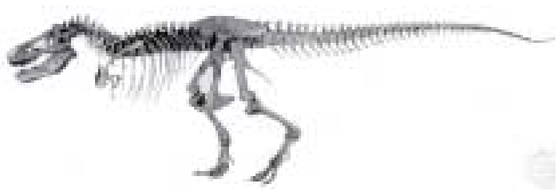
Musculoskeletal system

This chapter analyzes the gross aspects of the skeleton, muscles and tendons as a system of articulated levers operated by ropes, pulleys and contractile units. The object of this system is to exert forces of various kinds on the external world—for example to move the animal (locomotion) or to procure food.

1. Skeletons of land verterbrates



The verterbrate skeleton consists of bone[1], a composite material consisting of bone cells, collagen (a fibrous protein arranged in long strands), and inorganic rod-like crystals of $Ca_{10}(PO_4)_6(OH)_2$, perhaps 50 Å in diameter and 200 to 2,000 Å long.

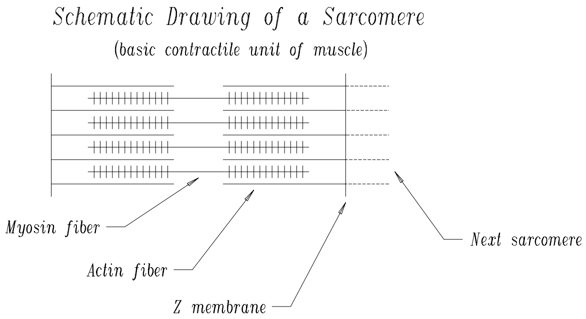
The quantitative properties of bone are given in the Table below:

Properties of Bone

Type of Stress	Ultimate Strength ($\times 10^8$ Nt/m^2)
Compression	1.5
Tension	1.2 – 1.5
Bending	2.1 – 2.2
Young's modulus	171 – 185

2. Muscle

Muscle tissue consists of basic contractile units called *sarcomeres*. The sarcomeres are attached end to end, with the demarcations marked by *Z-membranes*. At the microscopic level, the sarcomere contracts because the cross-bridges on the myosin fibers ratchet along the actin fibers. We discuss this in more detail in Chapter X, *Bioenergetics*.



The sarcomere can move only one way: it contracts. Thus (contractile) muscular force must be balanced by a weight, a spring, or an opposing muscle, in order that the fibers can be pulled back to their initial uncontracted state.

The important things to remember about muscles are

1. they can exert a *maximum stress* of 3×10^5 Nt/m^2; and
2. they can contract at most 20–25% of their overall length (*maximum strain* = 0.2–0.25).

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[1] Data on the properties of bone were taken from the article: “bone”, *Encyclopædia Britannica Online* (Copyright © 1994-2001 Encyclopædia Britannica, Inc.).

3. Mechanical (dis)advantage

We now analyze the muscular contraction force needed to lift a given weight. To do this we must take into account the articulated bones, which act somewhat like scissors jacks.

Because muscle can contact at most 25% of its length, the arrangement of vertebrate skeletal levers actuated by muscular contraction sacrifices mechanical advantage for range of motion. A secondary result is that the “output” achieves absolute speeds much greater than those of the muscular contractions.

A second constraint on the evolutionary optimization of organisms is the fact that muscles can only exert force while contracting. To make a muscle return to its uncontracted state it is necessary to pair it with a muscle that, when contracting, stretches the opposing muscle[2]. That is, all limbic muscles occur in pairs, called *flexors* and *extensors*.

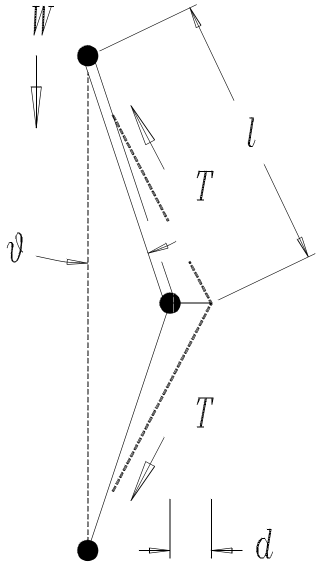
Virtual work

To analyze the levers and muscles comprising a limb, we apply the principle of *virtual work*[3]. For example, suppose the leg shown to the right raises the weight W by a distance δh, and thereby performs work $W\,\delta h$. In so doing, the angle of the femur (thighbone) from the vertical changes from θ to $\theta - \delta\theta$.

Taking the femur and tibia (shinbone) to be the same length L, and the muscles and tendons to have the (greater) length l, we see from the (Pythagorean theorem) that

$$l^2 = L^2 + 2Ld\sin\theta + d^2$$

where d is the offset of the muscle attachments. The muscle exerts a force T over the distance δl hence does work $T\,\delta l$. Since the tendon attaches below the knee, we set



$$W\,\delta h \approx 2T\,\delta l$$

and noting that

$$\delta h = -2L\sin\theta\,\delta\theta\,,$$

at last find

$$T = W\tan\theta\left(1 + 2\Gamma\sin\theta + \Gamma^2\right)^{1/2}$$

where Γ is the ratio ${}^{L}\!/_{d}$. For small angles from the vertical, very little tension is needed to raise or

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[2] This is not universal—exoskeletal animals like spiders extend their muscles using a hydraulic system, whereas certain other muscles compress springy tissues that expand when the muscles relax.

