

A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition

Andy Ruina^{a,*}, John E.A. Bertram^b, Manoj Srinivasan^a

^aTheoretical and Applied Mechanics, Cornell University, Ithaca, NY 14853, USA

^bCell Biology and Anatomy, Faculty of Medicine, University of Calgary, Alta., Canada T2N4N1

Received 19 October 2004; received in revised form 24 March 2005; accepted 1 April 2005

Available online 14 June 2005

Abstract

Terrestrial legged locomotion requires repeated support forces to redirect the body's vertical velocity component from down to up. We assume that the redirection is accomplished by impulsive leg forces that cause small-angle glancing collisions of a point-mass model of the animal. We estimate the energetic costs of these collisions by assuming a metabolic cost proportional to positive muscle work involved in generating the impulses. The cost of bipedal running estimated from this collisional model becomes less than that of walking at a Froude number ($v^2/g\ell$) of about 0.7. Two strategies to reduce locomotion costs associated with the motion redirection are: (1) having legs simulate purely elastic springs, as is observed in human running; and (2) sequencing the leg forces during the redirection phase; examples of this sequencing are the *ba-da-dump* pattern of a horse gallop and having push-off followed by heel-strike in human walking.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Locomotion; Collision; Energy; Walk; Gallop

1. Introduction

The footfall pattern of a galloping horse has been a curiosity at least since the famous studies of [Muybridge \(1887\)](#) and [Marey \(1874\)](#). Through high-speed photographs and hoof sensors ([Fig. 1](#)) [Muybridge](#) and [Marey](#) observed that a moderate speed gallop (or canter) consists of an aerial flight phase alternating with a support phase. At the start of support a rear foot lands, then the other rear foot and a front foot land together, and finally the remaining front foot lands. Modern data reveals the same pattern (e.g. [Eaton et al., 1995](#); [Potard et al., 1998](#); [Minetti, 1998](#)). This three-beat *ba-da-dump ba-da-dump* is familiar from the horse gallop we hear in Rossini's William Tell Overture (e.g. TV's *The Lone*

Ranger theme). Why should a horse prefer sequenced footfalls, *ba-da-dump*, to, say, a prong where all four feet hit simultaneously? We approach this and related questions from an old and intuitive perspective,

“A perpetual law of Nature consists of acting with the smallest work ...” [Borelli \(1680\)](#)

more recently championed by [Alexander \(2001\)](#).

The general energetic view comes into sharper focus by considering these two points

- *Only losses cost:* In a complex mechanism moving in complex ways it is easy to forget that muscular work is only required to make up for loss of mechanical energy. As a rule, no energy is required for the dizzying array of passive (e.g. “pendular”) energy exchanges that can occur in a multi-segmented animal or machine.

*Corresponding author.

E-mail address: ruina@cornell.edu (A. Ruina).

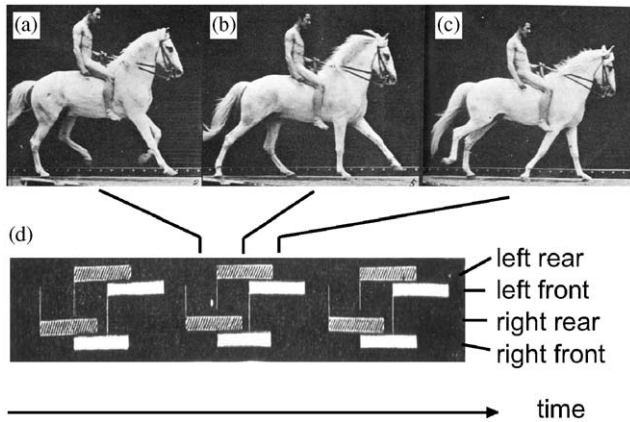


Fig. 1. (a–c) Plate 57 (panels 3, 5 and 7) from the 1957 Dover edition of Muybridge’s 1887 photos of a cantering horse. Shown are (a) initial rear foot contact, (b) simultaneous diagonal contact, and (c) front foot contact. The time between the photos shown is 0.112 s. The approximate instants of the Muybridge photos is indicated on (d) the footfall pattern of a galloping horse as recorded by Marey (1874). Each horse foot had a pneumatic sensor which drove a pen on a rotating drum. The bars indicate times of high pressure.

- *Collisions are big losses:* In legged locomotion, a big mechanical energy loss is associated with the feet pressing on the ground to redirect body motion. Thus the coordination strategies employed by terrestrial animals might be designed to minimize the cost of this redirection during stance.

One of nature’s design issues when using legs for terrestrial locomotion is this: after gravity pulls an animal down, either during a parabolic free flight or over an inverted pendulum arc, how does the animal get going back up again with least energy cost? This paper is centered around two model-based results

1. Leg forces that act elastically (as in running) are energetically beneficial, even in the extreme case that all the spring-like behavior is from positive muscle work with no genuine elasticity whatsoever.
2. Deflection of the body from downwards to upwards is accomplished with about half the energy dissipation if accomplished with two leg impulses in sequence instead of just one, and one-third the cost if with three sequenced impulses.

Nature seems to use both of these mechanical results to its advantage, as is explained in more detail below.

1.1. The plan of the paper

We start with a general discussion of rigid-objects modeling of locomotion followed by motivation for the collisional perspective. To avoid ambiguity we next describe our assumptions concerning work and

metabolic cost. The point-mass collisional model of legged locomotion, the associated vocabulary, and some general collisional formulas are next presented in detail. These formulas are applied to various special locomotion cases, especially running, galloping and walking, with an emphasis on coordination strategies that minimize energetic costs. Finally, model predictions are compared to human and animal behavior and metabolic data.

2. Rigid-body and muscle models for locomotion

We start with some central ideas and vocabulary.

2.1. Mechanically consistent models of locomotion

Our overall view is to model an animal as one would model a robot. One easily imagines a robot as being accurately modeled by assuming that the parts are rigid, that the bearings are frictionless, and that the motors have well-characterized torque–velocity relationships. Animal joints also have low friction, body parts that move almost as linked rigid objects with small deformation, and air friction is also often relatively small. So as a first approximation, one can use physical robots as models of animals, and one can use the robot-modeling assumptions for the description of animals. The robot modeling assumptions provide a test-bed for general locomotion analysis techniques. In particular, we are interested here in the analysis of energetics. If a mechanical energy accounting scheme is to make sense for animals it should make sense for robots, real or simulated, where all the quantities of interest are more precisely defined. In this paper, the mechanical model is simple in the extreme, so all quantities are particularly easy to track.

In these idealized robotic models dissipation of mechanical energy is mostly due to two overlapping mechanisms, collisions and negative muscle work. Understanding negative muscle work and collisional losses are thus central to understanding locomotion energetics.

2.2. Positive and negative muscle work

The overall energy accounting of muscle work starts by considering the work of one muscle. The rate at which a muscle does work on its environment is

$$\dot{W}_{musc} = (\text{tension}) \times (\text{shortening rate}).$$

\dot{W}_{musc} and all other quantities are defined in the glossary in Appendix B. In a so-called ‘concentric’ (towards the center) contraction, a shortening muscle has substantial tension and does mechanical work on the skeleton ($\dot{W}_{musc} > 0$). In turn, the skeleton can gain gravitational

potential energy, be accelerated or do work on the outside world. In an ‘eccentric’ (away from the center) ‘contraction’ a muscle still in tension (muscles never have substantial compression) lengthens and thus absorbs mechanical work ($\dot{W}_{musc} < 0$) from the skeleton, slowing it down, lowering it, or indirectly absorbing work from its environment.

2.3. Muscle work and metabolic cost

Our underlying assumption that animals minimize energy use is probably best expressed as a minimization of food fuel use, that is, a minimization of metabolic cost. So we need to relate muscle use to metabolic cost. The correlation between muscle activity and energy consumed (as food digested, ATP hydrolyzed, or oxygen consumed) depends, in complex and as yet poorly understood ways, on the molecular dynamics of contraction, activation and energy conversion within the muscle. There currently are no molecular-based and in vivo tested equations relating muscle activity to use of chemical energy from food.

Empirical curve-fits and guesses for the rate of metabolic energy use include dependencies on rate of contraction based on Hill-type equations (e.g. Minetti and Alexander, 1997), dependence on the integral of muscle tension over time, and more subtle dependencies on force and time (Kram and Taylor, 1990). We resort to an older more-approximate constant-efficiency model (e.g. Margaria, 1976; Alexander, 1992). This way the simplicity of our muscle modeling matches the simplicity of the mechanics. We use a metabolic cost rate

$$\dot{E}_m = \begin{cases} b_1 \dot{W}_{musc} & \text{if } \dot{W}_{musc} \geq 0, \\ b_2 |\dot{W}_{musc}| & \text{if } \dot{W}_{musc} < 0, \end{cases} \quad (1)$$

where b_1 and b_2 are positive constants. Typically $b_1 \approx 4$ and $b_2 \approx \frac{5}{6}$ (Margaria, 1976). Margaria motivates Eq. (1) by measurements of oxygen consumption for people walking uphill and downhill. More generally Eq. (1) may be expected to be a reasonable approximation if most of the individual muscle contraction and lengthening rates are mostly in an intermediate (near-optimal efficiency) regime where muscle efficiency is not highly sensitive to rate.

More elaborately one might imagine a slightly more sophisticated cost-law for muscle that includes a sum of terms. One, say, for work, one for force (for the costs of isometric contractions), one for force rate, etc. With such a more accurate constitutive law in mind, where the work accounting here is just one term in a series, the metabolic cost calculated in this paper may be viewed as that part of the metabolic cost associated with muscle work and not including the part associated with maintaining force, etc.

2.4. Mechanical energy balance

As complex as legged locomotion appears, the basic mechanical energy balance equation for steady locomotion over level ground is simply

The net positive muscle work is equal to the net mechanical energy lost.

All work production, absorption and energy conversions are subsumed by this simple relation. Over an average step at steady speed a body’s kinetic energy is unchanged. The main force that the muscles are superficially fighting, gravity, is orthogonal to the average motion so uses up no net work. Thus, no net work goes into increasing either kinetic or potential energy. We term the sum of positive muscle work increments over a fixed period of time ($0 \leq t \leq T$, one full stride, say) over all muscles as W_{pos} , and the sum of negative muscle work increments as W_{neg} with

$$W_{pos} \equiv \int_0^T \sum_{\text{muscles}} [\dot{W}_i]^+ dt, \\ W_{neg} \equiv \int_0^T \sum_{\text{muscles}} [-\dot{W}_i]^+ dt. \quad (2)$$

$[x]^+$ indicates what electrical engineers call ‘rectification’ and is x if $x \geq 0$ and 0 if $x \leq 0$. Neglecting air friction and friction in joints, and neglecting non-collisional material deformation, mechanical energy balance gives

$$W_{pos} = |W_{loss}| = |W_{neg}| + |W_{diss}|, \quad (3)$$

where W_{loss} is the total of mechanical energy sinks including negative muscle work and other dissipation. W_{diss} is the collisional dissipation not already taken up in negative muscle work; W_{diss} accounts for energy absorbed by deformation other than the lengthening of muscle (deformation of material that in non-collisional circumstances is approximated as rigid).

2.5. Energy balance and metabolic cost of locomotion

We can now use our relation between muscle use and metabolic cost with the energy balance equations to get a simpler estimate of metabolic cost. Combining Eqs. (1) and (3) the metabolic cost over a gait cycle is

$$E_m = b_1(|W_{neg}| + |W_{diss}|) + b_2|W_{neg}| \quad (4)$$

$$= bW_{loss} \quad (5)$$

$$= bW_{pos}, \quad (6)$$

where Eq. (5) defines b . In detail, the value of b depends on whether the loss is from negative work ($W_{diss} = 0$ so $b = b_1 + b_2$), from other dissipation ($W_{neg} = 0$ so $b = b_1$) or a mixture ($b_1 \leq b \leq b_1 + b_2$).

With reference to Eq. (1) it is often said that positive work is performed with efficiency (ratio of work to fuel

use) of about $1/b_1 \approx 25\%$, whereas negative work is more efficient at $1/b_2 \approx 120\%$ (sometimes more accurately reported as -120% efficiency). Similarly, it is noted that negative work only costs $b_2/b_1 \approx 21\%$ of an equal amount of positive work. However, a periodic gait cycle implies that a given amount of negative work needs to be compensated by an equal amount of positive work. Conversely, a given amount of positive work performed needs to be lost by an equal amount of dissipation or negative work. This symmetry is reflected in the similarity between Eqs. (5) and (6). Thus in the context of locomotion, it is more revealing to say that

Over a full gait cycle, any extra negative work must be balanced by an equal amount of extra positive work, and vice versa, so any increment in negative work has about the same net metabolic consequence as any increment in positive work.

The primary metabolic cost of negative muscular contractions is not the direct effect characterized by b_2 but the indirect effect characterized by the larger b_1 . In words, Eq. (5) says that, to the extent that fuel use is related to muscle work,

the metabolic cost of locomotion is approximately proportional to the energy lost

with little difference whether this loss is from eccentric contractions (metabolic cost = $b_1 + b_2 \approx 483\%$ of negative work) or from non-muscular dissipation losses (metabolic cost = $b_1 \approx 400\%$ of dissipation). For simplicity, when numbers are needed, we over-estimate the cost using $b = b_1 + b_2 \approx 5$.

