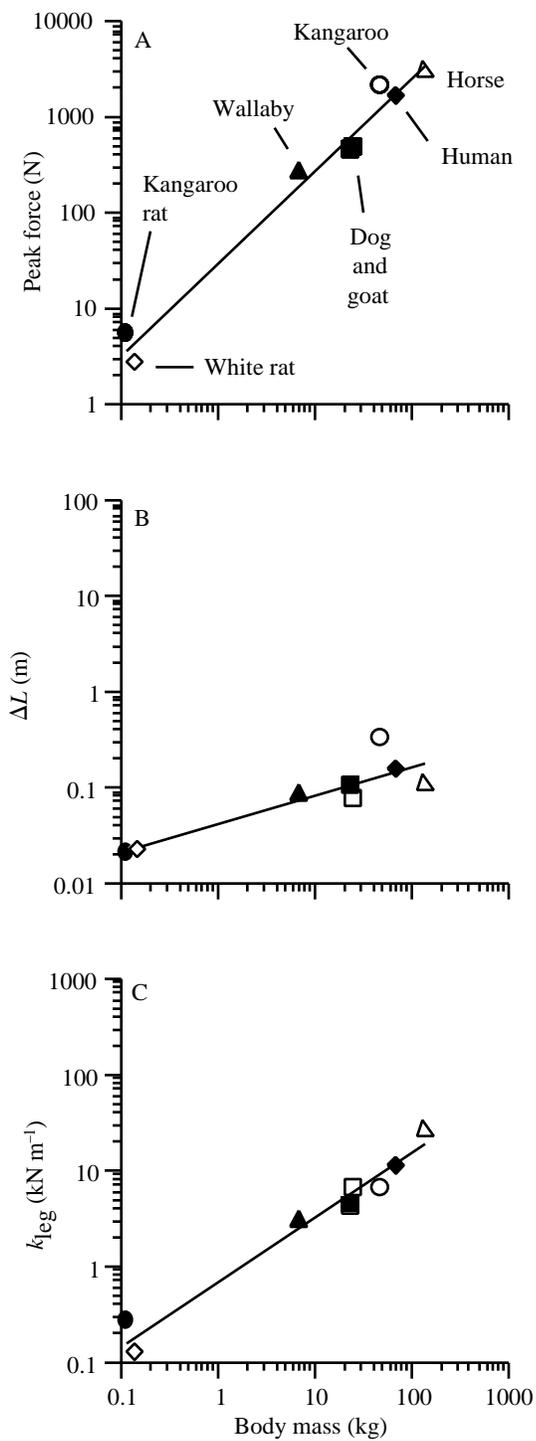
Fig. 3

mechanical work rate of the center of mass (P_{com}) was also nearly independent of body size ($P_{com} \ M^{0.12}$) (calculated from Heglund *et al.* 1982*a*). It is important to note that these comparisons were made at physiologically equivalent speeds and not at the same absolute speed (Table 1). Heglund *et al.* (1982*a*) showed that the mechanical work rate of the center of mass increases with speed in a similar way in mammals of all sizes and, as a result, is independent of body mass at the same absolute speed. In our study, the larger animals used higher absolute speeds (u) than the smaller animals ($u \ M^{0.12}$), so the mechanical work rate of the center of mass increased slightly with body mass. Our finding that the mechanical work rates of the center of mass and of the leg spring are similar at physiologically equivalent speeds in all the animals supports our assumption that the leg spring behaves as a simple linear spring. This finding also provides evidence that the spring-mass model accurately describes the mechanics of locomotion over a large size range of animals.

Discussion

The spring-mass model we use in this study is the simplest possible model for describing the mechanics of bouncing gaits (Fig. 1). This model lumps the mass of the whole body at the hip and represents the entire musculoskeletal spring system as a single linear spring (the leg spring). In reality, the musculoskeletal spring system consists of a complicated system of muscle, tendon and ligament springs which act across nearly every joint in the body (Alexander, 1988). Because of the difference between the simplicity of the spring-mass model and the complexity of the actual musculoskeletal spring system, it is remarkable how well the model describes and predicts the mechanics of locomotion (Blickhan, 1989*a*; Full and Blickhan, 1992; McMahon and Cheng, 1990; He *et al.* 1991).

In the context of this simple spring-mass model, we have been able to find general principles about how the musculoskeletal spring system operates in trotting, hopping and running mammals. In each of these bouncing gaits, the stiffness of the leg spring is nearly the same at all speeds. The spring system is adjusted to operate at higher speeds by increasing the angle swept by the leg spring while it is in contact with the ground rather than by increasing the stiffness of the leg spring. Consequently, at higher speeds, the leg spring experiences greater vertical forces, which result in larger compressions of the leg spring. Furthermore, it sweeps through a greater angle and the center of mass follows a flatter trajectory. The combination of these effects results in an increased vertical stiffness and a decreased period of ground contact.

