PREFERRED SPEEDS IN TERRESTRIAL VERTEBRATES: ARE THEY EQUIVALENT?

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Summary

Terrestrial animals have 'preferred speeds' within each gait, that are used much more frequently than others for moving along the ground. Energy costs reach minimal values at these speeds within each gait. In this study we asked whether these speeds are mechanically equivalent among different animals (i.e. speeds where the same levels of peak muscle stress occur). If so, this would help in establishing a link between the energetics and the mechanics of the active muscles at these speeds, providing a first step in understanding why energy costs are minimal. We also asked whether peak muscle stress reaches a similar fraction of the maximal isometric stress at these speeds. If so, this would suggest that muscles are structured so that a similar reserve capacity remains, with a similar safety factor for avoidance of injury in response to prolonged repetitive loading. We compared two species that use quite different locomotory methods at their preferred speeds: white rats that gallop and kangaroo rats that hop. We measured peak stress in the ankle extensor muscles of these two species, as they moved at their preferred speeds, using a force platform/ciné analysis technique. We also measured the maximum isometric force that this muscle group could develop in situ in the same individuals. We found the ankle extensors of white rats and kangaroo rats developed virtually identical levels of peak stress at their preferred speeds (70 ± 6 kPa and 69 ± 6 kPa, respectively, mean ± s.e.), despite a fourfold difference in peak ground reaction force per unit body mass exerted on each limb. The values of peak isometric stress in situ were also virtually identical (206 ± 17 kPa and 200 ± 9 kPa, respectively). Our finding that the peak muscle stress is about one-third of maximum isometric stress at the preferred speeds is consistent with the idea that these are mechanically equivalent speeds, where the same fraction of available muscle fibres is recruited. Finding nearly identical values in two species that move in such different ways (galloping vs hopping), and have such large differences in ground reaction force exerted by each limb, suggests this may be true more generally for terrestrial vertebrates.

Key words: locomotion, speed, muscle force, gait.

Introduction

Terrestrial mammals exhibit clear preferences for the speeds they use in nature, although they are capable of utilizing and, on occasion, sustaining a wide range of speeds. These preferred speeds were observed by Pennycuick (1975) in wildebeest, gazelles and zebras as they migrated across the African plains. The domestic horse has also been found to have a preferred speed within each gait (Hoyt & Taylor, 1981); and many species have been observed to use certain speeds much more frequently than others when they move along a runway containing a force platform (Cavagna, Heglund & Taylor, 1977; Heglund, Cavagna & Taylor, 1982a; Perry, Blickhan & Taylor, 1986).

Why are these speeds preferred? Hoyt & Taylor (1981) found that the energy cost of locomotion reached a minimum value at the preferred speeds in horses, and it seems likely this will also prove to be the case for other vertebrates. In an attempt to explain why cost is minimal at these speeds, the mechanics of the locomotory system have been linked with the energy consumption of the animals (Heglund & Cavagna, 1985; Taylor, 1985). It has been suggested that preferred speeds are mechanically equivalent speeds among different species, where muscle stress (force/cross-sectional area) and bone strain (change in length/total length) reach the same optimal levels. This would reflect both the similar material properties of muscle and bone and a similar structure so that the same reserve capacity would remain at the preferred speeds. This design might be important not only for minimizing cost but also for avoiding injury during prolonged repetitive loading (Biewener & Taylor, 1986; Taylor, 1978).

Maximum isometric stress appears to be a nearly invariant property of mammalian striated muscle (Close, 1972), reflecting a basic similarity in the sarcomere, the force-generating element. *In vivo* muscle stress is the same when mammals are: (1) using their muscles in similar ways (with respect to force–length and force–velocity relationships) and (2) using the same fraction of their muscle cross-sectional area. Evidence that terrestrial mammals use their muscles in similar ways for sustaining a constant speed along the ground comes from studies in which mammals as diverse as kangaroos and dogs were shown to use their muscles to operate the same 'pendulum' and 'spring' mechanisms (Cavagna *et al.* 1977). There is little evidence that mammals use the same fraction of their muscle at preferred speeds. However, it seems reasonable to suppose that mammals are structured so that their muscles have the same reserve capacity at these speeds.

A second reason to expect similar muscle stresses at preferred speeds is that limb bones, the other basic element involved in the support and movement in mammals, have similar strains. Biewener & Taylor (1986) have shown that bone strains are similar at equivalent speeds in goats, dogs and horses. The safety factor of their limb bones is also the same because the failure stress of mammalian bone is uniform (Biewener, 1982).