[3] See, *e.g.*, H. Goldstein, *Classical Mechanics, 2nd ed.* (Addison-Wesley Publishing Co., Reading, MA, 1980), p. 17ff.

lower the weight. However, for angles beyond 45° the force rises very rapidly indeed. For my leg the ratio Γ is about 3.3, hence at an angle of 45° the mechanical (dis)advantage (at 45°) is about 4. Thus the tension must equal 4 times the weight to be lifted. But at an angle of 60° the tension rises to 7 times the weight. This is why exercise physiologists warn us not to perform knee bends at angles exceeding 45°—we can damage our knee ligaments at higher angles!

Example

Let us estimate how much I can bench press. My upper arm has a circumference of 15 inches or 38 cm. Setting this to $2\pi r$ I find the radius of my upper arm muscles (biceps and triceps) to be $r \approx 6$ cm. Their total cross-section is thus some 114 cm^2. The cross-section of the upper arm bone (humerus) is perhaps 3 cm^2, so we may take the area of the triceps to be about 74 cm^2 (about ⅔ the difference). Multiply by the maximum stress, 3×10^5 Nt/m^2, to get a net force of 2220 Nt per arm muscle. From the preceding analysis we see that the net weight I can lift (using my triceps alone) is

$$W = T_{\max}\frac{d}{l}\cot\theta\,;$$

with $L = 32$ cm and $d = 7$ cm, and with $\theta = 45^\circ$, we get

$$W \approx 2\times\frac{2220}{5.3}\,\text{Nt} \approx 189\text{ lb}\,.$$

This is very close to the amount I can currently bench press (10 repetitions), about 180 lb.

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4. Hill's Law

Many of the ideas in this section are taken from the excellent book by C.J. Pennycuick.[4] The physiologist A.V. Hill proposed the following empirical relationship[5] between the absolute speed of muscular contraction and the force being exerted by the muscle:

$$v = v_0\,\frac{F_{\max} - F}{F_0 + F}$$

where $F_{\max}$, F_0 and v_0 are empirically determined parameters. It turns out to be convenient to express Hill's equation in terms of the stress,

$$\sigma \overset{df}{=} \frac{F}{A}\,,$$

and the *strain rate*

$$\psi \overset{df}{=} \frac{1}{\delta t}\,\frac{\delta x}{L} \equiv \frac{v}{L}\,.$$

We can express the stress in terms of the strain rate,

$$\sigma = \frac{\sigma_{\max}\psi_0 - \sigma_0\psi}{\psi_0 + \psi}$$

and use the result to calculate, for a given strain rate, the power output per unit volume of muscle tissue:

$$P = \sigma\,\psi\,.$$

Different types of muscle tissue contract at different maximum rates[6]. The so-called "fast" muscles are (relatively) anærobic in their metabolism. (That is, they use a chemical reaction that does not require free oxygen to generate their energy.) Anærobic muscles contain fewer mitochondria (the sites of oxidative phosphorylation) and lower density of myoglobin (myoglobin is related to hæmoglobin; it is used by muscle cells to store

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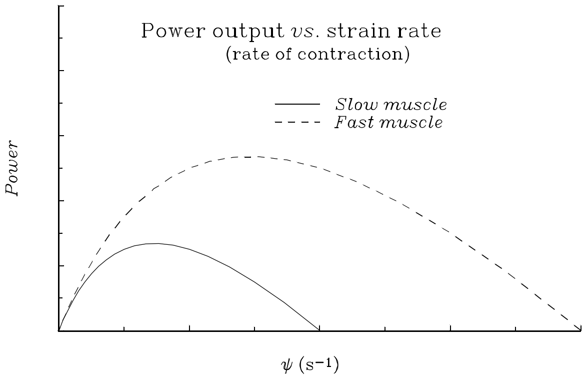
[4] C.J. Pennycuick, *Newton Rules Biology* (Oxford U. Press, Oxford, 1992).

[5] A.V. Hill, *Proc. Roy. Soc.* Ser. B **126** (1938) 136-195; see also *Science Progress* **38** (1950) 209-230.

[6] We are speaking here of striated rather than smooth muscle tissue. The latter behaves very differently and is not involved in locomotion.

oxygen), than the “slow” muscles. In other words, “fast” muscle tissue is usually paler in color than “slow” muscle tissue.

