

FORCE DEVELOPMENT DURING SUSTAINED LOCOMOTION: A DETERMINANT OF GAIT, SPEED AND METABOLIC POWER

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SUMMARY

This paper develops three simple ideas about force development during sustained locomotion which provide some insights into the mechanisms that determine why animals change gait, how fast they can run, and how much metabolic energy they consume. The first idea is that the alternate stretch-shorten pattern of activity of the muscles involved in locomotion allows muscle-tendon units to function as springs, affecting the amount of force a given cross-sectional area of muscle develops, and the metabolic requirements of the muscles for force development. Animals select speeds and stride frequencies which optimize the performance of these springs. The second idea is that muscle stress (force/cross-sectional area) determines when animals change gait, how fast they run and their peak accelerations and decelerations. It is proposed that terrestrial birds and mammals develop similar muscle stresses under equivalent conditions (i.e. preferred speed within a gait) and that animals change gaits in order to reduce peak stresses as they increase speed. Finally, evidence is presented to support the idea that it is the time course of force development during locomotion, rather than the mechanical work that the muscles perform, that determines the metabolic cost of locomotion.

MUSCLE-TENDON SPRINGS

Locomotion at a constant speed is a cyclic process with the mechanical events repeated once during each stride. Major muscle groups (e.g. the limb extensors) are alternately stretched and then shorten while they are active during each stride (Goslow *et al.* 1981). Work is performed on the active muscles as they are stretched and much of this energy can be stored in elastic elements of the active muscle-tendon systems. Some of this elastic energy can be recovered during the subsequent part of the stride as the active muscles and tendons shorten. The recovery of this stored elastic strain energy reduces the amount of metabolic energy consumed by muscles as they shorten, thereby reducing the metabolic energy that an animal consumes to sustain a constant speed. The importance of elastic strain energy in locomotion was first demonstrated in the classic study of human locomotion by Cavagna, Saibene &

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Margaria (1964). These authors found that more than half of the energy supplied to lift and reaccelerate the centre of mass during each stride could be recovered from elastic energy stored as the centre of mass fell and decelerated earlier in the stride. Cavagna, Heglund & Taylor (1977) extended these studies to other animals. They found that the same elastic storage mechanisms existed in running bipedal birds, hopping bipedal mammals and running and galloping quadrupeds.

The alternate stretch-shorten pattern of muscle activity typical of terrestrial locomotion has major effects on the force developed/cross-sectional area of muscle, the force-velocity curve, the relationship between efficiency and shortening velocity, the recruitment pattern of motor units and other parameters normally used to relate the mechanics and energetics of isolated muscle or muscle fibres to the mechanics and energetics of locomotion. Norm Heglund and Giovanni Cavagna consider how these effects are related to recovery of elastic strain energy in their papers in this volume.

EVIDENCE FOR 'TUNED' SPRINGS DURING LOCOMOTION

There are several lines of evidence that suggest animals operate their muscle-tendon springs in a manner that maximizes storage and recovery of elastic strain energy. Pennycuick (1975) observed that African plains animals utilize only very narrow speed ranges within each gait as they move about in nature. Yet in the laboratory, the animals will sustain steady state locomotion over a two- to three-fold range of speeds within each gait while moving on a motor-driven treadmill (Taylor, Heglund & Maloiy, 1982). What, if anything, is special about the speed animals select in nature? In a careful study of the energetics of locomotion within gaits, Don Hoyt and I (Hoyt & Taylor, 1981) found that horses moving along the ground choose the most economic speeds within each gait (in terms of metabolic energy consumed). Energy cost for moving a given distance increased significantly at faster or slower speeds within each gait. Interestingly, the minimum cost was the same for each gait (walk, trot and gallop). This minimum energy cost at the preferred speed is suggestive of a tuned mechanical system operating at its optimal efficiency.