Our findings also show that the resonant period of vertical vibration is greater in larger animals in spite of their stiffer vertical springs. This is possible because, as body size

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Fig. 3. (A) At equivalent speeds, the peak force in the leg spring increased in direct proportion to body mass ($F=30.1M^{0.97\pm0.14}$, $r^2=0.974$). (B) The peak displacement of the leg spring (ΔL) increased slightly with body mass ($\Delta L=0.0428M^{0.30\pm0.15}$, $r^2=0.803$). (C) The stiffness of the leg spring (k_{leg}), calculated from the ratio $F/\Delta L$, increased with body mass ($k_{leg}=0.715M^{0.67\pm0.15}$, $r^2=0.957$). The symbol for each species is the same in A, B and C, and the lines are least-squares regressions. The values for the human were taken from He *et al.* (1991).
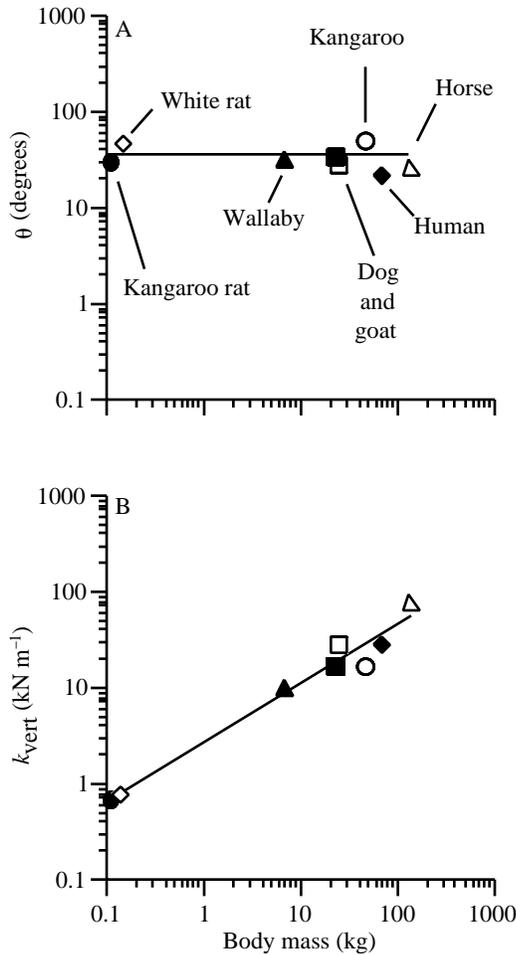
Fig. 4. (A) Half of the angle swept by the leg spring (θ) was nearly independent of body mass ($\theta = 34.35 M^{-0.034\pm0.092}$, $r^2 = 0.123$). (B) The effective vertical stiffness of the spring-mass system increased with body mass with nearly the same scaling exponent as the leg spring stiffness ($k_{vert} = 2.64 M^{0.61\pm0.10}$, $r^2 = 0.970$). The symbol for each species is the same as in part A. The lines are least-squares regressions. The values for the human were taken from He *et al.* (1991).

increases, the spring stiffness increases less steeply than body mass. The predicted half-period of vertical vibration ($T/2$) is proportional to $(M/k_{vert})^{0.5}$. Because k_{vert} is proportional to $M^{0.61}$ (Fig. 4), $T/2$ is proportional to $(M^{1.0}/M^{0.61})^{0.5}$ or $M^{0.19}$ (Fig. 5). The increase in the predicted half-period of vertical vibration in larger animals parallels the increase in the measured ground contact time ($t_c M^{0.19}$).

The results of this study also show that mammals of different sizes move in a dynamically similar manner. Dynamic similarity is a paradigm that proposes how it is possible for animals of different sizes to move in ways that are easily recognizable as
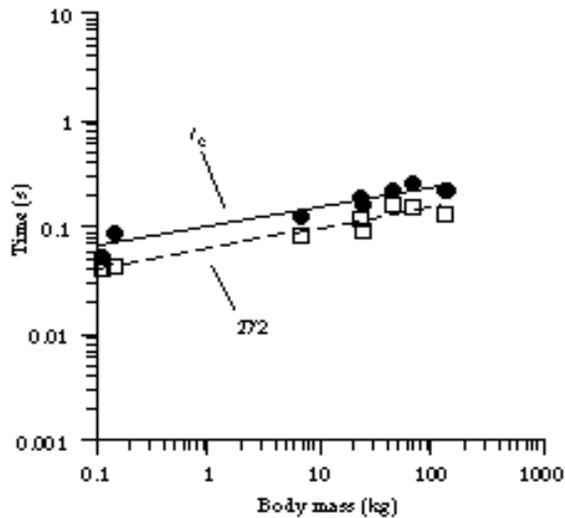
Fig. 5. The ground contact time (t_c) and the resonant period of vertical vibration of the spring-mass system ($T/2$) increased with body mass with nearly the same scaling exponent ($t_c=0.0994M^{0.19\pm0.06}$, $r^2=0.927$; $T/2=0.0611M^{0.19\pm0.05}$, $r^2=0.911$). The filled circles denote the ground contact time, and the open squares denote the resonant period of vertical vibration. The solid and dashed lines are least-squares regressions for t_c and $T/2$ respectively. Values for humans are included and were taken from He *et al.* (1991).
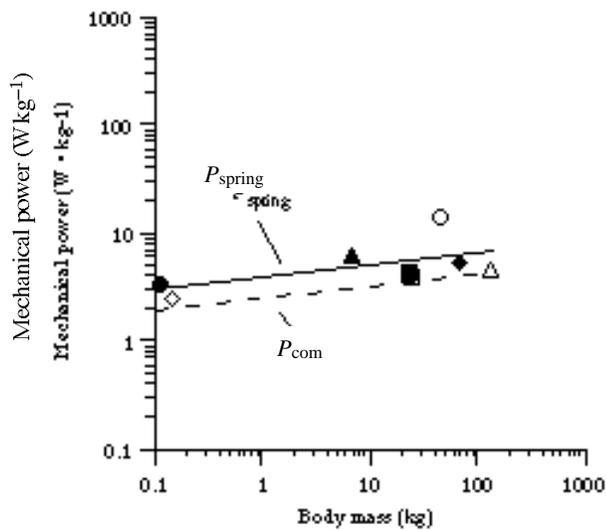