The (qualitative) specific power curves for the two types of muscles are shown in the figure below. We see that the maximum power is developed by fast muscles at a higher strain rate. Another factor that influences the ratio of fast to slow muscle fibers in a given muscle group is their endurance. Anærobic metabolism (which all cells are capable of, to some extent) generates lactic acid which must be removed by the usual transport mechanisms lest it interfere with muscle function. Thus, the ærobic muscles are for sustained effort at moderate speeds, whereas the anærobic ones are for emergency speed in short bursts.



We conclude that there is an optimum speed for each type of muscle, and that evolutionary selection will lead to the optimal adaptation of muscle types to the demands made on them.

5. Basics of locomotion

We shall concentrate here primarily on human locomotion, although the general principles apply to all land animals. First, we note that all locomotion requires cyclic motions of the legs: after one period the pattern repeats.

We define three parameters of locomotion. The speed v is obvious; the stride length s is the distance between successive placements of the same foot; and the stepping frequency f is the inverse of the time interval Δt between successive placements of the same foot: $f = 1/\Delta t$.

Clearly these parameters are related by[7]

$$v = \frac{s}{\Delta t} \equiv s f .$$

If an animal must increase its speed of locomotion, it can only do so by increasing its stepping frequency, its stride length, or both.

Broadly speaking, only two types of gait are observed in locomotion: walking and running[8]. The distinction is that in walking, the animal always has at least one foot on the ground; whereas at some point in running all the animal’s feet are off the ground. This distinction profoundly affects the animal’s performance.

Walking

According to D’Arcy Thompson[9], animals walk faster by increasing their stride length, or as he put it, “stepping out”. In fact, a simple experiment on a treadmill demonstrates the falsity of this claim: the graph on p. 27 below presents data from the author’s walking and running on a treadmill. It is

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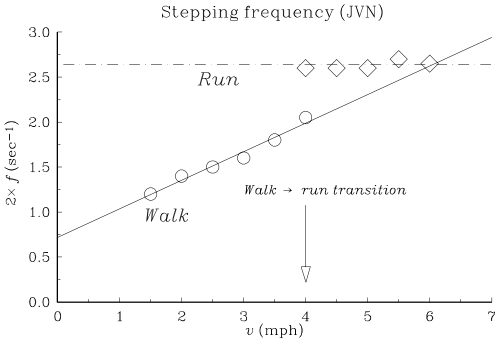
[7] This is exactly the same as the relation between frequency, wavelength and propagation speed.

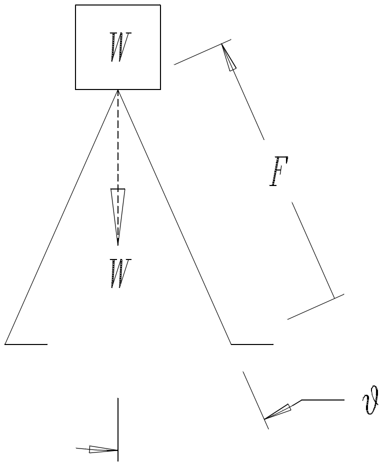
[8] The elephant’s amble (or shamble) is a walk, whereas the trot, canter and gallop are variations of running gaits distinguished by the order in which the legs move.

[9] D’Arcy Wentworth Thompson, *On Growth and Form* (Cambridge U. Press, New York, 1961), p. 29. (This is an abridged and annotated version of the 1917 edition.)



easy to see that for a wide range of walking speeds my stepping frequency is proportional to my speed. (This experiment has been repeated by my students, with essentially the same results.) That is, I increase my walking speed by increasing my pace, not my stride length.

When we look for an explanation of this observation, we realize that nothing else is possible. In walking the legs are always bearing the animal's weight. The diagram below relates the forces along the leg bones to the opening angle of the legs. As we can see, the force increases rapidly as the opening angle increases. That is, the forces that must be exerted by the muscles, simply to keep the animal from sprawling, must increase beyond the point of efficiency. (You can try this if you wish, but be careful!)



$$F = W/(2\cos\vartheta)$$

Another viewpoint treats the leg as a rigid pole with a mass on its end. When the foot is planted, the pole rotates about the point of contact.

The initial angular momentum of a mass m moving horizontally at speed v, a vertical distance $l\cos\theta_0$ above the ground, is

$$J = mv\,l\cos\theta_0\,.$$

Once the end of the pole is planted in the ground, the mass rotates about the point of contact. The angular momentum is then

$$J = m\,l^2\,\dot{\theta}$$

since the moment of inertia is $m\,l^2$. We now use conservation of angular momentum to say that

$$J = mv\,l\cos\theta_0 = m\,l^2\,\dot{\theta}\,.$$

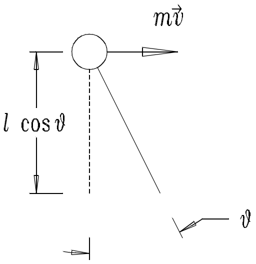
The equation of motion of an inverted pendulum of the form shown below is

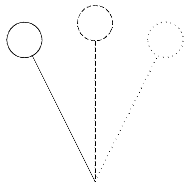
$$m\,l^2\,\ddot{\theta} = mgl\sin\theta$$

from which we can see, by integrating once[10] with the integrating factor $\dot{\theta} = \frac{d\theta}{dt}$ that

$$\dot{\theta}^2 + 2\omega^2\cos\theta = \dot{\theta}_0^2 + 2\omega^2\cos\theta_0 = \text{const.}$$

(This is also the equation of conservation of energy, once the rotation begins.[11])





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[10] See any standard reference on mechanics, such as Goldstein (*op. cit.*) or ordinary differential equations.