Additional evidence for a tuned spring system during locomotion comes from measurements of hopping and galloping frequencies. Hopping kangaroos (Dawson & Taylor, 1973) and galloping quadrupeds (Heglund, Taylor & McMahon, 1974) utilize nearly the same stride frequency over a two- to three-fold range of speeds. McMahon (1975) has proposed that this frequency is the resonant frequency of the body (represented as a large multi-jointed spring). Galloping frequency changes with body mass and body dimensions in a manner that is consistent with the changes in resonant frequency predicted by his multi-jointed spring model.

The most direct evidence for the hopping-galloping frequency being a tuned resonant frequency of a 'whole body spring' comes from current experiments on human hopping in our laboratory. (Three undergraduates, Manuel Perez, David Kessler and Claire Farley, are carrying out these studies in our laboratory together with Reinhard Blickhan, N. C. Heglund, T. A. McMahon and myself.) Hopping people, like hopping kangaroos and galloping horses, utilize a nearly constant

frequency over a wide range of speeds (from 0.25 to 2.2 m s^{-1}) (Fig. 1). A very important additional observation is that the same frequency was utilized when the treadmill was turned off (zero speed).

People hopping in place on a force platform under steady state conditions while oxygen consumption is measured provide an experimental system where both mechanical energy output and metabolic energy input of the muscles can be quantified (Thys, Cavagna & Margaria, 1975). The amount of energy contained in the ATP provided to the muscles can be calculated from the stoichiometry of the aerobic pathways by assuming a P/O ratio of 6 (approx. $8.04 \text{ J l}^{-1} \text{ O}_2$). People can hop over a range of constant frequencies by matching their frequencies to that of a metronome. Thus, the average rates of mechanical energy produced and metabolic energy consumed as ATP can be measured over a range of hopping frequencies.

A lower limit for the rate at which elastic energy must contribute to the mechanical energy supplied by the muscle-tendon system during a hop can be calculated by subtracting the metabolic energy supplied to the muscles from the mechanical work they perform. This lower limit is a very conservative estimate that assumes: all of the metabolic energy consumed by the animals is utilized by the active muscles involved in hopping; and that all of the metabolic energy released as ATP is broken down into ADP and P_i is transformed into mechanical energy (100% efficiency of this chemical-mechanical link).

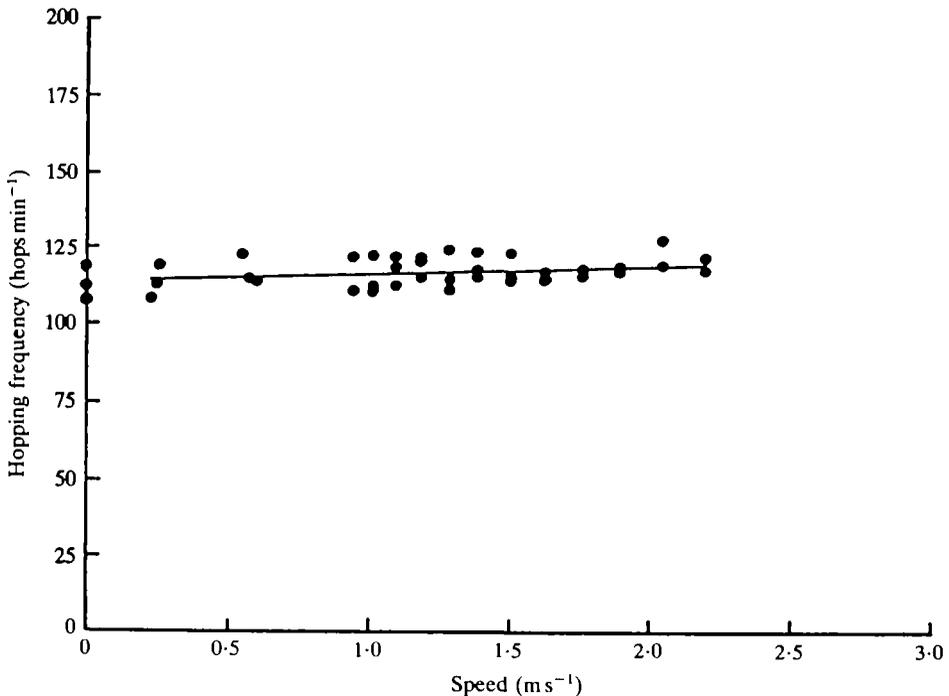


Fig. 1. Hopping frequency as a function of tread speed for three humans (average body mass 63 kg) hopping bipedally on a treadmill. Note that the hopping frequency changed very little with speed and was the same when the treadmill was turned off (zero speed).