To investigate whether muscle stresses are the same at the preferred speeds, we chose two mammals of similar body mass which use very different modes of

locomotion at their preferred speeds: the white rat, which gallops, and the kangaroo rat (*Dipodomys spectabilis*), which hops.

Materials and methods

Animals

Six white rats (average mass 239 g) and six kangaroo rats (average mass 106 g) were used in the study. The animals were housed in standard rodent cages and were accustomed to the force platform, although they were not exercised on a regular training schedule.

Determination of preferred speed

Each animal's preferred speed was determined from a series of 5–20 hops (kangaroo rats) or gallops (white rats) across a force platform. The animals were free to choose their speed. The average velocity of each run was calculated from the time required for the animal to interrupt a pair of light beams, 0·5 m apart, near the middle of the platform. The fore–aft horizontal force was monitored to determine that the animal was not accelerating or decelerating during the run. Only even, steady-state runs were accepted.

Muscle force during locomotion

The ankle extensor muscles (gastrocnemius, plantaris and soleus) were chosen for analysis because they act similarly about the ankle, and the ankle joint position can be accurately observed. The anatomy of this muscle group is basically the same for these two rodent species. All three muscles are aligned roughly parallel to the tibia and act about the ankle at the end of the calcaneus (heel bone). The gastrocnemius and soleus insert (*via* a common tendon) onto the calcaneus, and the plantaris tendon passes over the end of the bone to insert onto the digital phalanges. The gastrocnemius and plantaris both originate from the epicondyles of the femur, and the soleus arises from the head of the fibula. Several digital flexor muscles also originate from the caudal aspect of the shank, but their tendons pass close to the centre of rotation of the ankle, and consequently their contribution to ankle extension was assumed to be negligible.

Calculations of muscle force and stress during ground contact were made using a force platform and simultaneous high-speed ciné films. The force platform was composed of a series of seven contiguous 25×25 cm force plates of the type described by Heglund (1981). The central plate of the series was divided longitudinally into two independent plates. The force was recorded independently from each end of the half-plate closest to the camera. In this way both the force exerted by individual feet on this plate and the point of application of the force could be determined. The point of application, in the fore–aft direction, was proportional to the ratio of the force measured at one end to the total force measured by the plate. The natural frequency of the plate was 300 Hz in the

longitudinal direction and 400 Hz in the vertical direction, with cross-talk of no more than 2 % between the two channels. The dependency of the force reading on the point of application on the plate surface was no more than 2 % of the force. The smallest resolvable force was 10 mN. The position calculation was accurate to ±0·5 mm after being corrected for cross-talk. To determine whether the animal was running at a constant average speed, we also measured the total ground reaction force by summing all the vertical and all the fore–aft horizontal force outputs (lateral forces were ignored) from the seven plates.

Each animal was filmed in lateral projection (Photosonics 16 mm model 1PL camera) at 200 frames s^{-1} as it ran across the central split plate. Prior to filming, the hindlimb of each animal was shaved and marked with a black felt-tip pen to aid in locating the joints on the film. Data were collected through seven channels of an analogue to digital converter, including the following signals: split-plate vertical and horizontal force, split-plate single-end vertical force, whole-platform vertical and horizontal (fore–aft) force, film synchronization (one pulse for each film frame), and photocell output. Each channel was sampled at a rate of 1000 Hz. The force data were digitally filtered using a low-pass filter with a cut-off frequency of 100 Hz.

Runs were selected for analysis if the average speed of the run was nearly constant and within the animal's preferred range, within one standard deviation of the mean of the animal's preferred speed. Joint coordinates were digitized (Vanguard motion analyser) and entered into the microcomputer (IBM PC).

Ankle extensor muscle force was calculated from the individual moments of the vertical and longitudinal ground reaction forces, as illustrated in Fig. 1. This calculation assumes that no antagonistic muscles are active about the ankle and that inertial forces required to accelerate the foot during mid-support are negligible. These assumptions have been shown to be valid by comparing muscle forces measured directly with a tendon force transducer and indirectly with this force platform/ciné technique (Biewener et al. 1988).