In contrast, for applications to robots powered by, say, 80% efficient but non-regenerative electric motors one might set $b \approx 1.25$.

2.6. Energetic cost of transport

It is convenient to have a simple dimensionless measure of the energy required for locomotion. A commonly used dimensionless cost-to-benefit ratio is the specific energetic cost of transport,

$$c_m = \frac{E_m}{(\text{weight moved}) \cdot (\text{distance moved})}$$

(Note that c_m differs by a factor of g from another oft-used dimensional measure that has units of J/kgm.) Because we approximate metabolic cost E_m as proportional to energy losses (Eq. (5)),

$$c_m = b \frac{W_{\text{loss}}}{mgvT}, \quad (7)$$

where m is the body mass, g is the gravity constant, v is the average forward speed, and T is the period over which the work is measured. Sometimes it is useful to

consider the mechanically defined work-based cost of transport which here would be $c_w = c_m/b$.

3. The collisional perspective

In locomotion muscles have various functions. We can roughly divide these into a cost of support and a cost of swinging the limbs about. This paper concerns the cost of support. In particular, the metabolic cost we calculate here is from muscle used to redirect an animal's body motion from generally down to generally up during the support phase. This redirection from large leg forces will be modeled as a collision.

A collision is the sudden change in relative motion between two solid objects associated with large brief contact-interaction forces.

In the model here, one object is a mass representing the body of the person or animal and the other is the immovable ground. The brief contact-interaction forces are the leg forces causing the down-to-up redirection of the center of mass. Our emphasis here will be on energetic aspects of this collisional redirection.

3.1. Passive-dynamic walking

Collisional energy accounting is especially useful for analysis of the *passive-dynamic* walkers first developed by McGeer (1990a, 1990b). These machines are basically a collection of solid parts connected by hinges, with no motors and no controls. That such machines, appropriately designed and appropriately launched, can walk down a gentle slope with a rather human-like appearance (Collins et al., 2001) suggests that they may be relevant to human walking.

Exactly in theory, and approximately in practice, the full energetic cost of locomotion for passive-dynamic walkers is passive dissipation at collisions. Essentially, all of this collisional loss is at heel-strike (knee-strike, the collision of a leg with itself as it straightens, generally uses a near-negligible fraction of the energy budget, Garcia et al., 2000).

A simpler point-mass passive-dynamic model of walking is detailed in Garcia et al. (1998). The collisional aspect of this model will be reviewed here later. The Garcia et al. (1998) model predicts that

$$c_w \approx 6.9 \left(\frac{v^2}{\ell g} \right)^{3/2}, \quad (8)$$

where ℓ is the leg length. Garcia et al. (2000) show that the proportionality in Eq. (8) holds with reasonable accuracy even for more complex passive-dynamic models with knees, rigid rounded feet, and distributed mass.

Passive-dynamic walkers are one class of biomimetic robots that have an energy budget accurately determined by collisional accounting. Further, the collisional losses seem well-approximated with a point-mass model.

3.2. Other collisional models of locomotion

Rashevsky (1944, 1948) seems to have been first to use collisional accounting to estimate the energetic cost of transport. The details of his point-mass model will be reviewed later. The rimless wheel, another famous collisional model of locomotion (e.g. Bekker, 1956; Margaria, 1976; Rubanovich and Formalskii, 1981), shows a connection between rolling and walking (also to be discussed more later). For energetic purposes (but not for study of the stability) a slight generalization of the rimless wheel (Alexander, 1991) has a point-mass that can place massless rigid legs on the ground at arbitrary angles or times. A related model adds a cost for leg swinging (Kuo, 2001, 2002).

3.3. Recent human walking research that uses collisional accounting

Recent studies (Donelan et al., 2002a, b; Kram and Taylor, 1990; Kuo, 2001, 2002) have shown a substantial metabolic cost for the “step-to-step transition” in human walking. Like the models here, this step-to-step transition research was inspired by analysis of passive-dynamic-based biomimetic robots. The walking “step-to-step transition” is one example of the “down-to-up” redirection we discuss here. The walking portion of the paper here formalizes and generalizes some portions of this work.

3.4. The lack of collisions in brachiation: Bouncing without springs

In contrast to common notions about running over-ground, brachiation (arm swinging from branch to branch) of gibbons uses a mechanism of apparent “bouncing” (Fig. 4a) that has no essential dependence on elasticity (Bertram et al., 1999). Ricochetal brachiation, analogous to upside-down running, has a flight phase between hand holds. If the velocity of the body at the end of free-flight is tangent to the circular path of the body at the beginning of the swing, then the redirection from downwards to upwards motions has no essential collisional loss. The ape effectively bounces, ricocheting along the curve determined by her extended swing arm. That is, the essence of the pendulum in ricochetal brachiation is not to exchange gravitational and potential energy, but to redirect the body motion from generally down to generally up. Of particular note is the fact that this apparent “bouncing” motion is not mediated by any spring-like exchange of energy. Rather,

energy is available to re-elevate the animal simply because it was not lost in the interaction with the supporting hand hold.

A 5-link muscle-free brachiation model (Gomes and Ruina, 2005) shows realistic-looking steady-state ricochetal brachiation (i.e. including a ballistic flight phase between contacts). These gaits were found by numerical searches for solutions with no collisional (or other) loss. Real gibbons seem to choose motions close to these collision-free motions: (1) the bounce from downwards to upwards motion is accomplished with an impact-free mechanism, and (2) the making of contact with the handholds is at near-zero relative velocity, also minimizing impact losses. For ricochetal locomotion collisional dissipation shows its importance not by the energy it demands, but by its avoidance.

3.5. Can an animal swing against the ground?

It is puzzling that gibbons can ‘run’, albeit sort of upside-down, with no dissipative collisional impacts, but that right-side-up legged locomotion seems tied to collisional loss. Are there corresponding collisional-loss reduction mechanisms for running right-side-up? Of course the obvious answer is yes, “springs” (e.g. Alexander, 1990). But because animal limbs are not passive elastic springs (apparent leg elasticity is achieved with at least some muscle work). A motivation for the present research was a hope of finding dissipation reduction schemes that, like the dissipation-avoidance schemes used by gibbons, are not tied to material elasticity.

4. The point-mass compressional-leg glancing collision model

Before we can discuss how metabolic costs of locomotion can be reduced, we first present our collisional model for calculating some of these costs. This collisional model allows simple approximate calculation of costs associated with leg forces that, when viewed in detail, are smooth and non-impulsive. All later discussions of biologically relevant cost-reduction mechanisms are based on the formulas developed in this section.

We approximate the body as a point mass and the leg as a massless strut that can only transmit forces along its axis (that is, for most of the discussion we neglect hip and shoulder torques during the collision). For calculations we assume, consistent with the assumption of short contact time, that during a collision gravity forces are negligible and that the leg angle changes negligibly. Within this context, our overall model of locomotion is of smooth flight or stance phases punctuated by sudden velocity changes caused by impulsive leg forces.

Our collisional model is similar to the “compression-restitution” model of point-mass collisions discussed in elementary mechanics books but with 4 differences

1. Here we have an emphasis on glancing, shallow angle collisions rather than normal (direct) impact,
2. Here, we take account that biomechanical collisions need not cause a reduction in system kinetic energy. In classical mechanics, a collision typically refers to a purely passive, dissipative interaction between two objects which approached each other rapidly. Here, a collision can involve both purely passive mechanisms and actively muscular mechanisms. Collisions here can increase kinetic energy. In this sense, these collisions are a generalization of conventional passive collisions.
3. Here, we look at one collisional episode as possibly made up of a sequence of sub-collisions, and
4. The energy accounting here considers the metabolic cost of doing work.

4.1. Energetics of a single collision

The velocity v^- of the animal center of mass H is initially at an angle ϕ^- with a line orthogonal to the nominal leg (see Fig. 2a). During the *absorbing* part of the collision, H gets closer to the nominal foot contact

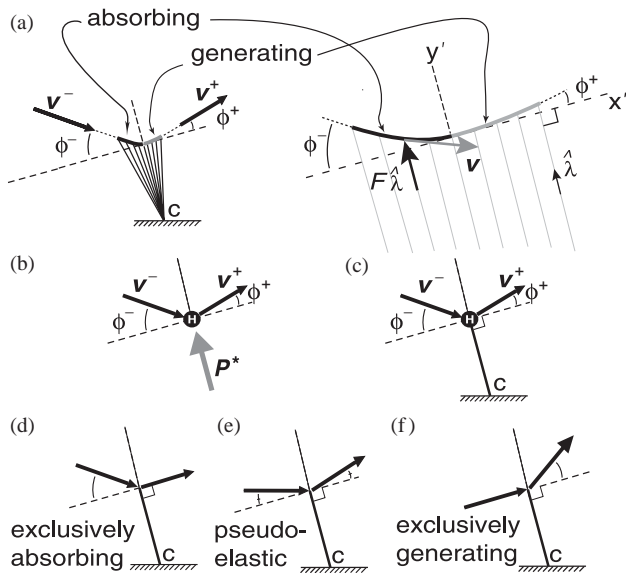


Fig. 2. The glancing collision model. (a) A particle collides with the ground through a single leg with a net deflection angle of $\phi = \phi^+ + \phi^-$. The force F during the collision comes from the leg whose direction is approximated as constant $\hat{\lambda}$ during the collision. (b) The net impulse of one leg on the mass m is \mathbf{P}^* . (c) The same collision viewed at a coarser scale where the details of the collisional interaction are not shown. (d) A point-mass has an *exclusively absorbing* (perfectly plastic) collision. (e) A point-mass has a *pseudo-elastic* collision and (f) A point-mass has an *exclusively generating* collision.

point C and the kinetic energy decreases. In this portion energy is absorbed by extending muscles and tendons (as joints flex) as well as by deformation of other tissues and the ground. Then at the point of maximum leg compression the distance CH begins to increase, the kinetic energy increases and work is *generated* by muscles, tendon recoil, and possibly ground recovery. In classical mechanics the generation phase is called the ‘restitution’ phase. But some collisions we consider here have no compression/absorbing phase, and the generating phase then has nothing to restitute. So we drop the classical vocabulary. Eventually contact is lost and the animal H completes the generation phase with velocity v^+ at an angle ϕ^+ with respect to the normal of the nominal leg orientation. We generally assume that both ϕ^+ and ϕ^- are nonnegative. The net deflection of the path in a single collision is

$$\phi = \phi^- + \phi^+. \tag{9}$$

Usually we think of both ϕ and $v^- = |v^-|$ as given. Throughout we are interested in locomotion, that is motion that is more sideways than up or down. We further assume that all portions of all trajectories are not far from level. So we simplify the formulas, at little cost in accuracy if the angles are indeed small, by using small angle approximations: $\sin \phi \approx \phi$ and $\cos \phi \approx 1$. Similarly ϕ^+, ϕ^- and ϕ are assumed small.

Conservation of linear momentum in the direction orthogonal to the leg (or, equivalently, angular momentum balance about the foot contact) demands that $v^- \cos \phi^- = v^+ \cos \phi^+$. Thus, $v^- \approx v^+ \approx v$. One can think of v as the average forward speed of the animal. Although the fluctuations of v are of central interest in the energetics, they are assumed to be a small fraction of v . The small velocity variations are made manifest in the energy terms discussed below.

The energy change is completely accounted for by changes in the component of velocity normal to the leg (from the collisional impulse).

$$\Delta E = -E_a + E_g, \tag{10}$$

where $E_a = m(\phi^- v)^2/2$ and $E_g = m(\phi^+ v)^2/2$.

E_a is the energy absorbed in leg shortening and E_g is the work done by the leg in the generating (lengthening) phase. Alternatively one may want to calculate the change in energy from the impulse \mathbf{P}^* where, with the small angle approximation $|\mathbf{P}^*| = mv\phi$. Either by rearranging Eq. (9) and (10) and making suitable geometric interpretations, or by the derivation in the appendix (Eq. (38)),

$$\Delta E = mv^2(-\phi\phi^- + \phi^2/2) = \mathbf{v}^- \cdot \mathbf{P}^* + |\mathbf{P}^*|^2/(2m). \tag{11}$$

In a single collision ΔE can be positive or negative.

4.2. Collision coefficients e_r and e_g

Collisions are commonly characterized by the coefficient of restitution

$$e_r \equiv \frac{\text{(separation speed)}}{\text{(approach speed)}} \\ = v \sin \phi^+ / v \sin \phi^- \approx \phi^+ / \phi^-.$$

In the case that $\phi^+ = 0$ the collision is equivalent to a ‘perfectly plastic’ (perfectly inelastic, coefficient of ‘restitution’ $e_r = 0$) frictionless collision against a surface normal to the leg. We call such a plastic collision *exclusively absorbing* (Fig. 2d).