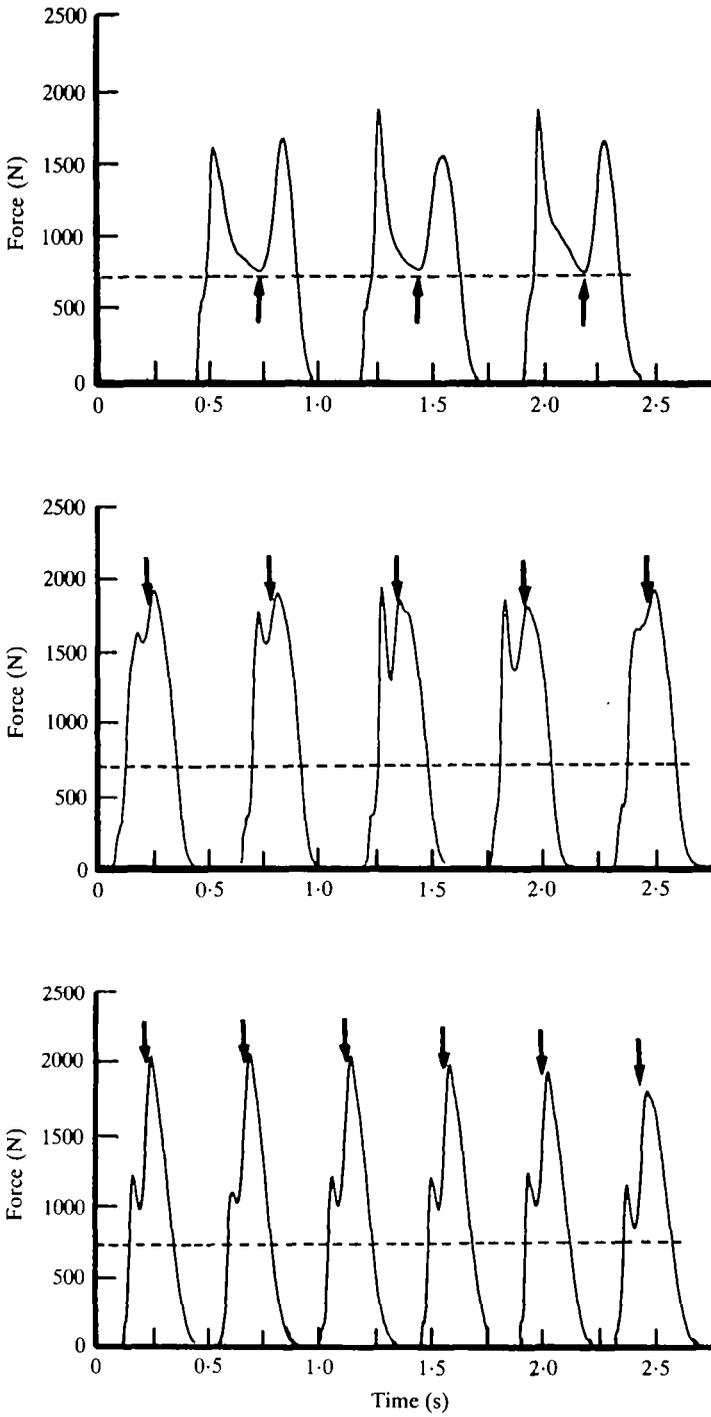


Fig. 2

The results of these experiments demonstrate that the role of elastic strain energy is maximized and that of metabolic energy is minimized when subjects hop at their natural frequency. Fig. 2 (middle graph) shows that the ground reaction force reached its maximum (2000 N) just before the centre of mass began to reverse direction (arrows) and accelerate upwards. Thus most of the energy that had been stored as elastic strain energy was available to contribute to the upward hop. The lower limit for the contribution of elastic strain energy to the mechanical energy of the hop was 43 % with metabolic energy contributing 57 % under these conditions. The lower limit of elastic strain energy decreased to zero when the subject hopped at a frequency about 36 % lower than the natural frequency. The ground reaction force reached about the same maximum and then decreased almost to body weight before the upward acceleration began (Fig. 2, top graph). Thus the elastic strain energy stored on landing was dissipated as heat before it could be utilized for the upward hop. Hopping at frequency about 20 % higher than the subject's natural frequency also decreased the relative contribution of elastic strain energy (from 43 % at the natural frequency to 29 %). Total mechanical energy per hop decreases at the high frequency by about 40 % while peak force remains at about 2000 N. Time of contact appears to be too short to utilize all of the elastic strain energy stored on landing during the upward hop. The behaviour of this system is what would be predicted for a tuned spring with its resonant frequency at the natural hopping frequency.

It seems reasonable to ask whether these human hopping experiments are relevant to bipedal hopping in animals that hop as a normal mode of locomotion or to quadrupedal galloping. The only link that we have established to this point is that all three mechanisms utilize a nearly constant stride frequency over a wide range of speeds. How do the absolute frequencies compare? To find out Manuel Perez (personal communication) analysed stride frequency as a function of speed for a large number of animals hopping and galloping on treadmills by using films that had accumulated in our laboratory from other studies over the last 14 years (expanding the number of galloping species analysed by Heglund *et al.* 1974 from 4 to 25 and including data on hopping mammals ranging from 30 g kangaroo rats to 30 kg red kangaroos). Surprisingly, he found the allometric relationship relating stride frequency and body mass for bipedal hoppers was not different from that for