Isometric force measurement

Maximum isometric force of the ankle extensor group was measured on each animal following the force platform and film recordings. All animals were anaesthetized using sodium pentobarbital. The isometric force measurements were made in situ in an apparatus designed to hold the leg rigidly over the range of joint angles normally encountered during locomotion. The femur and tibia were clamped with pins, screws and dental acrylic. The force transducer (Kistler model 9203) was clamped to the calcaneus directly along the line of action of the extensor muscle group. The force transducer had a resolution of 1 mN and a resonant frequency of 27 kHz.

The ankle extensor group was stimulated via the tibial nerve. Maximal muscle force was obtained using stimulation of 1 V at 100 Hz with square wave pulses of 0·5 ms duration. Supramaximal stimulation was ensured by doubling the voltage.
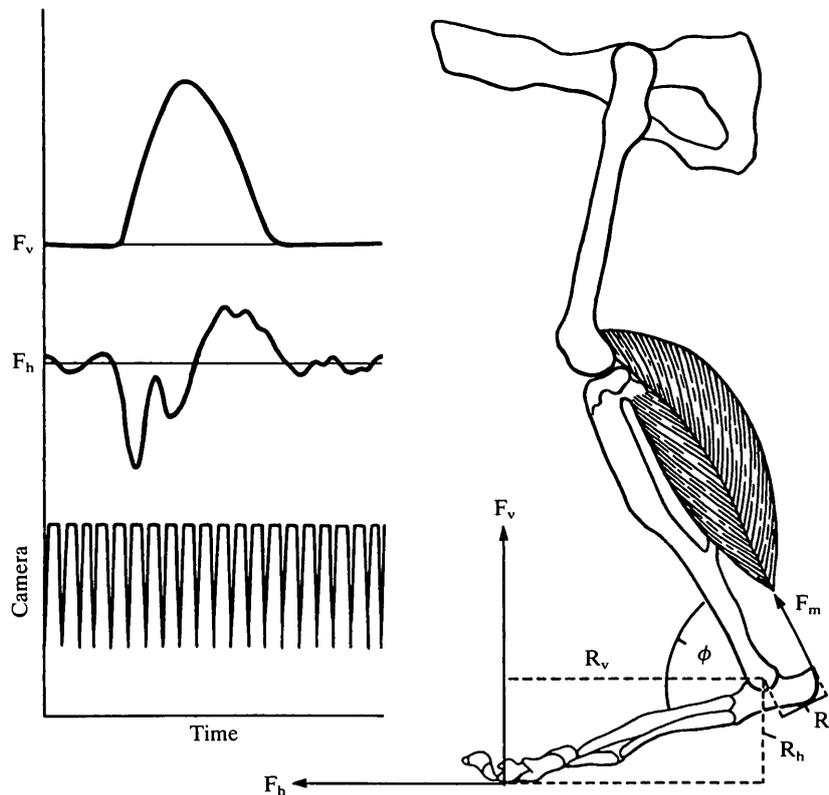
Fig. 1. Illustration of the method used for calculating muscle force (F_m) from force platform and high-speed film data. The force platform measured the vertical and horizontal components of the ground reaction force (F_v and F_h) and determined the point of application of the force. The film analysis provided the perpendicular distances (R_v and R_h) of these force vectors from the ankle joint as well as the angle of the ankle joint (ϕ). The ankle angle was defined as the angle formed by the intersection of the axes of the tibia and the calcaneus, the metatarsals being an unreliable indicator of this joint angle (we observed dorsiflexion of the foot between the ankle and the metatarsophalangeal joint). The moment about the ankle (M_a) of the ground reaction force was calculated from the individual moments of the horizontal and vertical components of the force: $M_a = F_vR_v + F_hR_h$. The ankle extensor moment arm (R_a) was obtained by morphometry. Ankle extensor force was calculated as: $F_m = M_a/R_a\sin\phi$. Film and force records were synchronized using the camera shutter pulse output.

The stimulator (Frederick Haer Pulsar 6bp) was connected to a pair of hooked silver electrodes positioned 1–2 mm apart on the nerve.

Anatomical measurements

Anatomical measurements were made on each animal at the conclusion of the experimental phase of this study. The length of the limb segments (shank, thigh and pelvis) and moment arm (the distance from the centre of rotation of the ankle to the end of the calcaneus) were measured with calipers to the nearest 0·1 mm.

Segment length was defined as the distance from the centre of rotation of one joint to the centre of rotation of the other.