If $\phi^- = \phi^+$ the collision is kinematically equivalent to a ‘perfectly elastic’ collision with $e_r = 1$ (Fig. 2e). We call such a kinetic-energy preserving collision a *pseudo-elastic* collision; it is elastic in effect, with the amount of work done equal to the amount previously absorbed. It is ‘pseudo’-elastic because the work in the generation phase may not be recovered elastic storage. Rather, the positive work could come in part or full from muscle work (see the concept of “pseudo-compliance” in Alexander, 1997).

If $\phi^- = 0$ the collision is *exclusively generating* (Fig. 2f). This is a classically ignored ‘super-elastic’ case with $e_r = \infty$. It’s like a backwards-run movie of clay hitting the floor. This $e_r = \infty$ case cannot be ignored here because muscles can do work even with no previous negative-work phase.

Thus, to avoid use of ∞ in formulas, we introduce a new collision coefficient, the coefficient of generation e_g ,

$$e_g \equiv \frac{\text{(separation speed)} - \text{(approach speed)}}{\text{(separation speed)} + \text{(approach speed)}} \\ = \frac{e_r - 1}{e_r + 1} \approx \frac{\phi^+ - \phi^-}{\phi}. \quad (12)$$

Inversely, $e_r = (1 + e_g)/(1 - e_g)$. The coefficient of generation e_g respects the symmetry between an exclusively absorbing collision ($e_g = -1, \phi^+ = 0$) and a exclusively generating collision ($e_g = 1, \phi^- = 0$). For the energetically neutral pseudo-elastic collision $e_g = 0$ ($\phi^- = \phi^+$). For intermediate cases the pre- and post-collision angles can be calculated from the net collision angle ϕ and the coefficient of generation e_g by $\phi^+ = (1 + e_g)\phi/2$ and $\phi^- = (1 - e_g)\phi/2$. From Eq. (10),

$$\Delta E = mv^2 \phi^2 e_g / 2. \quad (13)$$

Thus another interpretation of the coefficient of generation e_g is as the ratio of the collisional energy gain to that which would be lost for the same angular deflection in a totally plastic (dead, absorbing) collision with the same v and ϕ . That is, $e_g = \Delta E / (mv^2 \phi^2 / 2)$.

4.3. Elastic recovery r

Although the current discussion considers both active (muscle-determined) and passively mediated absorption and restitution, the terminology can be related to more commonly considered elastic behavior. The classical concept of elastic recovery is characterized by

$$r \equiv \text{fraction of } E_a \text{ stored and used for } E_g. \quad (14)$$

Thus the total positive muscle work during the collision, excluding the positive work contributed by parallel and series elastic components, is $E_g - rE_a$. The sum of dissipation and negative muscle work (excluding work absorbed by elastic tissue to be returned later) during the collision is given by $E_a - rE_a$. The elastic recovery r is an extra parameter that needs to be specified in order to calculate the metabolic cost of collisions. A truly elastic collision ($e_g = 0, r = 1$) is kinematically identical to a pseudo-elastic collision ($e_g = 0, r = 0$) where all incoming energy is lost but replaced by positive muscle work. Because we do not imagine elastic storage being used for anything but the subsequent generative phase, it is sensible to assume that for every collision or sub-collision that $rE_a \leq E_g$ so $r \leq E_g/E_a$ or $r \leq (1 + e_g)^2 / (1 - e_g)^2$.

4.4. Inferred energetic cost of a gait cycle with exactly one collision

A gait might involve positive and negative muscle work not only during collisions but also between collisions. The overall energy balance equation e.g. Eq. (3) concerns all of this work. In particular if $E_g > E_a$ then at least some negative work or other dissipation is needed in a non-collisional part of the gait cycle. On the other hand, if $E_g < E_a$ then at least some positive work need be done in a non-collisional part of the gait cycle. We take the *inferred energetic cost of collision over a gait cycle* to be the minimum possible cost based on the minimum positive work in the cycle, taking account that some positive work might have to be done between collisions in order to conserve energy.

The energy change across a collision $\Delta E = E_g - E_a = (E_g - rE_a) - (E_a - rE_a) = \text{(positive muscle work)} - | \text{(negative muscle work)} |$ can be negative, zero or positive. When $\Delta E < 0$, the positive muscle work during the collision $E_g - rE_a$ is less than the negative muscle work and dissipation $E_a - rE_a$. For energy balance over the whole gait cycle, the total positive work over the whole gait cycle (including that accounted for by the collision) must at least be $E_a - rE_a$. Thus, for $\Delta E < 0$ a lower bound on the total metabolic cost of a gait cycle is that inferred from the negative muscle work during the collision. Using the small angle approximation with Eqs. (10) and (14), the inferred collisional metabolic cost

per gait cycle E_m when $\Delta E \leq 0$ (and $e_g \leq 0$) is

$$\begin{aligned} \frac{E_m}{b} &= E_a - rE_a = (1 - r)E_a \\ &= \frac{(\phi^-)^2 v^2 m}{2} (1 - r) \\ &= \frac{\phi^2 v^2 m}{8} (1 - r)(1 - e_g)^2. \end{aligned} \tag{15}$$

Similarly, when $\Delta E \geq 0$ (and $e_g \geq 0$), the total inferred metabolic cost during the whole gait cycle is at least that due to the positive muscle work during collision. So the necessary inferred metabolic cost of collision per gait cycle is

$$\begin{aligned} \frac{E_m}{b} &= E_g - rE_a \\ &= \frac{v^2 m}{2} ((\phi^+)^2 - r(\phi^-)^2) \\ &= \frac{\phi^2 v^2 m}{8} [(1 - r)(1 - e_g)^2 + 4e_g]. \end{aligned} \tag{16}$$

The recovery r affects our interpretation of the metabolic energetics through Eqs. (15) and (16). However, r does not affect the kinematics (v, ϕ) which we take as given.

4.5. Multiple sequenced collisions per gait cycle

In one down-to-up redirection an n legged animal may have up to n sub-collisions. Each sub-collision i is expected to obey the equations above, each with its own $\phi_i, \phi_i^-, \phi_i^+, e_{gi}, \Delta E_i, E_{ai}, E_{gi}$ and r_i . From these it is possible to evaluate the energetic cost of the net down-to-up redirection.

The net changes in the collisional episode are given by

$$\begin{aligned} \phi &= \sum_{i=1}^n \phi_i, \\ \Delta E &= \sum_{i=1}^n \Delta E_i, \\ E_m &= \begin{cases} b \sum_{i=1}^n (E_{ai} - r_i E_{ai}) & \text{if } \Delta E \leq 0, \\ b \sum_{i=1}^n (E_{gi} - r_i E_{ai}) & \text{if } \Delta E \geq 0, \end{cases} \end{aligned} \tag{17}$$

where the expressions inside the sums can be expanded to look identical to Eqs. (15) and (16) with the subscript i added to ϕ, r and e_g . Fortunately, the relevant examples do not depend on the full generality and complexity of such expanded equations.

5. Examples, models and consequences

In this section we show some special cases. These illustrate the formulas above and in some cases hint at their biological relevance. A comparison of the predic-

tions here with human and animal behavior is given in the next section.

5.1. A glancing perfectly plastic collision can superficially appear elastic

Some subtlety in even the meanings of the words ‘elastic’ and ‘plastic’ are illustrated by the following example. Consider a perfectly absorbing ($e_r = 0, e_g = -1$) collision mediated by a single rigid massless leg (Fig. 2d). Just after the collision the outgoing velocity is orthogonal to the leg because the leg then pivots about the ground contact point. As discussed before, conservation of momentum orthogonal to the leg yields $v^+ = v^- \cos \phi$, where v^- and v^+ are the incoming and outgoing speeds and ϕ is the deflection angle. The post-collisional energy is $E^+ = E^- \cos^2 \phi$ and the fractional energy loss is $\Delta E/E^- = \sin^2 \phi \approx \phi^2$ (for small ϕ).

However, viewing this collision as occurring against the ground (ignoring the leg for a moment) one sees a redirection from downwards to upwards motion, a bounce. On the final upward path the overall speed of the object is slower than the approach (some energy loss has occurred). But the component of velocity normal to the ground after the collision could even be greater than before; the final upward velocity may be equal to or greater than the original downward velocity. Thus viewed as a collision with the ground this exclusively absorbing (plastic) collision has a corresponding positive coefficient of restitution ($e_r > 0$, and arbitrarily large). As discussed in, e.g. Chatterjee and Ruina (1998a), when collisional impulses have a tangential component, as here with the tipped leg, there is no fundamental relation between dissipation and the coefficient of normal restitution e_r between the object and ground.

Also, a plastic collision (plastic with respect to the leg) can have, say, an angle of incidence = angle of reflection (angles measured relative to the ground).

The plastic-collision mediated pole-vaulting in this example begins to hint that the concepts of bouncing and of elasticity are not so tightly related.

5.2. A pseudo-elastic collision with no recovery has one quarter the cost of a fully absorbing collision

The following example shows the energetic importance of pseudo-elasticity even in a collision that has zero elastic recovery. Assume a mass m moving at speed v that is to deflect an angle ϕ at a single collision per cycle. Consider two types of collisions.

First consider a collision that is pseudo-elastic with no recovery; none of the restitution work is recovered from the absorption phase but is instead actively replaced in

the generative phase. For such a collision we have $e_r = 1, e_g = 0, r = 0, \Delta E = 0$, and by Eq. (15) (or by Eq. (16)) that

$$E_m = bmv^2\phi^2/8. \quad (18)$$

Next consider a collision that is fully absorbing. In this case $e = 0, e_g = -1, r = 0$, and

$$E_m = bmv^2\phi^2/2. \quad (19)$$

The cost (Eq. (19)) associated with the plastic collision is four times the cost associated with the elastic collision (Eq. (18)), even with *no* recovery ($r = 0$).

For the pseudo-elastic collision the positive work required for the generative phase is associated with a collision with a deflection angle of $\phi/2$. On the other hand for the fully plastic collision, positive work is needed to make up for all the dissipation associated with a collision with a glancing angle of $\phi = 2\phi/2$. Because the energy costs are proportional to the square of the relevant normal velocity, the pseudo-elastic collision, which has half the collision angle, has one-quarter the energy cost.

5.3. Pseudo-elastic collisions minimize energetic cost

Assume we have a gait cycle with only one collision but for which the coefficient of generation e_g can be chosen freely. Assume m, v, ϕ and r are given. For what e_g is the cost of collision minimized? By inspection, for $e_g \leq 0$ Eq. (15) is minimized by $e_g = 0$ and for $e_g \geq 0$ Eq. (16) is minimized by setting $e_g = 0$. Thus, over all choices $-1 \leq e_g \leq 1$ we find that $e_g = 0$ minimizes the metabolic cost.

This observation has a strong consequence:

even with no elastic recovery, it is energetically beneficial to make every collision a pseudo-elastic collision.

This result is made intuitively plausible by recognizing that the negative work E_a varies as the square of the absorbing portion ϕ^- of the deflection angle. This cost is quartered by the pseudo-elastic collision as compared to a plastic collision. On the other hand, reducing the absorbing angle further has an extra prohibitive penalty of demanding non-collisional negative work or dissipation at another part of the gait cycle.

5.4. Dividing one collision into two smaller collisions halves the cost

Consider a single plastic (perfectly absorbing) collision with deflection angle ϕ . The energy lost in the collision is the kinetic energy associated with the component of motion orthogonal to the eventual direction of motion (Fig. 2d). For small angles the loss is then $-\Delta E = mv^2\phi^2/2$. Now decompose that one collision

into two smaller collisional deflections each with deflection $\phi/2$. The energy loss in each of the smaller collisions is calculated identically but with $\phi/2$. Thus $-\Delta E = mv^2(\phi/2)^2/2$; one-quarter the loss of the single larger collision. The net loss of the combination of two half-deflection collisions is thus $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$ of the loss of the single larger collision.

The key idea is that the relevant energies in a glancing collision vary as the square of the deflection angle. Halving the angle quarters the energy cost of a collision. So two half-angle collisions together have half the energy budget of a single full-angle collision. This hints at the utility of sequencing leg collisions.

5.5. Dividing one collision into n sub-collisions reduces the cost by a factor of n

Here we generalize the preceding result. Consider one collision A with a mass m moving at speed v and deflected by an angle ϕ with coefficient of generation e_g and recovery r .

Now consider replacing that one collision with a sequence B of n sub-collisions each of which has deflection angle $\phi_i = \phi/n$ and $e_{gi} = e_g$ and $r_i = r$ as the original collision. All energy terms in the smaller B collisions are smaller by a factor of n^2 than in the original larger A collision. Thus from Eq. (15), (16) and (17).

$$\frac{E_m^B}{E_m^A} = \frac{1}{n}. \quad (20)$$

Also, because $\Delta E^B = n(\Delta E^A/n^2)$ from Eqs. (13) and (17), we have that $\Delta E^B/\Delta E^A = 1/n$. That is, if the collision is divided into n smaller collisions both the work needed for generation during the collision and the kinetic energy lost during the collision are reduced by a factor of n .

As for the previous three examples, we gain an intuitive understanding by noting that the energies associated with a collision scale with the deflection angle squared. Breaking a collision into n smaller collisions makes each of the n sub-collisions have $1/n^2$ the energy associated with it. So the total energy cost is that of n collisions each with $1/n^2$ the cost.