Fig. 2. Ground reaction forces during a hop for a 69 kg human hopping at a low frequency (36 % below natural); a natural frequency; and a high frequency (20 % above natural). The arrows indicate the point where the centre of mass reverses direction. The dotted line is the force equal to the body weight of the subject. The mechanical energy of each hop, the metabolic energy contained in ATP consumed by the muscles during each hop, and the lower limit for amount of elastic energy stored and recovered during each hop (see text) for each hopping frequency are:

	Top graph Low frequency 1.17 hops s ⁻¹ J hop ⁻¹	Middle graph Natural frequency 1.83 hops s ⁻¹ J hop ⁻¹	Bottom graph High frequency 2.23 hops s ⁻¹ J hop ⁻¹
Mechanical	137	120	76
ATP	137	68	54
Elastic	0	52	22

quadrupedal gallopers. Also, human hopping frequency was predicted almost exactly from body mass by these relationships. Thus there seems to be a fundamental similarity between human hopping, bipedal hopping (in animals using this as a normal mode of locomotion) and galloping whereby mass of the entire body determines stride/hop frequency. All of the evidence is consistent with the idea that all three modes utilize tuned multi-jointed springs that normally operate at the same resonant frequency.

PEAK MUSCLE STRESS HYPOTHESIS

Our laboratory is currently trying to test a hypothesis that has grown out of our studies of the mechanics of locomotion. We have proposed that peak stress in the major locomotory muscles is the same in all species under equivalent conditions (e.g. preferred speed within each gait, gait transitions, top speed, peak accelerations and decelerations, etc.). The hypothesis can be tested directly by measuring muscle stress in limb extensors during locomotion in animals of different size and/or in animals adapted for different levels of performance. This type of data is not available yet, but I think it is worthwhile to review some of the indirect evidence that led us to formulate this hypothesis.