The average muscle cross-sectional area of the ankle extensors was determined by dividing the muscle volume by the mean fibre length (Alexander, 1974). The muscle volume was determined from muscle mass, assuming a muscle density of $1060 \, \mathrm{kg \, m^{-3}}$; mean fibre length was calculated as the average of 10 determinations made on each muscle. This method of calculating muscle cross-sectional area ignores muscle pinnation; however, in both species the angle of pinnation in the ankle extensors did not exceed $23°$, which introduces less than a 7 % error in the estimate of fibre cross-sectional area (Alexander, 1981). Muscle stress was calculated as muscle force divided by fibre cross-sectional area.

Results

Preferred speed

Each animal showed a clear preference for a narrow range of speeds when it moved along the runway at a constant average speed. Occasionally animals would move at higher or lower speeds. Indeed, it is possible to obtain a series of experiments spanning a wide range of speeds, as we have reported in previous force platform studies (Cavagna et al. 1977; Heglund et al. 1982a), but only after many trials. This clustering of experimental speeds is illustrated in Fig. 2 for a white rat and a kangaroo rat. The two graphs present data from the individuals of each species showing the widest distribution of speeds obtained in this study (a range of $0.8 \, \mathrm{m \, s^{-1}}$ for the white rat and $1.0 \, \mathrm{m \, s^{-1}}$ for the kangaroo rat). However, the animals are capable of sustaining constant average speeds over a nearly four-fold greater range of speeds.
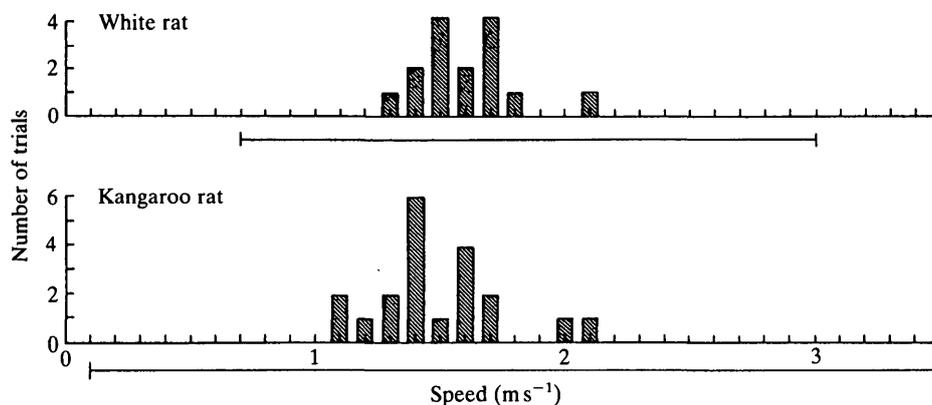

Fig. 2. The speeds which a white rat (top) and a kangaroo rat (bottom) used, when moving along a runway at a constant average speed, clustered within a narrow range of those that the animals could easily sustain. The data presented illustrate the widest range of speeds that were obtained for any individual of each species. Bars under histograms represent the range of sustainable constant average speeds for each species.

Table 1. *Means and variations of freely selected speeds of white rats (galloping) and kangaroo rats (hopping) clearly indicate preferred speeds within a narrow speed range in both species*

Animal	Mean body mass (g)	Mean speed (m s^{-1})	N	Standard deviation	Coefficient of variation (%)
White rat	266	1·65	15	0·39	24
	216	1·40	10	0·18	13
	215	1·33	5	0·09	7
	220	1·42	15	0·19	13
	320	1·58	15	0·19	12
	195	1·53	12	0·12	8
Mean	239	1·48			
Kangaroo rat	94	1·28	10	0·31	24
	109	1·31	10	0·14	11
	106	1·17	10	0·18	15
	117	2·08	6	0·25	12
	98	1·44	15	0·23	16
	113	1·48	20	0·27	18
Mean	106	1·46			

The gait preferred by the white rats was a gallop, and the mean speed observed for all experiments was about 1·5 m s^{-1} (Table 1). On a treadmill, white rats of the size used in these experiments (200–300 g) changed gaits from a trot to a gallop at a speed of about 0·7 m s^{-1}, and could sustain speeds up to 3 m s^{-1} for short intervals. The lowest speed obtained in these experiments was 1·2 m s^{-1}, nearly twice the speed at which the animals switch gaits from a trot to a gallop. Likewise, the highest speed obtained in our experiments was well below the highest speed easily achieved on a treadmill.