In order that the pole vaulter complete his vault, the angular velocity must not vanish before the angle decreases to 0 (top of the arc—note: angles are usually taken to be positive in the counter-clockwise direction). This means that

$$\dot{\theta}_0^2 \ge \frac{2g}{l}\left(1 - \cos\theta_0\right),$$

or, imposing conservation of energy,

$$\frac{v^2}{2gl} \ge \sec\theta_0\left(\sec\theta_0 - 1\right).$$

That is, if the angle between the legs is too large the walker has difficulty completing his stride.

Of course the above argument is only schematic—realistic walking involves bending the knee and a pelvic rotation (because the legs are actually angled to keep the body's center of mass over the feet). We also use the rotation of the foot about the ankle joint to prolong the time of contact with the ground while our center of mass rises and falls. Thus the center of mass need not rise as much as it would with rigid legs. Nevertheless, the constraints of statics and dynamics tend to keep the leg angles roughly constant, meaning that the ratio of stride length to leg length remains essentially independent of walking speed. The conclusion is that the best way for a walking animal to increase its speed is to increase its stepping frequency.

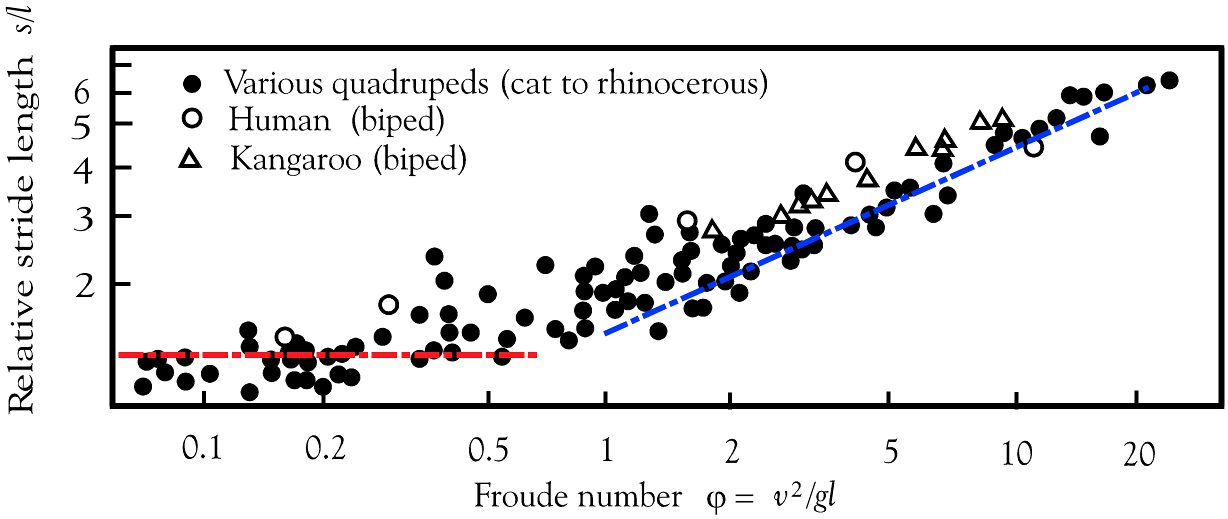
Scaling arguments

R.M. Alexander[12] has graphed the (dimensionless) ratio of stride length to leg length, *vs.* the dimensionless *Froude number*

$$\varphi \overset{df}{=} \frac{v^2}{gl}$$

for a variety of animals. One such graph appears below. The line through the data represents a regression (least-squares) fit. Also note that both the horizontal and vertical scales are logarithmic (equal distances represent factors of 10). That is, Professor Alexander is saying that he expects to discover a relation in the form of a power law,

$$\frac{s}{l} = f(\varphi) \sim \alpha\,\varphi^{\beta},$$



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[11] We note that energy is not conserved in the initial collision of the pole with the pivot point—if it were, the vaulter and pole would recoil!

[12] R.M. Alexander, "How dinosaurs ran", *Scientific American* April, 1991, p. 130ff.

where α and β are constants.

A rough argument that might justify such an expectation goes as follows: since

$$v = sf$$

and since, for a pendulum (inverted or otherwise) a characteristic frequency is

$$f \propto \left(\frac{g}{l}\right)^{1/2},$$

we see that

$$\frac{s}{l} \propto \left(\frac{v^2}{gl}\right)^{1/2} = \varphi^{0.5}.$$

In fact, the slope of the line at the fastest gaits does approach 0.5 (meaning that the exponent β is close to ½).