5.6. An infinite sequence of plastic sub-collisions can produce one elastic collision

Now we take the $n \rightarrow \infty$ limit of the previous result. Using Eq. (20) we see that

both the cost of collision E_m and the energy lost $-\Delta E$ in the collision tend to zero with increasing n .

This holds for arbitrary collision parameters including totally plastic collisions ($e_{gi} = -1$) with no recovery

($r_i = 0$). As an aside note, perhaps surprisingly, a sequence of super-elastic collisions $e_g = 1$ also tends towards an energetically neutral collision as the number of sub-collisions gets large.

5.7. The collisional cost of transport for a point mass runner

An estimate can be generated from the principles described above for that portion of human running cost that is derived from collisional loss. The presentation here is an extension of that given in Bekker (1956) and Rashevsky (1948). Consider running as a point mass collision followed by a parabolic flight followed by a collision, etc. We take the nominal (nearly constant) forward speed as v . Various cases of this model of running are pictured in Fig. 3.

The time of flight and distance per stride are $T = \phi v/g$ and $d = vT$ (Fig. 3). From Eq. (15), assuming $e_g \leq 0$, and Eq. (7) we have

$$\begin{aligned}
 E_m/(bT) &= \frac{\phi^2 v^2 m}{8T} (1-r)(1-e_g)^2 \\
 &= \phi v m g (1-r)(1-e_g)^2 / 8 \\
 &= d g^2 m (1-r)(1-e_g)^2 / (8v), \\
 c_m &= b \frac{E_m/T}{m g v} = b \frac{d g (1-r)(1-e_g)^2}{8v^2} \\
 &= b(1-r)(1-e_g)^2 \hat{\mathcal{F}} / 16. \tag{21}
 \end{aligned}$$

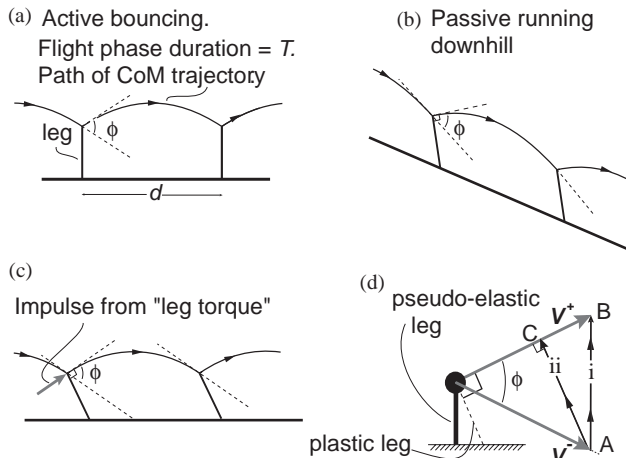


Fig. 3. (a) Collisional pseudo-elastic version of ‘pogo-stick’ (mass-spring) running. (b) Downhill passive running with no springs (plastic $e_g = -1$ collisions), energetically 4 times as costly as (a), even if (a) has no elastic recovery ($r = 0$). (c) Level-ground running propelled by hip torque, energetically identical to (b). (d) Hodographs show candidate trajectories for the tip of the velocity vector, during collision, as it moves from v^- to v^+ . Two cases are shown: (i) corresponding to pseudo-elastic running, and (ii) corresponding to hip-powered running.

The Froude-like number

$$\hat{\mathcal{F}} = (2gd)/v^2 = \frac{mgd}{mv^2/2} \tag{22}$$

is based on stride length d rather than the usual ℓ . $\hat{\mathcal{F}}$ is the ratio of the locomotion credit per step (weight \times step length = mgd) to the kinetic energy ($mv^2/2$). The usual Froude number $\mathcal{F} \equiv \sqrt{v^2/g\ell}$ does not simplify the collisional formulas here. Now, we can compare running without and then with emulating a spring with the legs.

5.8. Passive running with no springs may be like hip-powered running

Although apparently a silly idea, we can imagine a passive runner with no springs and no spring like behavior. This (Fig. 3b) is the running analog to the springless passive-dynamic walkers. Such a runner has a plastic collision ($e_r = 0, e_g = -1$) at each footfall. As mentioned above, because of the tipped leg the collision in some ways appears elastic, with the relative-to-ground angle of incidence equal to the angle of reflection. For this generation-free case there is no place to use recovery, so $r = 0$. From Eq. (21) the collisional cost is

$$c_m = b \frac{E_m/T}{m g v} = b \frac{d g}{2v^2} = b \hat{\mathcal{F}} / 4. \tag{23}$$

Energetically equivalent models can be considered that replace gravity work with another source. For now we do not allow use of work from an axial leg force. Another possible energy source is an externally applied impulse in the direction tangent to the outgoing path, as shown in Fig. 3c. Such a force impulse is mechanically equivalent (equipollent) to an externally imposed impulsive torque applied to the rigid leg at, say, the hip.

Within the context of the point-mass model, but for leg extension which we are excluding at the moment, no scheme can supply mechanical work from within the animal. But, as suggested by McGeer in the context of walking (McGeer, 1990a, 1992) and running (McGeer, 1990b, 1992), point-mass concepts might apply to bodies with extended mass. First, if the upper body is an extended mass hinged to the leg(s) at the center of mass (e.g. hip coincident with COM), the mechanics are identical to that of the point-mass model. Next imagine that, for collisional purposes, the COM is close enough to the hip that the collisional mechanics is little effected. But imagine that the center of mass is sufficiently forward of the hip that substantial hip torque is needed to balance the torque from the axial leg force (to prevent net body angular momentum increase over a stride). That is, Eq. (23) seems to apply, approximately, to an imagined runner that uses hip torques (Fig. 3c), rather than gravitational energy (Fig. 3b), to make up the collisionally absorbed energy.

5.9. Running with pseudo-elastic springs

A popular mathematical model for running has a massless foot connected to a rigid point-mass body by a perfectly elastic and massless leg-spring (called variously the mass-spring model, the Spring-Loaded Inverted Pendulum SLIP model, or the pogo-stick model). In flight the leg is positioned so the foot lands forward of the body. During the support phase the body compresses the spring, passes over the foot, and flies off again forward of the foot. In this model the ground collision involves no dissipation. This spring-mass model was the conceptual substrate of the highly successful running robots made by Raibert, students and colleagues (e.g. Raibert, 1986, 1990). A related passive runner with springs (and dashpots) is discussed in some detail in McGeer (1990b). But how important are actual springs to the energy savings provided by the mass-spring model?

In order to evaluate the potential saving of muscle-mediated contact strategies in running it is necessary to determine the potential costs incurred for running without passive elastic recovery. For this comparison we begin by taking the collisional limit (stiffness $\rightarrow \infty$) and use $e_g = 0$ and $\phi^- = \phi^+ = \phi/2$. For better comparison we assume no recovery $r = 0$ so that all of the generative phase comes from muscle work. Then by Eq. (21) the metabolic cost of transport for collisions is

$$c_m = b \frac{E_m/T}{mgv} = b \frac{dg}{8v^2} = b \hat{\mathcal{F}}/16. \tag{24}$$

Comparing Eqs. (23) and (24) we see again that the cost of transport is still 4 times less with a pseudo-elastic collision than with the positive work being done any other way. That is, for example, it is inefficient to use hip torque to make up for collisional losses.

5.10. Caveat on the neglect of leg-swing costs

The model here only considers the energetics of the redirection forces and thus cannot completely characterize locomotion energetics. Real animals move some body parts in non-passive, and thus energetically costly ways not directly associated with along-the-leg redirection forces considered here. Because we do not consider these non-collisional costs the utility of the calculations here are (1) as rough models that neglect some important terms, (2) as models for only part of the total cost, (3) as models for comparison between cases where the other costs are approximately fixed.

For example, note that in this running model the cost of transport at a given speed v tends to zero as the step length d tends to zero. This non-physical result is common to the locomotion models below as well. Thus when only counting collisional costs, optimization must be done only at fixed step length d or at prescribed total collision angle ϕ . Otherwise the optimum is zero-cost locomotion with step length tending to zero and frequency tending to infinity.

6. Galloping

Galloping is a high-speed running gait in large quadrupeds such as horses. Unambiguous mechanical characterization of this gait has been elusive, in spite of the horse being of substantial social and economic importance to the history of human civilization. Consideration of collisional cost provides insight into the functional advantage of using this gait at high speeds. However, before applying the collisional model to the horse gallop it is useful to discuss some motivational analogies.

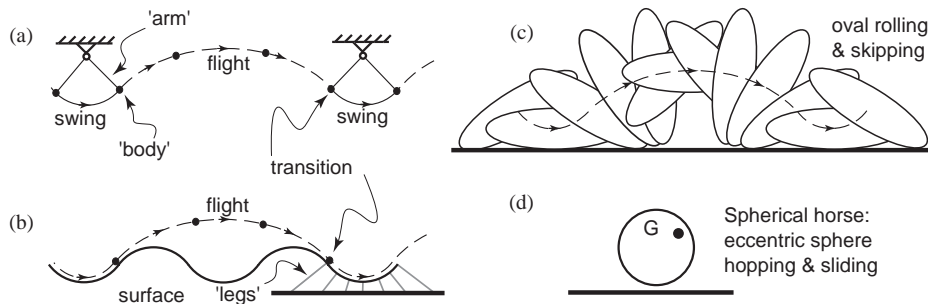


Fig. 4. (a) The point-mass ricochetal brachiation model from (Bertram et al., 1999). The dots show the body trajectory. The motion alternates between flight and an effective bounce at the branch-holding swing phase. There is no collision loss if the flight trajectory is tangent to the circular swing path at the transition. (b) A particle sliding on a frictionless corrugated surface can have motions identical to those in (a). The corrugated surface can be simulated by an infinite number of massless legs which contact in sequence. Each leg is orthogonal to the path and produces only an infinitesimal collision. Note, to match the path the legs have various lengths. (c) A football-like body can bounce with no elasticity if its rotation and downwards translation are phased so that ground contact point has zero velocity just before contact. The center-of-mass motion is shown as a dotted line. (d) If launched with the right spin, a sphere with an eccentric center-of-mass can hop on a rigid frictionless substrate, even with no elasticity.

6.1. Galloping as sliding on a bumpy surface

We initiated this research project by looking for a ground-support version of ricochet brachiation (Fig. 4a). Fig. 4b illustrates such a system. A point-mass slides on and skips over a frictionless corrugated surface. For both models the free-flight and sliding motion paths are tangent at the time of contact and there is no collisional dissipation.

Now we try to implement the idea using legs. As is intuitively acceptable and demonstrated by Eq. (20) an infinite number of infinitesimal glancing collisions, even if each is fully plastic, is equivalent to frictionless sliding. The right part of Fig. 4b shows that the frictionless surface could be simulated by an infinite number of massless legs each orthogonal to the path of the point-mass and each providing a compressional force along the leg. That is, a sequence of concave-down parabolic arcs approximates a polygon. The long hindmost leg lands first and the sequence of collisions proceeds through shorter and then longer legs to final lift-off mediated by the long foremost leg.

6.2. Assume a spherical horse

Even without a corrugated frictionless surface or an infinite number of varying-length legs, an oval-shaped rigid body can effectively bounce off a rigid flat surface without elastic recoil (Fig. 4c). The occasional high bounce of an end-over-end tumbling rugby or American football seems to roughly illustrate this phenomenon. In flight the lower-most point of the football oscillates up and down relative to the center of mass. With the right timing such a retraction can exactly cancel the downwards center of mass motion and the lower surface will touch the ground with zero downwards velocity. If the horizontal motion is also matched then the new contact is made with zero relative velocity. With no velocity discontinuity at contact there is no collisional dissipation. After a brief roll, the hop up proceeds with no energy loss.

The analytic treatment of such a dissipation-free yet *inelastic* collision is simplest with the vertical bouncing of a frictionless ball or sphere that has an eccentric center-of-mass, as discussed in Haggerty (2001). To make this bouncing more like locomotion, a uniform horizontal motion can be superposed to the center of mass motion so that there is zero horizontal velocity at ground contact. To recover the football-like motions we can impose a non-slip condition during the contact phase. Although rolling contact and sliding contact phases have different details, they both have collision-free motions and identical flight phases. (A technical caveat: for the no-slip motion the rolling contact must be with infinite coefficient of friction; a finite horizontal force is needed at first and last contact.). In the

bouncing-egg case the bottom curved surface replaces the continuum of legs in the point-mass model above. Note that in such non-dissipative bouncing, energy is not stored and returned. Rather, there is just no loss in the process. A related elasticity-free bouncing mechanism is pictured and briefly discussed in Tucker (1975).

We now try to emulate the gibbon-like corrugated-sliding and spherical-horse mechanisms with a finite number of collisions.