The only gait utilized by the kangaroo rat was a hop, and the mean hopping speed for all experiments was about 1·5 m s^{-1} (Table 1). On a treadmill, kangaroo rats of the size used here (about 100 g) could hop at a constant speed as low as 0·1 m s^{-1} for prolonged periods and reached speeds as high as 3·5 m s^{-1} for short intervals. In our experiments the animals hopped at constant speeds over only a very small fraction of this range of speeds. The lowest speed we obtained was 1·0 m s^{-1} and the highest was 2·1 m s^{-1}. The kangaroo rat, like the white rat, appears to have a speed it prefers to use for locomotion.

Muscle stress at preferred speed

Mean body mass of the white rats was twice that of the kangaroo rats (239 *vs* 106 g), whereas mean cross-sectional areas of the ankle extensors of both species were similar (133 *vs* 162 mm^2). Therefore the cross-sectional area of the ankle extensors, relative to the body mass that the muscles must support, was twice as great in the bipedal kangaroo rat as in the quadrupedal white rat. It is interesting that the bipedal kangaroo rat appears to compensate for the loss of the support

function of its front limbs in locomotion by having twice the cross-sectional area of muscles in its hindlimbs.

The peak forces measured in the ankle extensors of the white rats and the kangaroo rats were similar when the animals moved at their preferred speeds (8·9 vs 11·1 N). The similarity in peak forces at the preferred speeds and in the cross-sectional areas of the ankle extensors results in similar peak muscle stresses (Table 2). In fact, both the ranges of peak stresses observed in individuals and the mean values for all individuals were virtually identical at the preferred speeds (a mean of 69 kPa in the kangaroo rats vs 70 kPa in the white rats).

Maximal isometric stress

Maximal isometric forces of the ankle extensors measured *in situ* were also similar in these two species (27 N in the kangaroo rats vs 32 N in the white rats, Table 2). Maximal isometric force was not significantly different over the range of ankle and knee angles observed during locomotion. Maximal isometric stress, like peak locomotory stress, was virtually identical in the two species (206 kPa in the white rats vs 200 kPa in the kangaroo rats) (Fig. 3).

Discussion

Our finding that white rats and kangaroo rats have a preferred speed was expected, since preferred speeds have been observed both for animals in nature and for animals free to choose their speed as they run along an experimental runway, a track or a wheel. Pennycuick (1975) found that although wildebeest used gallop (canter) speeds spanning a range from 1·4 to 11·0 m s^{-1} in their migrations across the African plains, 80 % of the speeds measured were between 3 and 6 m s^{-1}. Hoyt & Taylor (1981) found that a 140-kg horse could gallop on a treadmill at speeds as low as 3·5 m s^{-1} and easily sustain the treadmill's top speed of 6·8 m s^{-1} for long periods. The same horse, galloping freely, used only a narrow range of speeds, from 5·0 to 5·8 m s^{-1}. Although we have not systematically investigated the preferred speeds used by different species, we have consistently observed in our force platform studies, involving a wide variety of birds and mammals, that we quickly obtained data over a narrow range of speeds; and that it proved difficult and time consuming to obtain data at other speeds (Cavagna *et al.* 1977; Heglund *et al.* 1982*a*).

The speeds used by the two species in this study spanned only a small fraction of their total range. The highest speed we obtained for a white rat was 2·1 m s^{-1}, although Wood (1972) reports a top speed of 2·7 m s^{-1} for white rats of similar body size. These animals can easily sustain constant speeds as low as 0·1 m s^{-1} on a treadmill (Taylor, Schmidt-Nielsen & Raab, 1970); yet despite the wide range of speeds available to the animals, more than two-thirds of our experiments from each animal fell within a speed range of only 0·3 m s^{-1}. The same preference for a narrow range of available speeds was also true of the kangaroo rats. Djawdan & Garland (1985) report a top speed of 8 m s^{-1} for a closely related species of

Table 2. *Maximum isometric ankle extensor muscle force and stress measured in situ compared with the average peak muscle force and stress measured during running and hopping at the preferred speed*