There is good evidence that the peak force exerted by limb extensors increases within a gait but decreases across gait transitions as animals increase their speed. We have found in our force platform studies (Biewener, Thomason, Goodship & Lanyon, 1983; Cavagna *et al.* 1977; Heglund, Cavagna & Taylor, 1982a) that the peak vertical force exerted on the force platform decreases dramatically as quadrupeds switch from a fast trot to a slow gallop. For example, peak vertical force in a dog increased from 1.3 times its body weight (1.3 G) at a slow trot to 2.5 G at a fast trot. Although the dog increased speed, peak force decreased from 2.5 G to 1.5 G as the dog changed gaits from a fast trot to a slow gallop. Peak force increased to 2.75 G at a fast gallop. Rubin & Lanyon (1982) have reported similar results using a force sensitive shoe attached to the foot of a horse. These results led us to suspect that some peak force is reached as speed increases within a gait which necessitates the redistribution of force over time in order for an animal to increase speed, and that this is accomplished by changing gaits.

The hypothesis of the same peak stress under equivalent conditions would predict that animals adapted for running fast would have greater cross-sectional areas of their locomotory muscles in order to run faster at the same muscle stress. If so, then equivalent muscle stresses at gait transitions should also occur at higher speeds than in non-adapted animals. Table 1 illustrates that the higher top speeds of the dog and horse compared to goat and cow are accompanied by higher gait transition speeds.

The hypothesis also predicts that locomotory muscle stresses would be the same for animals of different size at gait transitions, top speed, etc. The force platform data from animals of different size show that peak vertical force/body weight increases in a regular manner with decreasing body size (Cavagna *et al.* 1977; Heglund *et al.* 1982a). For example, Table 2 illustrates that it is nearly twice as large in a chipmunk as in a dog over the entire range of galloping speeds. If peak muscle stresses are the

same under equivalent conditions in these animals, then the mechanical advantage of the muscles, cross-sectional area of the active muscle groups, and/or time course of application of force must vary with size. Biewener (1983) has reported a regular change in mechanical advantage with size which could account for two-fold difference peak vertical forces/body weight observed for the chipmunk and dog.

TIME COURSE OF FORCE DEVELOPMENT AND COST OF LOCOMOTION

The transfer of metabolic energy into mechanical energy does not appear to be the key to understanding the metabolic cost of locomotion. Metabolic cost of locomotion can vary by more than ten-fold with speed and body size, yet these large differences are not reflected by parallel differences in the mechanical energy that the muscles supply to the limbs and body (Heglund, Fedak, Taylor & Cavagna, 1982*b*). For example, the ratio of metabolic power/mechanical power at the trot-gallop transition speed changes by nearly 60-fold as body size increases from 10 g to 100 kg (Table 3).

A priori, one might expect that a good place to look for an explanation of metabolic cost of locomotion would be metabolic cost of generating force. After all, muscles are machines for transforming metabolic energy into force. Only if they shorten while they are active and consuming energy do they convert the metabolic energy into

Table 1. Top speed* and speed at which animals change gaits from trot to gallop compared in animals adapted for high speed locomotion (dog and horse) and in animals of similar size that are not adapted for high speed locomotion (goats and cows)

	Goat	Dog	Cow	Horse
M_b (kg)	20	20	160	170
Top speed* ($m s^{-1}$)	4.25	8.98	6.43	10.4
Trot-gallop speed ($m s^{-1}$)	2.75	4.17	3.78	4.97
Strides/second at T-G transition	2.51	2.52	2.04	2.48

* Top speed sustained for 2 min on treadmill.
 M_b , body mass.

Table 2. Peak ground reaction forces/body weight over the observed range of galloping speeds of a 30 kg dog and a 130 g chipmunk

Gait	Dog		Chipmunk	
	speed ($m s^{-1}$)	F_v /body wt (G)	speed ($m s^{-1}$)	F_v /body wt (G)
Slow gallop	2.64	1.5	1.58	3.0
	2.86	1.75	1.70	3.2
	4.75	2.0	2.10	3.6
	7.25	2.75	2.55	4.1
Fast gallop			2.86	4.8

F_v , peak ground reaction force.

mechanical energy. If they do not change length while they are active, then they consume metabolic energy and generate force without producing any mechanical energy. Likewise if they are active while being stretched, they consume metabolic energy and absorb mechanical energy from the external environment. As discussed earlier, locomotion is a cyclic process with major muscle groups involved in locomotion being alternately stretched and then shortening within each stride. Therefore, it seems worthwhile to consider whether the metabolic cost of generating force during locomotion holds the key to understanding metabolic cost of locomotion.