6.3. The point-mass collisional model of galloping

We treat a three beat horse gallop as a point mass runner with each gait-cycle made up of three sub-collisions (see Figs. 1 and 7). Although one can consider other possibilities, for definiteness and simplicity assume each sub-collision is pseudo-elastic ($e_r = 1, e_g = 0$), $\Delta E_i = 0$ and with recovery r not specified. From Eqs. (5), (18) and (20) for each collision we get that $E_m = b\phi^2 v^2 m(1-r)/(8 \cdot 3)$. Thus, proceeding similarly to the running model calculation in Eq. (21), we have

$$\begin{aligned} c_m &= b \frac{(1-r)\phi}{24} = b \frac{(1-r)g}{24vf} = b \frac{1-r}{24} \left(\frac{gd}{v^2} \right) \\ &= b(1-r)\hat{\mathcal{F}}/48 \end{aligned} \quad (25)$$

Comparing Eqs. (24) and (25) we get a three-fold reduction in cost by using three legs, as expected from Eq. (20). Assuming a given speed v and stride length d the triplet collisions use three times less energy as would a pronk gait with one collision at each stride. This factor of 3 improvement holds for plastic, pseudo-elastic or with any other values of e_g and r , so long as the same values are used for the triplet as for the pronk.

7. Point-mass model of collisions in human walking

Here we consider the step-to-step transition in human walking from the point-mass glancing-collision perspective. The relevant issues are conveniently displayed (e.g. Kuo, 2001) by a nineteenth century visualization technique called a “hodograph” (Fig. 5). If the velocity vector is animated as it changes during the step-to-step transition, always putting its tail at the origin, the tip traces a curve. This velocity-trajectory curve is a hodograph. Fig. 5 shows the velocity before collision (\mathbf{v}^- with tip at A) and just after collision (\mathbf{v}^+ with tip at B). In this model \mathbf{v}^- and \mathbf{v}^+ are assumed to be orthogonal to the old and new stance legs, respectively. During a collision the tip of the velocity vector traces a path on the hodograph. Shown are several such velocity-tip trajectories, each with a different collisional meaning and each with a different energetic cost.

Even though we track the velocity trajectory in detail, the collisional model assumes that the path is traversed

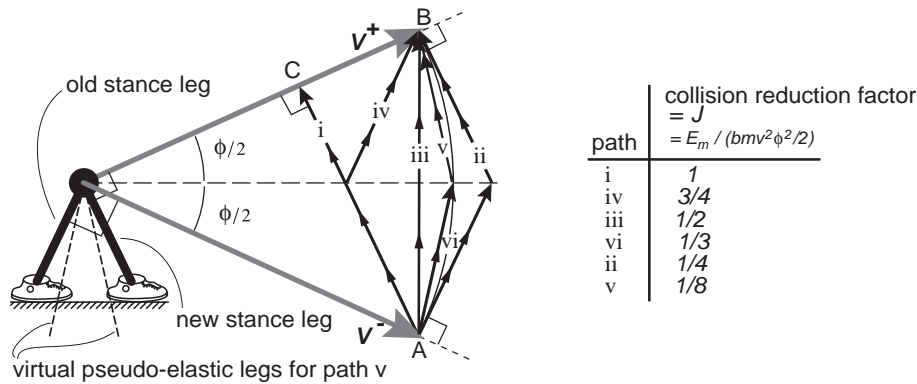


Fig. 5. Various collisional models for the step-to-step transition in walking. The hodographs show candidate trajectories for the tip of the velocity vector, during collision, as it moves from v^- to v^+ . All are for walking models with collisional impulses from two legs. Several cases are shown. (i) In passive-dynamic downhill walking, there is only impulse along the new stance leg. This case is the same for walking as for passive running with a dead leg. At every instant on path AC $dW = mv \cdot dv < 0$ and the collision is exclusively absorbing (the length of v is decreasing throughout). The work required to make-up the length of v^+ (path CB) is supplied by gravity. An energetically equivalent model has power supplied by the trailing old stance leg after motion is constrained to the new stance arc. (ii) In the toe-off then heel-strike model of walking there is a purely generative phase with a force along the old stance leg, followed by a purely absorbing heel-strike phase along the new stance leg. (iii) Using only impulses from the two legs the vertical path requires overlapping impulses. (iv) The least energetically favorable collision using two compressional impulses along the legs, in which the heel-strike impulse is complete before push-off starts. (v) In the new pseudo-elastic model proposed here there are two branches. One along the virtual leg from hip to toe ($\phi/4$ forward of the rear leg) and one along the virtual leg from hip to heel ($\phi/4$ behind the front leg). This path is the minimum-cost two-leg simultaneous collision for given ϕ . (vi) A trajectory of constant energy. This trajectory has precisely zero ‘external work’ yet requires leg work. Path (vi) can be traversed at no energy cost using a (slightly) rounded foot whose length is the step length.

in negligible time. In a sense we assume that a gait cycle can be characterized by two time-scales: the longer one associated with, say, the period of one step; and a shorter one associated with the collisional time. During the short collisional time, the longer stride time is treated as frozen.

The details inside the short collisional time have a huge effect on the energetics of the collision. Below we consider various collision scenarios. All have the same v^- and ϕ . All but one of these has the same net collisional impulse and the same impulses at each leg as the other cases. Yet, these different contact strategies have quite variable energetics.

7.1. The rimless wheel and passive-dynamic walking

A special simple case for the model here is the famous rimless wheel (Bekker, 1956; Margaria, 1976) with mass only in the hub (see Fig. 6a) analysed in detail in McGeer (1990a). The collision analysis is the same as for the Simplest Walker (Garcia et al., 1998). In this case the only collisional impulse is from the new stance leg. The trajectory is labeled (i) in Fig. 5. The deficit in the magnitude of v^+ must be made up by gravity (walking down an incline) if the system is strictly passive. Using the formalism here, the cost of this collision is, from Eq. (15), using $r = 0, e_g = -1$,

$$E_m = b\phi^2 v^2 m / 2. \tag{26}$$

This corresponds with path (i) on the hodograph of Fig. 5, the most costly model for walking.

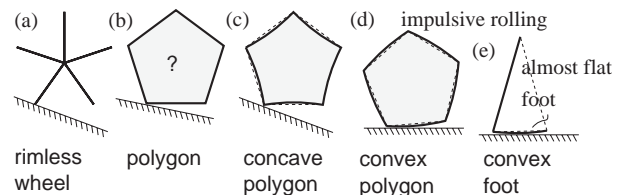


Fig. 6. Relation between walking and rolling. (a) The rimless wheel. (b) The rolling polygon, ill-defined (a distinguished limit). (c) The concave rolling polygon is a rimless wheel. (d) The slightly convex polygon rolls with no dissipation, but impulsively (e) An almost-flat foot with rigid ankle can, like the impulsive polygon, be part of the step-to-step impulse, but absorb no energy. On the hodograph of Fig. 5 the rounded foot with $d_f = d$ corresponds to constant energy motion on the constant v circular arc.

7.2. Active collision reduction: push-off preceding heel-strike

As mentioned in Tucker (1975) and again in McGeer (1993), the collisional cost of walking can be reduced by preceding the absorbing heel-strike collision with a push-off (plantar extension) which we model as a generative collision. At a given speed and step length the collisional cost can be reduced by a factor of 4 this way (Kuo, 2001).

Using the formalism here we can look at a sequence of two collisions with $\phi_1 = \phi_2 = \phi/2$. The first is a purely generative push-off collision with $e_{g1} = 1$ and the second a purely absorbing collision with $e_{g2} = -1$. Using Eqs. (15)–(17) and $r_i = 0$,

$$E_m = b\phi^2 v^2 m / 8 \tag{27}$$

giving, comparing with Eq. (26), a factor of 4 reduction in cost as compared to passive walking. Pushoff before heelstrike is shown as path (ii) on Fig. 5. For given ϕ this two leg walking collision is energetically identical to a single-leg pseudo-elastic collision (see Eq. (24)). Both have generating and absorbing phases with deflection angle $\phi/2$. For walking, however, the ‘restitution’ occurs before the absorption.

There are a few ways to understand the efficiency gain of using pushoff before heel-strike as compared to the purely passive, rimless-wheel collision. By pushing off before heel-strike the collision loss at heel-strike is reduced. Or, the angle at the absorbing part of the collision is cut in half, reducing the absorption E_a by $\frac{1}{4}$. Finally, using two legs with push-off before heel-strike is effectively using two legs to make up a single pseudo-elastic collision. Only a backwards pseudo-elastic collision, one having generation before absorption instead of the other way around.

7.3. Overlapping collisional force histories

Our sequenced collision calculations in Sections 4 and 6 have assumed that only one leg is in contact with the ground at a time. But real leg contact times do overlap, both in the horse gallop and in double-support in human walking. As mentioned in Tucker (1975) and discussed in detail by Donelan et al. (2002a, b), when two legs simultaneously apply force one can do work while the other absorbs work. So kinetic energy fluctuations are less than the muscle work that causes them.

Assume ϕ and v are given, the two impulses are assumed to be along the legs, and the net collision conserves energy ($\Delta E = 0$). Balance of momentum determines the two impulses and balance of energy determines that their total work is zero. But the collisional cost is not determined. The collision cost depends on the relative timing of the two impulses.

For example, consider truly simultaneous collisions. Assume the two forces at all times proportional, giving path (iii) in Fig. 5. The path integral from the appendix (Eq. (42)) gives

$$E_m = \frac{1}{2}mv^2\phi^2/2. \quad (28)$$

Comparing with Eq. (27) we see that truly simultaneous push-off and heel-strike has twice the cost of push-off entirely before heel-strike. For heel-strike entirely before push-off, path (iv) in Fig. 5, we get

$$E_m = \frac{3}{4}mv^2\phi^2/2. \quad (29)$$

This is a peculiar limiting case. The lead foot first applies an impulse, then waits for the trailing leg to apply an impulse, and then (non-impulsively) begins single stance. Considering only cases with compressional impulses applied between stance phases this cost, three

times more than that in Eq. (27), is the most costly down-to-up redirection.

A case mimicking passive downhill walking, path (i) in Fig. 5 is also possible on level ground. First a heel-strike collision occurs (with the full ϕ and with $e_g = -1$) following this both legs apply forces to bring the magnitude of v up to its pre-collision value along path CB in Fig. 5. This requires a physically unrealistic non-working tension force from the lead leg as the rear leg pushes off. Should this be implemented by a person or robot, the time of collision could be spread and the tension could be replaced by gravity, with identical net energetics (as implemented in Collins et al., 2005). Energetically this push-off-during-next-stance case is identical to that for passive walking (e.g. Eq. (26)).

7.4. A collision with ‘no work’ but with a muscle work cost

Another illustrative case is given by path (vi) in Fig. 5. At every instant in time the net force (the sum of the two leg forces) is orthogonal to the path. The kinetic energy is constant throughout the collision. The ‘external work’ is precisely zero. But each of the legs does some mixture of positive and negative work, a little more than in the sequential collision model (Fig. 5 path ii). As presented in the appendix, for this zero-external-work case we have

$$E_m = bmv^2\phi^2/6. \quad (30)$$

This cost is $\frac{4}{3}$ the cost of the push off entirely before heel-strike (Eq. (27)).

This zero-‘external-work’ example suggests that modeling double stance or a horse gallop as a sequence of independent collisions may be closer to the appropriate work accounting (e.g. the ‘individual-limbs’ method of Donelan et al., 2002b) than just associating a cost with the center-of-mass energy fluctuations (e.g. Minetti et al., 1999).

7.5. The optimal step-to-step transition

Considering the full range of force histories, which one is optimal? Minimization of the explicit formula (Eq. (41)) in the appendix, for given v^- and v^+ shows that, for forces along the legs, push-off entirely before heel-strike, path (ii), is energetically optimal.

7.6. Pseudo-elastic legs

The variety of possible collision strategies raises the following question. Given v^- and v^+ , if one assumes that the collision is mediated by forces along two virtual legs (not necessarily orthogonal to v^- and v^+), how should these legs be oriented and how should the separate force histories vary so as to minimize the net collisional cost?

A slightly involved argument shows that the solution is the path (v) of Fig. 5; a sequence of two pseudo-elastic collisions oriented at the quarter and three-quarter point of the splayed double-stance legs. All other trajectories based on forces along two legs, no matter what the leg orientations or how the forces are distributed in time, have greater cost.

The energetic cost of one such two-collision episode ($n = 2$, $e_{gi} = 0$, $\phi_i = \phi/2$) is

$$E_m = mb(1-r)\phi^2 v^2 / 16, \quad (31)$$

one-eighth the cost of passive-dynamic walking and one half of toe-off before heel-strike. This situation is essentially identical to the model for a horse canter, but with two beats here instead of the horse's three.

7.7. Collisional rolling

One model of walking, used in McGeer-like passive robots, is with round feet and locked ankles. To understand such a foot from the collisional perspective it is instructive to consider the subtle case of a rolling polygon (Fig. 6).