The first comment that we can make about the attempt to fit the data with a regression curve is that the data below $\varphi \approx 0.5$ (roughly where the gait changes from walking to running) should not scale at all. That is, since geometry limits the leg opening angle to a certain range, the ratio $\frac{s}{l}$ is more or less independent of speed, hence of φ. We can also argue that if locomotion is akin to vaulting, the angle θ_0 has to obey the inequality

$$|\theta_0| \le \cos^{-1}\left(\frac{2}{1+\sqrt{1+2\varphi\Gamma}}\right),$$

where Γ is a geometrical constant. The time for the pole vaulter to rotate from angle θ_0 to $-\theta_0$ can be computed by separating the variables in the equation of motion: we find

$$\omega\Delta t = \int_{-\theta_0}^{\theta_0} d\theta \left[\Lambda + 2\left(\cos\theta_0 - \cos\theta\right)\right]^{-1/2}$$

where Λ is the dimensionless parameter

$$\dot{\theta}_0^2/\omega^2 = \varphi/\cos^2\theta_0 .$$

Here is a table of φ, twice the stepping frequency (in terms of ω), and the initial leg angle, that illustrates this point:

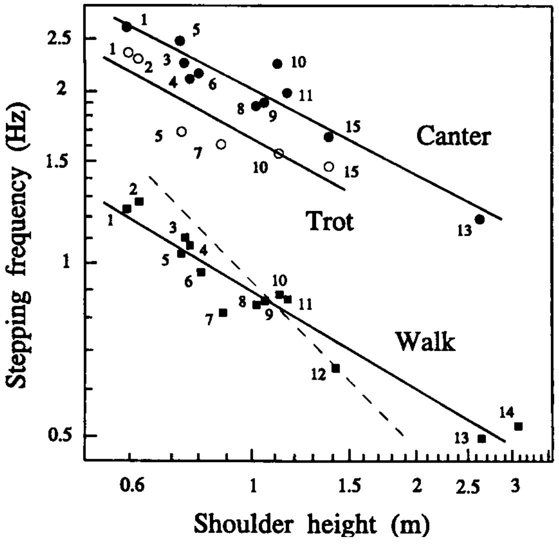
φ	$2f/\omega$ $(\Gamma = 1)$	θ_0 (deg)
0.1	0.399781	17.36
0.2	0.398596	23.64
0.3	0.397565	27.99
0.4	0.410874	30.00
0.5	0.439127	30.00
0.6	0.462887	30.00
0.7	0.483315	30.00
5.0	0.727090	30.00
10.0	0.790407	30.00
20.0	0.839795	30.00

We see $2f/\omega$ is nearly independent of φ, over a wide range of φ.

In other words, the data shown in Alexander's graph on the preceding page are better fit with two straight lines, one that is horizontal (exponent 0) and one with slope (exponent) 0.5 .

Timing

We now take a closer look at the stepping frequency. Pennycuick[13] has measured the stepping



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[13] *op. cit.*, p. 51.

frequencies of various African mammals, and determined that they scale as $l^{-1/2}$, as shown in the graph below.

This is, of course, what would be expected if locomotion were pendulum-like. However, consider the frequency for an animal of leg-length 1 m: from the graph it should be 0.9 Hz, whereas from the table above we extract a somewhat smaller number at the walk, namely about 0.6 Hz (note we must multiply by $\omega = \left(\frac{g}{L}\right)^{1/2} \approx 3.1$ Hz and divide by 2).

The same animal runs at a frequency of nearly 2 Hz. The predicted frequency of the pendulum model is 1.13 Hz, barely half that observed[14].

What are we to conclude from this disagreement? There are several alternatives:

1. The omitted details, such as bending the leg or damping, are so important as to materially change the numerical results.
2. The timing is not primarily determined by the kinematics of an inverted pendulum, but rather by some other aspect of the problem, such as the forces exerted by the animal's muscles.

I tend to favor the second possibility. The notion that an animal tends to walk "in resonance" with its pendulum motion (or at some other natural frequency) arose from the intuition that a swing goes higher if we push in time with it—that is, if we drive the system at resonance. This point of view misleads, however. While it is true that we can most easily store energy at resonance, the energy dissipated per cycle is just the integral of dissipative force times distance:

$$\Delta E = \oint \vec{F} \cdot d\vec{x}$$

where the integration follows one complete cycle (the integral does not vanish since the frictional force always opposes the motion, *i.e.* the integrand is negative). Since this is independent of the driving force, we expect the power dissipated in alternately contracting and relaxing muscles to be proportional to the contraction frequency.

In other words, there is no particular advantage, insofar as minimizing energy loss to friction is concerned, in driving the musculoskeletal system at a resonant frequency. Therefore in my opinion the scaling of stepping frequency as the inverse 0.5 power of the leg length, observed by Pennycuick and others, results from some other aspect of the problem. Or in other words, to conclude from this empirical scaling law that locomotion is best represented as a swing metronome is an example of the logical fallacy known as *post hoc, ergo propter hoc*[15].