Animal	Mean body mass (g)	Muscle cross-sectional area (mm^2)	Maximum isometric force (N)	Maximum isometric stress (kPa)	Mean peak locomotory force (N)	Mean peak locomotory stress (kPa)	Ratio of mean peak locomotory to maximum isometric force
White rat	266	153	31	202	7·9	51	0·25
	216	114	29	256	8·3	73	0·29
	215	184	25	136	9·9	54	0·40
	220	104	21	201	6·9	66	0·33
	320	135	28	208	12·2	90	0·44
	195	107	25	234	8·6	81	0·34
Mean ± S.E.M.	239 ± 20*	133 ± 13	27 ± 1	206 ± 17	8·9 ± 0·8	69 ± 6	0·33
Kangaroo rat	94	107	22	205	8·2	76	0·37
	109	160	38	238	8·7	54	0·23
	106	198	39	197	11·9	60	0·31
	117	157	27	173	14·2	91	0·53
	98	150	31	207	12·2	81	0·39
	113	199	36	181	11·4	57	0·32
Mean ± S.E.M.	106 ± 4*	162 ± 14	32 ± 3	200 ± 9	11·1 ± 0·9	70 ± 6	0·36

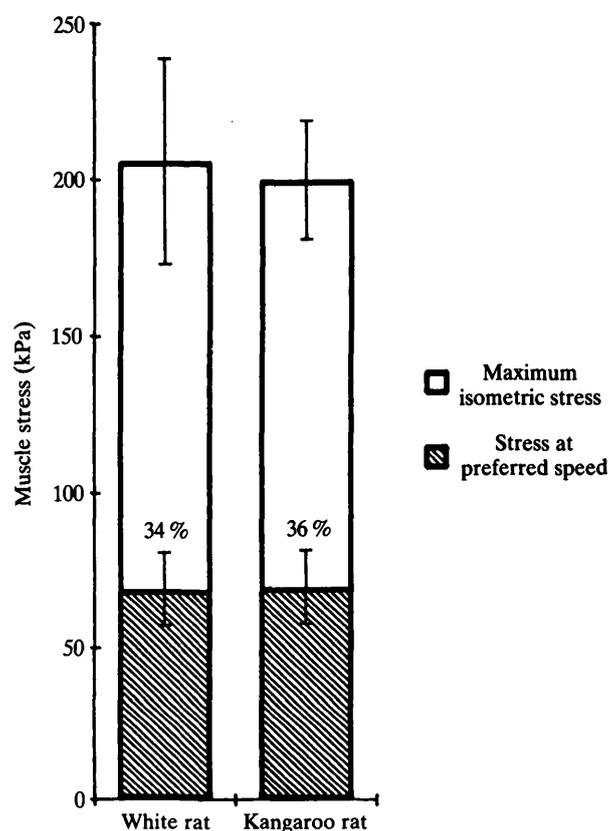* Significantly different between the two species ($P = 0.05$).

Fig. 3. Stress in the ankle extensors at the preferred speed of white rats (left) and kangaroo rats (right) is compared with maximal isometric stress developed by these muscles. Percentages indicate locomotory stress as a percentage of maximal isometric stress for each species. Error bars indicate 95 % confidence intervals. $N = 6$.

kangaroo rat of the same size. The top speed we observed was only $2 \cdot 1 \, \mathrm{m\,s^{-1}}$. These animals can maintain constant speeds as low as $0 \cdot 1 \, \mathrm{m\,s^{-1}}$ on a treadmill (Thompson, MacMillen, Burke & Taylor, 1980). However, more than two-thirds of our experiments with kangaroo rats fell within a range of only $0 \cdot 4 \, \mathrm{m\,s^{-1}}$.

In this study we asked whether preferred speeds were mechanically equivalent speeds where the same levels of peak locomotory muscle stress occurred among different animals. Our results clearly demonstrate that this is the case for the two species that we investigated. Both peak locomotory stress at the preferred speeds and maximal isometric stress of the ankle extensors were virtually identical for the two species. This is a remarkable finding, considering that, at this speed, peak vertical acceleration during each hop of the kangaroo rat (peak ground reaction force/body mass) is twice as great as in a stride of the white rat, and the peak acceleration per limb is on average four times as great because the animal is using two instead of four limbs. A combination of greater cross-sectional area, and a greater mechanical advantage of the muscles around the ankle joint, compensates

almost exactly for the large difference in forces applied to the ground, so that the stresses in the muscles are identical. Such precise compensation involving multiple factors seems to indicate the operation of a basic design principle rather than a fortuitous coincidence.