So far the collisional walking models considered are mechanically similar to the rimless wheel of Fig. 6a. For simplicity assume passive rolling without slip, and with all mass at the center point. One might think the rimless wheel is equivalent to a rolling polygon (Fig. 6b). But the polygon is ambiguous. Fig. 6c shows a concave polygon which is equivalent to the rimless wheel, no matter how small the concavity. On the other hand, Fig. 6d shows a convex polygon. This polygon rolls with no dissipation, no matter how small the convexity. Machined solids similar to the slightly concave and convex polygon, even if almost imperceptibly different, roll completely differently. The convex polygon rolls well and the concave polygon loses a considerable fraction of its energy at each collision. Thus, the regular polygon is (in math language) a distinguished limit with different behavior depending on whether it is considered an extreme case of concavity or of convexity.

A rolling, slightly convex polygon has motions that alternate between inverted pendulum motion (hinged at a vertex) and a collisional phase. The collisional phase is not dissipative but rather tracks path (vi) in Fig. 5, all in an instant. This is equivalent to having a continuum of legs.

From the collisional perspective we can treat rounded feet, even if close to flat, as a means to track path (vi) in Fig. 5. If the foot length is the step length d then there is no dissipation. If the foot length d_f is less than d then the relevant collisional length is $d - d_f$. This should replace d in any of our formulas involving collisional loss but not in formulas relating step length to speed. Thus, at a given speed and with a given collisional mechanism (be it passive walking, or push-off before

heel-strike), use of a rounded foot multiplies the collisional cost per step by $(d - d_f)^2 / d^2$; a rounded foot with length of half the step-length quarters the collisional cost.

7.8. Collision cost and the plethora of step-to-step transition models

For walking the collisional cost depends sensitively on the details of the step-to-step transition. We can summarize the various scenarios for the cost of one step-to-step transition, as

$$E_m = mbJ(1-r) \frac{d^2 v^2}{\ell^2 2}, \quad (32)$$

where reviewing, v is average forward speed, $b \approx 5$ is an average metabolic cost for negative work or absorption, $0 \leq r \leq 1$ is an elastic recovery, and $d \geq d_f$ and ℓ are step length, foot length and leg length, respectively. The collision reduction factor for walking, taking $d_f = 0$ is

$J = 1$ for passive dynamic walking.

$J = 3/4$ for heel-strike before push-off.

$J = 1/2$ for simultaneous push-off and heel-strike.

$J = 1/4$ for push-off before heel-strike.

$J = 1/8$ for a pseudo-elastic toe and heel at the $\frac{1}{4}$ and $\frac{3}{4}$ points.

If $d_f \neq 0$ the above values of J should be multiplied by $(d - d_f)^2 / d^2$ for the first four cases above.

8. Application to animals and people

The overly simple point-mass collisional models discussed above obviously do not capture all of the features of coordination in locomotion nor all of the energy costs. Nonetheless, it is interesting to check the predictions against human and animal behavior.

8.1. Human running

A popular observation is that human legs behave much like springs while running (e.g. Alexander, 1990, Blickhan, 1989, Farley and Gonzalez, 1996, McMahon, 1985). That is, a spring-mass model captures much about the ground forces and center-of-mass motion in running. This spring-like behavior is not claimed to be literally elastic behavior, but rather the relation between force at the foot and distance of the foot from the hip as mediated by nerves, muscles, tendons, ligaments and bones is similar to that which would result from spring-like elastic return.

Given that people's bodies are relatively large, that their legs are relatively light, and that muscles for activities other than leg compression have small strength, the mass-spring model must be a reasonable description at some level. But people could conceivably

run with other strategies than spring-like hopping. For example the leg collision could be more absorbing (with $e_g \approx -1$) as per Figs. 3b, c. The energy lost could be made up by hip torques. The collision calculation here shows that, even neglecting recovery, such motion would have four times the energetic cost of spring-like leg action, even with no energy recovery involved. So adding and using strong hip extensors would not be energetically beneficial, but rather more costly. Thus, the pseudo-elastic and “linear actuator”—only nature of the human leg in running is a prediction of this collision theory. The energetic favorability of the approach is independent of, although further enhanced by, any genuine elastic recovery.

What about quantitative prediction of the ground-contact costs of running? Applying the fastest forward running data point in Wright and Weyand (2001) to Eq. (24) we get

$$c_m^{VO2} = b(1 - r) \frac{dg}{8v^2}$$

$$0.36 \approx 5(1 - r) \frac{(1.33 \text{ m})(10 \text{ m/s}^2)}{8(3.5 \text{ m/s})^2}$$

$$\approx 0.68(1 - r), \tag{33}$$

which gives a superficially reasonable elastic recovery of $r = 48\%$, assuming the total cost of running was due to collisional small-angle ground contact.

8.2. Horse galloping

When Raibert built multi-leg robots, he simplified his control-algorithm design by first making multiple legs act like one, and then controlling that one virtual leg in

the same way that had worked for robots with one physical leg (e.g. Raibert, 1986; Raibert et al., 1986).

A proponent of the spring-mass model (e.g. Blickhan and Full, 1993) might suggest that what worked for Raibert’s robots might work in natural systems as well. According to this view animals should use multiple legs to simulate a single leg. Applying this idea to fast moving horses suggests they should pronk. But they do not. Although a horse trot may be considered a two-leg pronk, at higher speeds horses break their gait into a three-beat gallop (canter).

The collisional model predicts even more savings on the legwork cost by using a four-beat gait. And such is used by horses at still higher speeds. Here are some comparisons of the model predictions with what horses do during the down-to-up redirection in a canter:

- The first-contacting rear leg ground-contact force accelerates the horse and the last-contacting front leg retards the horse. This is clear in Fig. 7. Thus near mid-stance the horse is at maximum speed. In contrast, the mass-spring model predicts the opposite, that mid-stance is the time of minimum forward velocity. The horse canter is also the opposite of the normal spring-mediated-running paradigm for the phasing of kinetic and potential energy. Rather, the horse’s energy phasing is like that of human walking, as predicted by the sequential collision model here.
- The legs make contact from rear to front, not simultaneously as in a pronk. This is clear in Figs. 1 and 7. Although our point-mass model cannot distinguish front legs from rear legs, the analogy with the rolling egg (Fig. 4) suggests that extended-body considerations make landing on the rear most

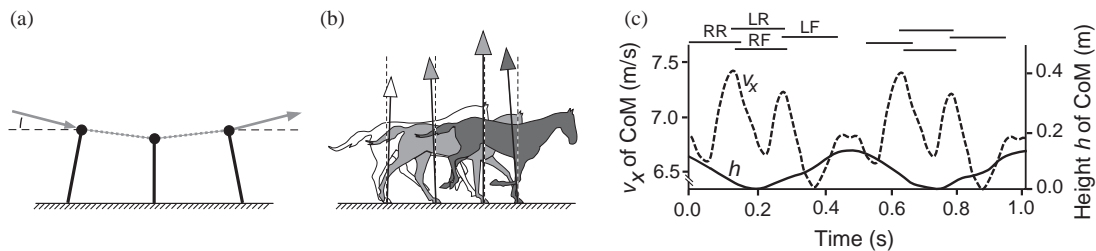


Fig. 7. (a) The three-pseudo-elastic-collisions model of the horse gallop. (b) schematic strobe of a horse shows mid-contact of the trailing rear limb (first contact, unshaded), contralateral lead rear and trailing fore limbs (contact together in canter, light shading) and lead fore limb (last contact prior to non-contact flight phase, dark shading). Arrows indicate measured (Merkens et al., 1993) average ground reaction force for the contact of each limb (shading matches corresponding image). The nearly simultaneous midfoot ground contacts (the two lightly shaded arrows) correspond to the middle of the three feet in (a). (c) Center-of-mass horizontal velocity v_x and height fluctuations h for a small horse galloping at 6.83 m/s (redrawn from Minetti et al., 1999). Two complete strides are illustrated (one data set cut and pasted) with corresponding approximate footfall timing (as per Fig. 1). The first contact after the flight phase occurs with the right rear (RR) limb. Horizontal velocity initially decreases slightly, but increases substantially over this limb’s contact time. Meanwhile h decreases. Contact of the diagonal pair of left rear (LR) and right front (RF) limbs also causes a transient decrease and increase in v_x . During this second contact phase the h reaches its minimum height. Finally the left front (LF) ‘lead’ (pronounced leed) limb makes contact and v_x decreases, bringing the instantaneous forward speed to the lowest in the gait cycle. During the lead-limb contact h increases as the animal vaults into the next flight phase. During each limb contact a horizontal deceleration and reacceleration occurs which is duplicated by a decrease and then increase in the total energy (not shown here). (Note, with better measurement the v_x curve would be more constant during the flight phases).

appropriate. In particular, because the first contacting leg has a primarily forwards force, its moment about the center-of-mass is less if it is applied at the rear of the horse. Similarly the moment of the rearwards force of the last-contacting leg is less if applied at the front of the horse.

- The fluctuations in v_x , shown in Fig. 7, closely mimic the fluctuations in the total energy (not shown). The three-dip-per-stride pattern thus shows that each leg absorbs and then returns energy (with the rear leg a bit stronger on the generative part and the front a bit stronger on the absorption). The collisional model predicts that such pseudo-elasticity is energetically advantageous (independent of recovery).

Overall, it seems, horses use a combination of two strategies discussed here. On the one hand they mimic the brachiation swing with a sequence of collisions. On the other, they make each of those collisions close to pseudo-elastic.

The metabolic energy of running horses has been relatively well studied (Hoyt and Taylor, 1981; Eaton et al., 1995; Potard et al., 1998; Langsetmo et al., 1997; Butler et al., 1993; Wagner et al., 1989; Minetti et al., 1999). Minetti et al. (1999) reports data from a horse cantering at about $v = 7\text{ m/s}$ with a stride frequency of about $f = 1/0.6\text{ s}$. Minetti et al. also report a rate of chemical energy expenditure of between 2 and 3 J/kg m. Using $g \approx 10\text{ m/s}^2$ this gives a specific energetic cost of transport of between 0.2 and 0.3:

$$0.2 \leq c_m \leq 0.3 \quad (\text{as measured by } \dot{V}\text{O}_2). \quad (34)$$

From Eq. (25) using $r = 0$, $b = 5$ we get a mechanical cost of transport due to collisions of

$$c_m = \frac{b(1-r)g}{24vf} \approx \frac{(5)(1)(10\text{ m/s}^2)}{24(7\text{ m/s})(1/0.6\text{ s})} \approx 0.18 \quad (35)$$

That is, naive application of the formulas says collisions account for about 60%–90% of the measured cost of locomotion in a galloping horse. However, there are three likely sources of error: (1) We have assumed no recovery $r = 0$; (2) the collisional cost is sensitive to the details of the collision (the value of e_g and whether or not there is force overlap); and (3) the collision model assumes a duty factor of zero, far from the combined-legs duty factor of about 0.75 observed in the horse data (and also inferable by counting the three beats and rest in each triplet of Rossini’s overture). The presence of non-zero recovery will reduce the predicted cost. Thus the support cost of transport, if estimated more accurately using a more detailed model, may be substantially less than 0.18.

8.2.1. Sequenced versus evenly spaced collisions

At the speed of a given gallop the collisional model gives about the same cost if there are 3 independent collisions (each with a parabolic arc in-between) in the time of one *ba-da-dump* cycle. Our model does not give one or the other gait much preference. A similar situation holds for the 4 beat gallop. Curiously, there are some horses that do have an even 4-beat gallop (the Icelandic tölt and a “full rack” of other breeds have a foot-fall pattern and timing of a fast walk).

8.3. Human walking

We can compare both the qualitative and quantitative predictions of the collisional model with human walking. Some considerations:

8.3.1. The metabolic cost of walking

Data from Bertram (2005) is plotted in Fig. 8. A range of frequencies are shown for 9 subjects with cost per step on the y -axis (normalized by mean translational kinetic energy) and dimensionless step length on the x -axis. The dimensionless axes chosen highlight the collisional cost. Also plotted is a fit from Eq. (32) where we use $r = 0$, $b = 5$, and $J = 1/4$. The data is unprocessed (A better fit to theory is generated by subtracting the cost of walking in place from each subject at each frequency). At larger step lengths the predicted collisional cost accounts for a large fraction of the total metabolic cost of walking. As discussed, the details (values of r , J , and d_f) significantly effect collisionally predicted cost.

8.3.2. Coordination patterns

Most significantly, as expected by the theory here (and anticipated by Tucker and McGeer), the energetic

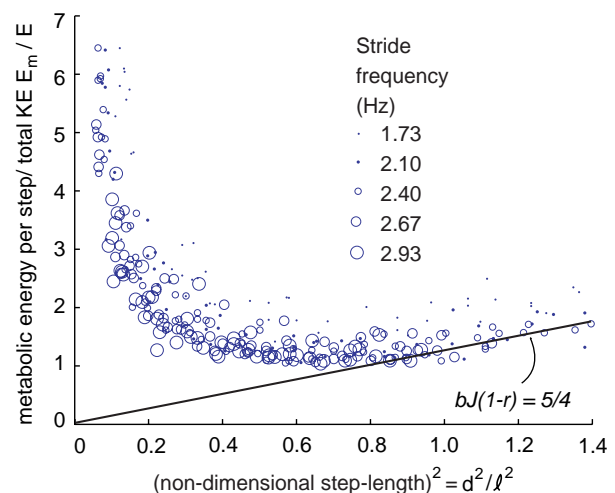


Fig. 8. Human walking data. Data from the data set used in Bertram (2005). A non-dimensional plot shows the contribution of the cost based on the collisional model to the total metabolic cost of walking.

favorability of using push-off to power walking might explain that coordination strategy of humans. Further, energetically favorable coordination features, as predicted by the collisional modeling, include

- having toes that push off, and heels that land extending in front and behind the ankle, respectively.
- having some energy absorption before toe-off and generation at the end of heel-strike (as shown clearly in Kuo et al., 2005). This model of walking is interesting in that it shows, perhaps, that the step-to-step transition is one where people choose not to simulate a single leg with two legs, but rather, to use their two legs (with heels and toes) to simulate 4: the rear stance leg to set up the initial pre-collision velocity, the toes for a pseudo-elastic collision, the heels for another pseudo-elastic collision, and the lead stance leg to impose the post-collision inverted-pendulum velocity.
- having push-off somewhat before heel-strike.