Fig. 6. The work rate of the leg spring (the points and the solid line) is nearly independent of body mass ($P_{spring}=3.80M^{0.11\pm0.15}$, $r^2=0.34$) and is similar to the mechanical work rate of the center of mass (the dashed line; $P_{com}=2.41M^{0.12}$). The mechanical work rate of the center of mass is calculated from Heglund *et al.* (1982*a*). The lines are least-squares regressions. Values for humans are included and were taken from He *et al.* (1991).

similar (Alexander, 1989; Alexander and Jayes, 1983). For example, if a horse and a rat trot in a dynamically similar manner, their feet will spend a similar fraction of a stride period on the ground and they will swing their limbs through similar angles. In the context of the spring-mass model, dynamic similarity between a large and small animal predicts that if they are moving at similar Froude numbers (forward velocity normalized for differences in leg length; Table 1), they will have (1) an equal compression of the leg spring relative to the rest length of the spring ($\Delta L/L_0$), (2) an equal angle swept by the leg spring while it is on the ground (2θ), (3) an equal fraction of the predicted half resonant period of vibration spent in contact with the ground [$t_c/(T/2)$] and (4) an equal ratio of peak force in the leg spring to the weight of the body (F/Mg).

Our findings support the hypothesis that mammals of different sizes move in a dynamically similar manner at physiologically equivalent speeds. This conclusion is based both on our results about the mechanics of locomotion and on the observation that the leg lengths of the animals in this study are proportional to $M^{0.34}$ (Table 1). First, we find that the compression of the spring (ΔL) is about 25% of leg length in animals of all sizes ($\Delta L/L_0$ $M^{0.30}/M^{0.34}$; Fig. 3B, Table 1). Second, as predicted by dynamic similarity, half the angle swept by the leg spring (θ) is similar in animals of all sizes (θ $M^{-0.034}$; Fig. 4A). This result is not significantly different from an earlier study which found that the angle swept by the hindlimb was proportional to $M^{-0.10}$ (McMahon, 1975). Third, the ratio of the ground contact time (t_c) to the predicted resonant period of vertical vibration ($T/2$) does not change in a regular way with body mass [$t_c/(T/2)$ $M^{0.19}/M^{0.19}$; Fig. 5].

The final prediction of dynamic similarity, that the peak force in the leg spring relative to the weight of the body should be independent of animal size, is on average supported by our findings. We find that for all of the animals running at physiologically equivalent speeds, the peak force in the leg spring is nearly proportional to body weight (F/mg $M^{0.97}/M^{1.0}$; Fig. 3A). However, it is important to note that the peak force in the leg spring is about twice as great in the bipedal hoppers (four times body weight) as in the quadrupedal trotters (twice body weight). This peak force refers to the peak vertical force during a ground contact phase and, therefore, is the sum of the forces exerted by both legs in contact with the ground. Our observation of higher peak ground reaction forces in hoppers than in trotters or runners agrees with the findings of earlier studies (Blickhan, 1989b; Full and Blickhan, 1992; Perry et al. 1988). Perry et al. (1988) found that the peak forces in the ankle extensor muscles of a hopping kangaroo rat are about twice as great as in a galloping white rat at their preferred speeds. However, because the kangaroo rat has twice the cross-sectional area of ankle extensors as the white rat, the muscle stresses are similar in both animals.

In spite of the simplicity of the spring-mass model, it describes and predicts many aspects of the mechanics of hopping, trotting and running in animals that vary in body mass over three orders of magnitude. Our observation that the stiffness of the leg spring is nearly constant at all speeds applies equally well to trotting, hopping and running animals. We conclude that a constant-stiffness leg spring may be a basic and invariant principle of running.

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