The metabolic cost of generating force during locomotion has been investigated by Taylor, Heglund, McMahon & Looney (1980). Animals were trained to carry loads evenly distributed along their backs. The accelerations of the centre of mass of the animals and the masses of their limbs were not altered by carrying the loads, therefore the increases in forces exerted by the extensor muscles were directly proportional to the increases in the mass of the loads that were carried. Metabolic cost of generating force measured in this way exactly paralleled the changes in metabolic cost of locomotion as a function of speed and body size (Table 4).

The key to understanding both cost of generating force during locomotion and metabolic cost of locomotion appears to lie in the time course of the cyclic event, the stride. Development of each Newton of force by a small animal requires much more metabolic energy than development of a Newton of force by a large animal, but the force has to be developed and decay at a much faster rate because small animals go

Table 3. *Rates at which metabolic energy is consumed (Taylor, Heglund & Maloiy, 1982) and mechanical work is performed (Heglund, Fedak, Taylor & Cavagna, 1982b) by each kilogram of large and small animals moving at a physiologically equivalent speed (trot-gallop transition)*

Body mass	10 g	1.0 kg	100 kg
Metabolic power (ATP) (W kg^{-1})	19.1	8.96	5.19
Mechanical power (W kg^{-1})	0.60	2.06	8.80
Ratio: metabolic/mechanical	32	4.4	0.59

Table 4. *Metabolic cost of locomotion (Taylor, Heglund & Maloiy, 1982) and metabolic cost of generating force (Taylor, Heglund, McMahon & Looney, 1980) of large and small animals moving at a physiologically equivalent speed (trot-gallop transition)*

Body mass	10 g	1.0 kg	100 kg
Metabolic cost of locomotion (ATP) (W kg^{-1})	19.1	8.96	5.19
Metabolic cost of force generation (ATP) (W N^{-1})	1.95	0.91	0.53
Ratio: locomotion/force	9.8	9.8	9.8

Table 5. *Metabolic cost of locomotion and metabolic cost of generating force during locomotion divided by the number of times the force must be generated and decay per unit time (stride frequency) for large and small animals moving at a physiologically equivalent speed*

Body mass	10 g	1.0 kg	100 kg
Metabolic cost of locomotion per stride (ATP) ($\text{W kg}^{-1} \text{stride}^{-1}$)	2.24	2.00	2.21
Metabolic cost of force generation (ATP) ($\text{W N}^{-1} \text{stride}^{-1}$)	0.23	0.21	0.23

through many more stride cycles/unit time than large animals. Table 5 presents the metabolic cost of force generation and the metabolic cost of locomotion normalized for the time of force generation (by dividing costs by the number of times the force must be generated and decay per unit time, i.e. stride frequency). The results are remarkable. Both cost of generating force and metabolic cost of locomotion appears to be directly proportional to stride frequency (i.e. to $1/\text{time}$ involved in a cycle of force generation and decay). Thus the time course of force generation and decay appears to determine the energetics of steady state terrestrial locomotion.

CONCLUSIONS

During steady-state running, hopping and galloping major muscle groups are alternately stretched and then shorten during a stride. This enables them to operate in concert with their tendons as spring systems. Energy is stored in these springs (as elastic strain energy) during one part of a stride and recovered during another. Speeds and stride frequencies that animals normally utilize within gaits are those where storage and recovery of elastic strain energy is maximized. Peak muscle stresses are reduced when animals change gaits from a trot to a gallop, reflecting a redistribution of force over time, and the recruitment of a larger more compliant spring system. Operating these 'muscle-tendon spring systems' for locomotion requires that they be alternately turned on and off during each stride cycle. The energetic cost of locomotion and the cost of generating force during locomotion both appear to be directly proportional to the frequency at which the muscles are turned on and off (i.e. stride frequency) when muscle stresses are the same (at gait transitions).

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