To understand what is going on, then, we must return to our understanding of muscle tissue. As we saw, each type of muscle has an optimal contraction speed, or in dimensionless terms, an optimal strain rate ψ. Presumably what we are observing is that strain rates, optimized for the entirety of an animal's lifestyle to maximize the probability of species survival, scale as $L^{-1/2}$. Whether we can model the factors that lead to such optimization sufficiently well to explain the empirical scaling law, is another question.

Walking power

We have seen by direct measurement (p. 27) that walking gaits maintain constant stride length and vary speed by varying the stepping frequency. We

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[14] These results are insensitive to Γ.

[15] "After this, therefore on account of this."

now attempt to estimate the mechanical power consumption of walking and compare it with data.

From the inelasticity of the collision of a leg with the ground, assuming the correctness of the pole-vault model, we see that the mechanical energy loss per step is

$$\Delta E = \frac{1}{2} m v^2 \sin^2\theta_0 .$$

The power input, to keep a constant pace is therefore

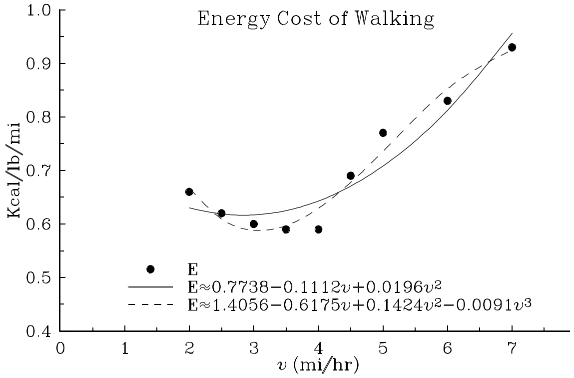
$$P = \frac{\Delta E}{\Delta t} = \frac{1}{2} m v^2\, 2 f \sin^2\theta_0 \approx \frac{m v^3}{4s} = \frac{m v^3}{8l} ,$$

where we have taken $\theta_0 = 30^{\circ}$. For a 100 Kg person walking at 3.5 mi/hr (1.6 m/sec) with leg length 1 m, we find a (mechanical) power loss of 51 Watts.

Let us compare this with the actual power consumption, taken from the table shown below[16]

Energy cost of walking at various speeds

	Weight (lb)						
mi/hr	100	120	140	160	180	200	220
2.0	65	80	93	105	120	133	145
2.5	62	74	88	100	112	124	138
3.0	60	72	83	95	108	120	132
3.5	59	71	83	93	107	119	130
4.0	59	70	81	94	105	118	129
4.5	69	82	97	110	122	138	151
5.0	77	92	108	123	138	154	169
6.0	86	99	114	130	147	167	190
7.0	96	111	128	146	165	187	212



According to this table, the rate of energy consumption in this exercise is 130 Kcal/mi. If we convert this to power, we obtain

$$\frac{1.3\times10^5 \cdot 4.2 \cdot 3.5 \ \text{joules}}{3600 \ \text{sec}} \approx 530 \ \text{watts} ,$$

a factor of 10 greater than our estimate. We must ask wherein lies the discrepancy. First, as we shall see when we study some thermodynamics, the efficiency of conversion of chemical (food) energy to mechanical work is only 20%-25% in humans. This accounts for a factor of, say, 4 or 5. But then we have also neglected internal friction in our book-keeping, as well as losses from imperfect restitution by the (springy) tendons. These dissipative effects could easily amount to another 50 watts of mechanical power consumption, which would account for everything. Finally, it is not clear whether the above value of 130 Kcal/mi includes basal metabolism (which amounts to some 50-75 W) for that person.

Our simple model predicted that the energy cost to transport a unit mass a unit distance should be independent of mass and should vary as the square[17] of the speed. The data from the table do indeed predict a mass-independent cost, and do

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[16] …cited on an exercise website, *http://walking.about.com/sports/walking/library/how/blhowcalburn.htm*

[17] The power per unit mass varies like v^3 so the energy per unit distance varies like one less power of v.

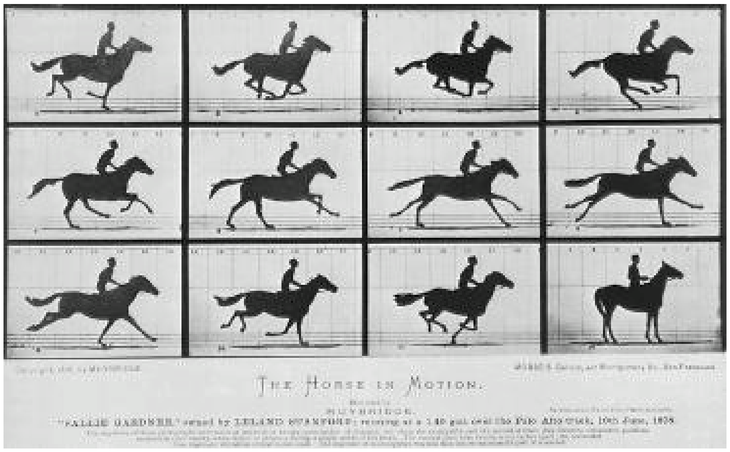
seem to increase asymptotically as v^2. However, the data exhibit a dip—that is, there seems to be a speed at which the efficiency of converting food into transport is maximum.