Although other studies have not examined the question of stress at preferred speeds, reported values of muscle stress during locomotion are consistent with our findings, lending support to the idea that peak muscle stress is the same at preferred speeds in terrestrial birds and mammals. Using data presented in another study of kangaroo rats moving over force platforms (Biewener, Alexander & Heglund, 1981), we calculate similar values of about 60 kPa for muscle stress in the ankle extensors at the preferred speed, and find that muscle stress approximately doubles as speed doubles, reaching a value of about 100 kPa at $2 \cdot 7 \, \mathrm{m \, s^{-1}}$. At this speed, which is well below the animal's top speed, the locomotory stress would have increased from 35 % to about 50 % of maximal isometric stress. In a bird, the quail, Clark & Alexander (1975) report stresses of 50–100 kPa during running, values which are much the same as we have observed in our two species of rodents. Studies of animals operating at speeds close to their maximal speeds have yielded higher stress values, approximating values of maximal isometric stress. For example, Alexander & Vernon (1975) report values of 150 kPa for the ankle extensors of a wallaby and 170 kPa for the ankle extensors of a big red kangaroo hopping at high speeds. Thus it appears that animals operate with muscle stresses only about one-third of their maximal isometric stress at their preferred speeds, but they are capable of developing stresses nearly equal to maximal isometric stress at their highest speeds.

The finding that animals have peak muscle stresses approximately one-third of their maximal isometric stress at preferred speeds indicates that a similar fraction of the cross-sectional area of their muscles is active. This follows from the reasonable assumption, discussed in the Introduction, that the muscles are operating over similar ranges of their force–velocity and force–length relationships. However, until we can determine where the muscles are operating with respect to these relationships, it is not possible to make a reasonable estimate of the fraction of cross-sectional area that is active. Assuming the muscles operate only over their optimal length in terms of force generation (on the plateau of the force–length relationship), this fraction of the cross-sectional area could be between 20 % (if the force is generated on the negative side of the force–velocity curve) and 100 % (if the muscle shortens at approximately one-third of maximum shortening velocity, where its power output and efficiency are maximal).

Peak muscle stress probably occurs when an animal lands on each stride, and its muscles and tendons are stretched (storing strain energy). Under these conditions stresses can reach values up to 1·6 times the maximal isometric stress (Katz, 1939). If this is the case, then a considerable reserve capacity would remain at the preferred speed, since only 20 % of the cross-sectional area of the muscles would be required to generate the peak muscle stress observed at these speeds (one-third maximal isometric stress). The observation that at top speed animals generate

peak stresses 3–4 times as high as at the preferred speed is consistent with the peak stresses being generated when the muscle is on the negative plateau of the force–velocity relationship; these peak stresses would require only 60–80 % of the muscle to be active.

However, the classic analysis of Hill (1950) of muscular performance during locomotion assumes that peak stresses occur when the muscles shorten as the animal accelerates its limbs during each stride. Under these conditions the maximal mechanical power output and maximal efficiency of the muscles occur at about one-third of the maximum shortening velocity, and the muscle only generates one-third of its maximal isometric stress. To achieve the peak stresses observed at the preferred speeds under these conditions would require that almost all of the muscle be active, and would leave little or no reserve capacity. Furthermore, muscle stress approaching maximal isometric stress, observed at the fastest speeds of locomotion, would clearly not be possible in a muscle shortening at one-third of its maximum shortening velocity.

We have observed that the energy consumed by each gram of muscle is directly proportional to the stride frequency at another mechanically equivalent speed, the trot–gallop transition speed. Both stride frequency and energy consumption increase by a factor of about five as body size decreases from 170 kg ponies to 30 g mice, but the cost per stride per gram is constant (Heglund, Fedak, Taylor & Cavagna, 1982b). We would anticipate that cost per stride per gram at the preferred speeds would also be independent of body size, that storage and recovery of elastic strain energy would be maximized, and that this might explain the minimization of energy costs at these speeds. This matter certainly merits further and more detailed investigation.

Although the finding of similar muscle stresses at the preferred speeds does not necessarily indicate an optimal safety factor to injury, it is suggestive. Presumably this relatively low value of stress allows prolonged repetitions of force generation without damage, although damage may occur with progressively fewer repetitions as maximal isometric stress is approached at top speed. This interpretation is consistent with our observations of muscle soreness in humans asked to train at higher levels of muscle stress than they prefer to use, and with the finding that muscle tissue is damaged in white rats subjected to high levels of peak muscle stress by running down an inclined treadmill (Armstrong, Ogilvie & Schwane, 1983).

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