8.3.3. The walk to run transition

Because we do not account for leg swing cost, we cannot fairly examine the unconstrained walk-to-run transition. If, however, we assume that a person is given a speed of locomotion (say on a treadmill) and also a given frequency (say with a metronome) we can compare the cost of locomotion of the two gaits using the small angle collisional theory here. Using, say, Eq. (32) with $J = \frac{1}{2}$ and $r = 0$ for walking we have $c_m = bdv^2/(4g\ell^2)$. Using Eq. (21) with $r = 0$, $e_g = 0$ for running we have $c_m = bdg/(8v^2)$. The cost of running is less than that of walking for $v^2/(g\ell) > \sqrt{1/2}$. Note that the transition speed turns out to depend only on speed and leg length and to be independent of frequency.

In effect, the walk to run transition is thus explained as occurring at that speed for which the collisional angle in running (meeting of parabolic arcs) becomes less than that of walking (meeting of circular arcs). This explanation may be contrasted with the usual explanation based on the centrifugal acceleration at mid-stance in walking.

8.4. Children's skipping

As noted in Marey (1874) and Minetti (1998) children's skipping, with two foot falls between successive flight phases, has a resemblance to galloping. One version (asymmetric or unilateral skipping) is called 'galloping' by children. These gaits would correspond to $n = 2$ (Minetti, 1998) and according to the theory here should have an initial (rear) foot contact with a forward thrust. Immediately following this the next foot (front) should redirect the mass upward into the next flight phase while slowing the forward motion. Both these features appear to be true for human children. And, as is

true for horse galloping, the phasing of kinetic energy for skipping is predicted to more resemble human walking than human running (see the local maximum in E_{kx} at mid double-support in Fig. 3b of Minetti, 1998).

As noted, the collisional model, without other costs, is not sufficient to explain why children and astronauts on the moon like to skip and adults on earth generally do not. However, given a velocity and stride length, the collision-loss minimization of this sequential-collision gait make it preferable to hopping with both feet together. One does not need fancy equipment to find that repeated jumping is more tiring than skipping.

8.5. Classification of gaits

Gaits can be classified any number of ways (e.g. number of legs on the ground at a time, existence or not of a flight phase, duty-cycles of legs, phasing of various energy terms, the order of leg contact, whether legs are compressed or extended mid-stance, etc). From the collision perspective we can classify gaits into two types

- Gaits that use sequenced collisions and thus have a maximum v_x in the midst of the down-to-up redirection. These gaits include walking, cantering, galloping, and children's skipping.
- Gaits that do not use sequenced collisions and thus should have a minimum v_x in the middle of the down to up redirection. These gaits include human running and horse trotting. The Icelandic horse tölt may also be in this class.

8.5.1. If collision costs are bad, why do not animals avoid collisions entirely?

One can imagine, say, a walking gait where the center of mass moves at a constant speed at a constant height. Simple experiments (Farley and Ortega, 2003; Gordon et al., 2003) show that such smooth motion seems to add to metabolic cost. We expect that simple theory will also predict that smooth motions should have a higher metabolic cost than the oscillatory (and thus somewhat collisional) motions that animals choose.

9. Discussion

The leg of a bipedal animal typically contains many muscles, which act in concert to produce legged locomotion. Some of this work goes into swinging the leg. This we have ignored. Also, no account is made here for the costs of producing forces without work, in isometric contractions. We have focused on the other substantial fraction of locomotor metabolic cost: the work of the leg on the upper body, to redirect its motion. In particular, we have assumed that mechanical

work correlates with metabolic cost. Of course, this correlation is only approximate in detail.

In this paper, we approximate this cost by one that is derived from a point mass model with a single actuator. Why is this likely to be a good approximation? Firstly, if we believe that muscles do not fight each other, it might be reasonable to assume that in any given phase of the gait cycle, muscles do mostly positive work or mostly negative work but not both in comparable amounts simultaneously. Given that this is true, the energetics of a complex mechanism might be captured by a point-mass model—the collisional energetics depends on the foot-to-ground mass matrix (Chatterjee and Ruina, 1998a,b) whose dominant term will generally highly correlate with the total mass.

The metabolic cost thus estimated is closely related to some older energy accounting schemes. Complex animal motion data is sometimes reduced using König's decomposition of total kinetic energy into a center-of-mass energy, fluctuations of which define “external work”, plus a relative-to-center-of-mass energy, fluctuations of which define various “internal work” measures (e.g. Cavagna et al., 1976, 1977; Fenn, 1930). For a fictitious (or simulated) animal which is literally a point-mass, the classical external work is the same as our metabolic cost, if only one leg is on the ground at any given time.

The idealized model here does neglect some important mechanical features of locomotion. For example, as mentioned before, we have not accounted for the costs of moving limbs to and fro. Without this cost, the model here predicts optimal energy performance by means of having very small strides. Inclusion of such a cost, as in Kuo (2001), makes such small strides energetically unfavorable and can result in realistic predictions of preferred step lengths.

We have simplified the analysis considerably by assuming that the work is done by large leg forces of short duration, abstracted as collisions here. This assumption, however, can lead to over-estimation of the metabolic cost. An extended stance can sometimes produce a metabolic cost lower than that of a collisional stance phase.

No detailed account has been made of how real elasticity in the leg muscle–tendon complex can affect choices. Rather we have assumed that the elastic recovery fraction is independent of the details of the task. The point-mass body assumption also rules out other possible elastic mechanisms, for example, in the back (Alexander, 1993) and neck (Gellman and Bertram, 2002) in horse galloping. Another energy saving mechanism available only for non-point-mass models, is the possibility of kinetic energy storage (as is used by the hopping egg model discussed earlier).

Together these missing effects preclude our explaining here various scale effects.

10. Conclusions

The paper presents a simple model for evaluating a dominant fraction of the metabolic cost of locomotion. The model demonstrates two basic points *independent of the presence or absence of any elastic recovery mechanisms*.

- Pseudo-elastic collisions are more energy effective than more plastic-like collisions that demand work to be made up elsewhere.
- Two, three, or more sequenced collisions per given stride length and velocity are more energy effective than a single collision.

Biologically relevant predictions are:

- Human walking should use, at double support, sequenced collisions.
- Walking is less costly than running at speeds below about \sqrt{gl} (depending on details of the collisional model for running and walking).
- At each stride of a gallop, horses should go ba-da-dump instead of pronk. And they do. With the first foot-falls accelerating the horse and the later ones retarding the horse.
- Human and horse legs should simulate elastic behavior. This is well documented with human running. There is evidence in support of this prediction in human walking. The individual foot falls of the galloping horse also seem to follow this trend.
- The range of estimated collisional costs explains a reasonable fraction of the metabolic cost of human running, horse galloping, and human walking.

We have shown that three apparently distinct gaits, brachiating (swinging from branches) in primates, galloping in horses and human walking, all use similar collision-loss avoidance strategies. The qualitative correlation between the model predictions and animal behavior and architecture suggests that the energetic cost of the down-to-up motion redirection during the support phase is a key aspect of legged locomotion.

Acknowledgements

Thanks to Alberto Minetti for discussions that stimulated the pondering of horses; and Joe Burns, Mike Coleman, Steve Collins, Art Kuo, Tad McGeer, Saskya van Nouhuys, Jim Usherwood, Phil Holmes and Anindya Chatterjee for technical and editorial suggestions. NSF biomechanics and robotics grants partially supported this work.

Appendix A. Work of impulsive forces

A.1. Work of one impulse

Eqs. (10)–(16) were developed using kinetic energy changes for a given deflection angle. Here we calculate the work of the impulsive force for given impulse. Assume mass m , pre-collisional velocity \mathbf{v}^- and the collisional impulse \mathbf{P}^* are known (Fig. 2b). Linear momentum balance gives that $m\mathbf{v}^+ = m\mathbf{v}^- + \mathbf{P}^*$ so, by the work-energy relation

$$W = \Delta E = \frac{m}{2}(|\mathbf{v}^+|^2 - |\mathbf{v}^-|^2) = \mathbf{v}^- \cdot \mathbf{P}^* + |\mathbf{P}^*|^2/(2m). \tag{36}$$

For use below, here is a more tortuous derivation of Eq. (36). Assume that the impulsive force \mathbf{F} is always in the direction of constant unit vector $\hat{\lambda}$. Thus

$$\mathbf{P}^* = \int_{t_1}^{t_2} \mathbf{F} dt = \hat{\lambda} \int_{t_1}^{t_2} F dt, \tag{37}$$

where the period of force application is between t_1 and t_2 . The partial impulse is $\mathbf{P}(t) \equiv \int_{t_1}^t \mathbf{F}(t') dt' = p\mathbf{P}^*$ with parameter $0 \leq p \leq 1$ expressing the degree of collision completeness. We can calculate the work as

$$\begin{aligned} W &= \int dW = \int_{t_1}^{t_2} \mathbf{v} \cdot \mathbf{F} dt \\ &= \int_0^{\mathbf{P}^*} \underbrace{(\mathbf{v}^- + \mathbf{P}/m)}_{\mathbf{v}} \cdot \underbrace{d\mathbf{P}}_{\mathbf{F} dt} \\ &= \int_0^1 (\mathbf{v}^- + p\mathbf{P}^*/m) \cdot \mathbf{P}^* dp \\ &= \mathbf{v}^- \cdot \mathbf{P}^* \underbrace{\int_0^1 dp}_1 + \frac{\mathbf{P}^* \cdot \mathbf{P}^*}{m} \underbrace{\int_0^1 p dp}_{1/2} \\ &= \mathbf{v}^- \cdot \mathbf{P}^* + |\mathbf{P}^*|^2/(2m), \end{aligned} \tag{38}$$

where we recover the result from Eq. (36), having derived a special case of the work–energy relation. The formula (36) gives the net work. If $\mathbf{v}^+ \cdot \hat{\lambda}$ is of different sign than $\mathbf{v}^- \cdot \hat{\lambda}$ then W is a difference between positive and negative work terms, $W = |W_{pos}| - |W_{neg}|$. To calculate $|W_{pos}|$ and $|W_{neg}|$ requires dividing the work integral into its absorbing and generative portions. If the interaction is entirely absorbing or entirely generating then Eq. (38) suffices.

A.2. Work of two simultaneous impulses

Collisional episodes may include multiple impulsive forces in various directions. If, within an episode, the entire integral of force in one direction is complete

before force in another direction climbs above zero, then the collisions are sequential and the net collision energetics is calculated by successive use of Eqs. (10)–(16) or Eq. (36).

Now we allow the possibility of overlap of the collisional forces (see Fig. 9). Assume mass m , pre-collisional velocity \mathbf{v}^- and both collisional impulses, \mathbf{P}_1^* and \mathbf{P}_2^* are known. As for the case of a single impulse (Eq. (36), we can calculate the net work as

$$\begin{aligned} m\mathbf{v}^+ &= m\mathbf{v}^- + \mathbf{P}_1^* + \mathbf{P}_2^*, \\ W = \Delta E &= \frac{m}{2}((v^+)^2 - (v^-)^2). \end{aligned} \tag{39}$$

For the cases of main interest we can assume that each impulse only does work with one sign. For definiteness assume \mathbf{P}_1^* is totally generative and \mathbf{P}_2^* is totally absorbing

$$\begin{aligned} W_1 \geq 0 &: \mathbf{v}^- \cdot \hat{\lambda}_1 \geq 0 \quad \text{and} \quad \mathbf{v}^+ \cdot \hat{\lambda}_1 \geq 0, \\ W_2 \leq 0 &: \mathbf{v}^- \cdot \hat{\lambda}_2 \leq 0 \quad \text{and} \quad \mathbf{v}^+ \cdot \hat{\lambda}_2 \leq 0. \end{aligned}$$

So W in Eq. (39) is

$$W = |W_2| - |W_1|, \tag{40}$$

where W_1 and W_2 are the work generated by, and absorbed by the two impulsive forces. However, the separate works cannot be determined. That is, unlike the case of a single impulse, *the collisional energetics are not fully determined by knowledge of the two impulses*. We will now reduce this indeterminacy to a single parameter, $0 \leq s_o \leq 1$ which characterizes how much overlap there is between the nominally simultaneous impulses.