What leads to this minimum? We recall from the figure on p. 26 that each type of muscle has an optimal contraction speed, at which it produces maximum mechanical power output. Thus we should expect, for each animal, an optimum speed of locomotion. Of course the minimum is much flatter than the maximum in the graph of power *vs.* strain rate, since the inherent power requirement of walking is growing as v^3.

6. Transition to running

When we analyze running gaits (trot, canter, gallop) we see that at some point in the cycle the animal's feet are entirely free of the ground. That is, running consists of a series of forward bounds. Among bipedal animals like humans and ratite birds (ostrich, emu, *etc.*) this is true at every step. It is also true of the cheetah, which leaps twice each stride. In heavier quadrupeds such as horses, rhinoceri and giraffes, the animal is airborne only once per complete stride. Presumably larger animals must take some extra steps per stride to correct their balance and adjust their takeoff position.

Precise observations of the gaits of running animals were not possible until near the end of the 19th Century. The persistance of human vision precluded early observers from being able to determine, for example, whether a horse keeps three, two or one feet on the ground while galloping. Controversy has raged over the precise number, probably since the first painter drew a galloping animal on the wall of his cave. No one, prior to the sequential photographs[18] of Eadweard Muybridge (1830-1904) would have been so bold as to hazard the opinion that the horse becomes fully airborne. This is shown in the second and third frames of the figure below.



The question now arises, "Why does an animal *bother* to run?" Manifestly it is to move faster than a walk will accomplish. But for the physicist the question is why running works better than simply moving the legs faster.

We recall that the speed of locomotion is given by

$$v = sf$$

and that in walking s remains fixed and f increases proportionately to speed, for the geometric reasons we have discussed. In running, the opposite happens: the stepping frequency remains nearly constant and the stride length is proportional to the speed. In fact, the stride length is the distance of the jump[19],

$$s = \frac{2v_x v_y}{g},$$

where the velocity vector at takeoff is

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[18] Muybridge's work, financed by the railroad baron Leland Stanford, led eventually to Edison's kinetiscope, thence to the motion picture, and all the consequences thereof.

[19] The student will recognize this as the formula for the range of a projectile.

$$\vec{v} = \begin{pmatrix} v_x \\ v_y \end{pmatrix}$$

and as usual x is the horizontal and y the vertical direction. If the height h of jump is a constant, then the stride length is proportional to the speed, and this explains Alexander's results for running:

$$\frac{s}{l} = 2\left(\frac{h}{l}\right)^{1/2}\left(\frac{v^2}{gl}\right)^{1/2} \propto \varphi^{0.5},$$

where h is the maximum height of the jump. (It may also explain the spread in Alexander's results, since h/l is certainly not the same for all species.)

Running power

Finally, we look at the power requirement of running. By definition,

$$\frac{P}{m} = \frac{\Delta E}{\Delta t} = (1-\eta)\,\frac{g v_x}{4}\left(\lambda + \lambda^{-1}\right)$$

where

$$\lambda = \frac{v_y}{v_x}.$$

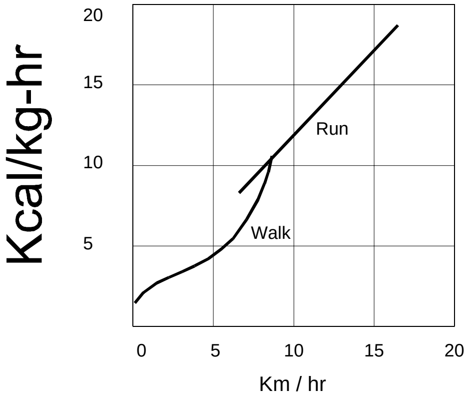
Here η is the fraction of kinetic energy that can be stored in the stretching of tendons and restored as kinetic energy for the next stride. The minimum value of $\lambda + \lambda^{-1}$ is 2, but to avoid excessive stress on takeoff and landing, most animals tend toward values of λ much smaller than unity.

In retrospect it should not surprise us that running power may be written

$$P = \zeta\, m g v_x$$

where ζ is a dimensionless constant. Clearly the average force an animal exerts in running at constant speed must be proportional to its weight, mg; since power is force times speed, voila!

The upshot is that running power increses only as the first power of speed. Margaria, *et al.*[20] have measured the energy cost of walking and running as a function of speed, using trained athletes as test subjects. Their data appear in the graph below. We note that as we expect from our previous results, walking power increases (at least as fast) as v^3 whereas running power is linear in v. Therefore, at some speed v_{crit} the power cost for walking will exceed that for running, and the animal will change gaits. From the graph I have extracted the empirical relation (in MKS units)



$$\frac{P}{m} = 0.6 + 4.6\, v_x .$$

If we suppose 75% of the energy is stored and that the power is minimized, we find the coefficient of v_x to be

$$0.125\, g = 1.225 \text{ J/kg-m},$$

which, when multiplied by 4 to convert to total energy usage, gives 4.9—close enough to the empirical value of 4.6. The constant term, 0.6, must be related to basal metabolism. If a 70 Kg person eats 2000 Kcal/day to maintain body weight, then this is about 1.4 watts/kg. It is close enough to the 0.6 W/kg in the above formula that we may conclude they are the same (especially since the latter figure is suspect).

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[20] R. Margaria, P. Cerretelli, P. Aghemo and G. Sassi, J. Appl. Physiol. **18** (1963) 367-370.

Other considerations

I stated that the power cost of walking grows *at least* as fast as v^3; in fact, because the stride length in walking is fixed, and because the stepping frequency is limited by the maximum contraction frequency of the leg muscles, the chemical power requirement becomes infinite at some walking speed. A better way to say this is that the rate of energy consumption is inversely proportional to a factor that vanishes at a finite maximum strain rate of muscle tissue. The reason for this is that the chemical energy to make a myosin cross-bridge switch from one actin site to another is constant. Hence the chemical energy needed to contract a muscle a certain distance is independent of the strain rate. However, empirically, the mechanical power output is zero at zero strain rate and also at the maximum strain rate. This is just Hill's Law discussed in §4 above. Hence to get the same mechanical power output when the strain rate is higher than optimum the body recruits more muscle fibers. This process ends (short of infinity!) when all the available muscle is in use.

Maximum speed

The transition from walking to running therefore is an economy measure, that reduces the rate of increase of power with speed. The upper limit on speed may be imposed by two factors:

1. The maximum power output the organism can sustain. Since 75-80% of the energy produced must be dissipated as heat, the strain on an exothermic animal's cooling system can become severe. For example, assuming the power requirement to be similar to that of humans, an animal running at 5 m $\sec^{-1}$ generates power at the rate of 23 Watts Kg^{-1}. If the heat is to be dissipated by water evaporation, the rate of evaporation will be about 0.008 gm $\sec^{-1}$. For a 70 Kg animal this amounts to water loss of 4 Kg in the course of a 42 Km run. It is thus not surprising that Phidippides (who bore the news of victory from Marathon to Athens in 490 BC) died at the end of his run, nor that modern marathon runners carry liquid with them and drink as they run.
2. The maximum stress the animal's tendons and ligaments can sustain. Each time an animal reverses its vertical direction it must subject itself to substantial vertical acceleration—several *g*'s, in fact. The harder the running surface, the greater the shock. (This is the origin of "shin splints", wherein the tendons of the lower leg separate painfully from the bone.)

   A human sprinter has a top speed of about 23 mi/hr. The horse, giraffe, buffalo and rhinocerous can gallop at about 30 mi/hr. Cheetahs and gazelles are said to be capable of 60 mi/hr bursts of speed. To achieve such speeds an animal must be capable of leaping higher than the norm—and cheetahs and gazelles are indeed excellent leapers. They are also relatively light, and are built on a particularly springy plan, hence they are less liable to injure themselves on takeoff and landing.

Whether it is stress or heat dissipation that most limits the top speeds of running mammals, however, is not definitely known. The cheetah's ability to sustain a sprint extends to perhaps 100 or so meters. The effort clearly exhausts them, as much video footage of their hunts confirms.

Animals that cannot run

As we have seen, the time a running animal can be airborne is

$$t_{hang} = \frac{2v_y}{g}$$

The average acceleration an animal experiences in changing from landing to takeoff is of order

$$2g\frac{h_{\max}}{\Delta h} = \frac{v_y^2}{\Delta h} = \frac{v_y^2}{\gamma l}$$

where Δh is the stopping distance, which we suppose to be a fraction γ of the leg-length.

The maximum (momentary) acceleration humans can sustain without serious injury is about 5 *g*.

Since strength-to-weight ratio scales as $M^{-1/3}$, an elephant's maximum sustainable acceleration should be a bit over 1 *g*. That is, an elephant has no safety margin for anything as athletic as jumping. In consequence, elephants must not leave the ground during locomotion, consequently their ability to run may be primarily limited by their ability to withstand stress.

Of course this may also be a sort of chicken-and-egg problem. Since the maximum height of a jump does not scale with body size, and since, empirically, the stepping frequency scales inversely as $\sqrt{l}$, an elephant or larger animal may not be able to run because it has literally "run out of time"—it cannot get its legs back and forth in the available time, so it does not try to. It walks—or rather, shambles[21].

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[21] But don't make an elephant angry—it can shamble along at 15 mi/hr, a lot faster than anyone but a trained runner can go!