Duplicating the notation and argument used for Eq. (38), using $0 \leq p \leq 1$ and $0 \leq q \leq 1$ to parameterize the partial impulses $\mathbf{P}_1 = p\mathbf{P}_1^*$ and $\mathbf{P}_2 = q\mathbf{P}_2^*$, we

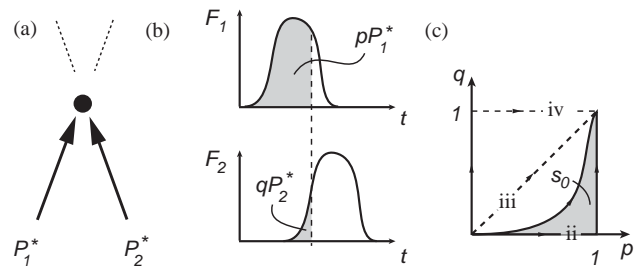


Fig. 9. A point-mass is acted upon by two impulses \mathbf{P}_1^* and \mathbf{P}_2^* which accumulate in time as $\mathbf{P}_1(t) = p(t)\mathbf{P}_1^*$ and $\mathbf{P}_2(t) = q(t)\mathbf{P}_2^*$. The area under a cross-plot of q vs. p defines an overlap parameter s_o which is 0.5 if the impulses are truly simultaneous. The parameter allows the calculation of the impulse work in Eq. (41). The various paths in the p - q plane are labeled to correspond with the paths in Fig. 5.

can calculate

$$\begin{aligned}
 W_1 &= \int dW_1 = \int_{t_1}^{t_2} \mathbf{v} \cdot \mathbf{F}_1 dt \\
 &= \int_0^{\mathbf{P}_1^*} (\mathbf{v}^- + (\mathbf{P}_1 + \mathbf{P}_2)/m) \cdot d\mathbf{P}_1 \\
 &= \int_0^1 (\mathbf{v}^- + (p\mathbf{P}_1^* + q\mathbf{P}_2^*)/m) \cdot \mathbf{P}_1^* dp \\
 &= \mathbf{v}^- \cdot \mathbf{P}_1^* \int_0^1 dp + \frac{\mathbf{P}_1^* \cdot \mathbf{P}_1^*}{m} \int_0^1 p dp \\
 &\quad + \frac{\mathbf{P}_1^* \cdot \mathbf{P}_2^*}{m} \underbrace{\int_0^1 q dp}_{s_o} \\
 &= \mathbf{v}^- \cdot \mathbf{P}_1^* + |\mathbf{P}_1^*|^2/(2m) + (\mathbf{P}_1^* \cdot \mathbf{P}_2^*)s_o/m. \quad (41)
 \end{aligned}$$

Similarly,

$$W_2 = \mathbf{v}^- \cdot \mathbf{P}_2^* + |\mathbf{P}_2^*|^2/(2m) + \mathbf{P}_1^* \cdot \mathbf{P}_2^*(1 - s_o)/m. \quad (42)$$

The overlap parameter s_o fully characterizes the degree to which the collision is simultaneous (see Fig. 9). When $s_o = 0$, \mathbf{P}_1^* is complete before \mathbf{P}_2^* starts, and when $s_o = 1$, \mathbf{P}_2^* is complete before \mathbf{P}_1^* starts. When $s_o = 0.5$, as would be the case if the impulses progressed proportionally (i.e. $F_1(t)/F_2(t) = \text{constant}$), then the collision might be called truly simultaneous. Eq. (41) is used in the text to describe various scenarios for the double-stance collision in walking.

A.2.1. Application to walking

For walking we take \mathbf{P}_1^* to be the impulse from the trailing old stance foot and \mathbf{P}_2^* to be the impulse from the leading new stance foot. We can find the various terms in these formulae using small angle formulas as: $\mathbf{v}^- \cdot \mathbf{P}_1^* = 0$, $\mathbf{v}^- \cdot \mathbf{P}_2^* = -mv^2\phi^2/2$, and $|\mathbf{P}_1^*|^2 = |\mathbf{P}_2^*|^2 = \mathbf{P}_1^* \cdot \mathbf{P}_2^* = m^2v^2\phi^2/4$.

Thus, we can have an alternative derivation to Eq. (27) (push-off before heel-strike). Using $s_o = 0$ Eq. (42) gives $E_m = b|W_2| = bmv^2\phi^2/8$ again.

For truly simultaneous collisions, the diagonal path (iii) on Fig. 9, $s_o = .5$ and Eq. (42) gives $E_m = b|W_2| = bmv^2\phi^2/4$.

For heel-strike before push-off, path (iv) on Fig. 9, $s_o = 1$ and $E_m = b|W_2| = 3bmv^2\phi^2/8$.

For the circular arc (vi) in Fig. 9 the trajectory can be parameterized, for small angles, by p and q with $p = 2\sqrt{q} - q$. Thus $s_o = \int q dp = 1 - \int p dq = \frac{1}{6}$. So, from Eq. (42), $E_m = b|W_2| = bmv^2\phi^2/6$.

For any s_o the cost is minimized with $\Delta E = 0$. For a given $\Delta E = 0$, the cost $E_m = b|W_2| = -bW_2$ in Eq. (42) is minimized by $s_o = 0$, with push-off entirely before heel-strike.

Appendix B. Glossary

b	average metabolic energy per unit of negative or dissipated work over a periodic gait cycle, $b_1 \leq b \leq b_1 + b_2$. $b \approx 4$ or 5
b_1	metabolic energy cost per unit of positive muscle work, reciprocal of muscle efficiency, $b_1 \approx 4$
b_2	metabolic energy cost per unit of negative muscle work, $b_2 \approx \frac{5}{6}$
c_m	specific metabolic cost of transport = energy/(weight*distance), approximated as bc_w
c_w	specific positive-work-increment based energetic cost of transport
e_r	traditionally defined coefficient of restitution. $\phi^+v^+ / (\phi^-v^-)$
e_g	coefficient of generation, a new parameter replacing e_r . $e_g \approx (\phi^+ - \phi^-) / \phi$
d	stride length. Here defined as distance of travel from one support phase to the next
E	kinetic energy, $E = mv^2/2$
ΔE	kinetic energy increase in collision, $E_g - E_a$
E_a	kinetic energy lost in absorbing part of a collision ($E_a \geq 0$)
E_g	kinetic energy increase in the generating part of a collision ($E_g \geq 0$)
E_m	inferred net metabolic cost of all the sub-collisions over a stride
\dot{E}_m	average rate of metabolic energy use due to collisions, averaged over one or more strides
$\mathbf{F}, \mathbf{F}_1, \mathbf{F}_2$	forces of legs on body during an impulse
$\hat{\mathcal{F}}$	A Froude number based on step length, $2gd/(mv^2)$
g	local gravity constant (e.g. $\approx 10 \text{ m/s}^2$)
J	collision reduction factor in walking, $E_m/(bmv^2\phi^2/2)$. Characterizes the effectiveness of a deflection. Small J is high effectiveness
ℓ	leg length
m	mass of the animal—a point-mass
$\mathbf{P}^*, \mathbf{P}_1^*, \mathbf{P}_2^*$	net impulses of legs on body
P, P_1, P_2	partial impulses: $P = p \mathbf{P}^* $, $P_1 = p \mathbf{P}_1^* $, $P_2 = q \mathbf{P}_2^* $
p, q	dummy variables to parameterize the work path-integral. $0 \leq p \leq 1, 0 \leq q \leq 1$
r	recovery, fraction of absorbed energy that is used, at no metabolic cost, in the subsequent generative part of the collision
s_o	characterizes force overlap in a nominally simultaneous collision, $0 \leq s_o \leq 1$. $s_o = 0$ or 1 if P_1 is entirely before or after P_2 ,

	respectively. $s_o = 0.5$ for a truly simultaneous collision
T	step period = time from one step to the next. For instantaneous collisions T is the stance time in walking and the flight time in running and galloping
v	nominal locomotion speed, close to v^- and v^+
v^-, v^+	speeds before and after a collision
W_1, W_2	net work of legs 1 and 2 in a simultaneous collision
W	net work of legs in a collision, $W = \Delta E$
W_{pos}	positive muscle work
W_{neg}	negative muscle work
W_{loss}	lost work, combined dissipation and negative work, $W_{diss} + W_{neg}$
\dot{W}_{loss}	rate of mechanical energy loss, averaged over one or more steps
W_{diss}	dissipation other than negative muscle work, e.g. from soft tissue deformation
\dot{W}_{musc}	muscle power = (muscle tension) \times (shortening rate) added over all muscles, approximated here as (leg compression force) \times (leg lengthening rate)
ϕ	Deflection angle of path in a single collision (McGeer's $\alpha = \phi/2$) $\phi = \phi^- + \phi^+$. For calculations $\phi \ll 1$
ϕ^-	angle of incoming velocity (just before collision) relative to the normal of the leg
ϕ^+	angle of the outgoing velocity
ϕ_i	deflection at a single sub-collision i in a re-direction phase made up of sub-collisions
$\hat{\lambda}, \hat{\lambda}_1, \hat{\lambda}_2$	unit vectors in the direction of leg impulses

References

- Alexander, R.Mc.N., 1990. Three uses for springs in legged locomotion. *Int. J. Robot. Res.* 9, 53–61.
- Alexander, R.Mc.N., 1991. Energy-saving mechanisms in walking and running. *J. Exp. Biol.* 160, 55–69.
- Alexander, R.Mc.N., 1992. A model of bipedal locomotion on compliant legs. *Philos. Trans. R. Soc. London B* 338, 189–198.
- Alexander, R.Mc.N., 1993. Why animals gallop. *Am. Zool.* 28, 237–245.
- Alexander, R.Mc.N., 1997. Invited editorial on “Interaction of leg stiffness and surface stiffness during human hopping”. *J. Appl. Physiol.* 82, 13–14.
- Alexander, R.Mc.N., 2001. Design by numbers. *Nature* 412, 591.
- Bekker, M.G., 1956. *Theory of Land Locomotion*. University of Michigan Press, Ann Arbor.
- Bertram, J.E.A., Ruina, A., Cannon, C.E., Chang, Y.-H., Coleman, M., 1999. A point-mass model of gibbon locomotion. *J. Exp. Biol.* 202, 2609–2617.
- Bertram, J.E.A., 2005. Constrained optimization in human walking: cost minimization and gait plasticity. *J. Exp. Biol.* 208, 979–991.
- Blickhan, R., 1989. The spring-mass model for running and hopping. *J. Biomech.* 22, 1217–1227.
- Blickhan, R., Full, R.J., 1993. Similarity in multilegged locomotion: bouncing like a monopode. *J. Comp. Physiol. A* 173, 509–517.
- Borelli, J.A., 1680. *On the Movement of Animals (De Motu Animalium, Pars prima)* (P. Maquet, Trans.) Springer, Berlin, p. 152 (1989).
- Butler, P.J., Woakes, A.J., Smale, K., Roberts, C.A., Hillidge, C.J., Snow, D.H., Martin, D.J., 1993. Respiratory and cardiovascular adjustments during exercise of increasing intensity and during recovery in Thoroughbred racehorses. *J. Exp. Biol.* 179, 159–180.
- Cavagna, G.A., Thys, H., Zamboni, A., 1976. The sources of external work in level walking and running. *J. Physiol. (London)* 262, 639–657.
- Cavagna, G.A., Heglund, N.C., Taylor, C.R., 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* 233, 243–261.
- Chatterjee, A., Ruina, A., 1998a. A new algebraic rigid body collision law based on impulse space considerations. *J. Appl. Mech.* 65, 939–951.
- Chatterjee, A., Ruina, A., 1998b. Realizability of arbitrary local mass matrices in single-point rigid body collisions. *Proceedings of the International Symposium on Impact and Friction of Solids, Structures and Intelligent Machines*, Ottawa, Canada.
- Collins, S.H., Wisse, M., Ruina, A., 2001. A three-dimensional passive-dynamic walking robot with two legs and knees. *Int. J. Robot. Res.* 20, 607–615.
- Collins, S., Ruina, A., Tedrake, R., Wisse, M., 2005. Efficient bipedal robots based on passive dynamic walkers. *Science* 307, 1082–1085.
- Donelan, J.M., Kram, R., Kuo, A.D., 2002a. Mechanical and metabolic costs of step-to-step transitions in human walking. *J. Exp. Biol.* 205, 3717–3727.
- Donelan, J.M., Kram, R., Kuo, A.D., 2002b. Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* 35, 117–124.
- Eaton, M.D., Evans, D.L., Hodgson, D.R., Reuben, J.R., 1995. Effect of treadmill incline and speed on metabolic rate during exercise in thoroughbred horses. *J. Appl. Physiol.* 79, 951–957.
- Farley, C.T., Gonzalez, O., 1996. Leg stiffness and stride frequency in human running. *J. Biomech.* 29, 181–186.
- Farley, C., Ortega, J., 2003. Flattening the center of mass trajectory increases the cost of walking. *Proceedings of the 27th Annual Meeting of the American Society of Biomechanics*.
- Fenn, W.O. (1930). Work against gravity and work due to velocity changes in running. *Am. J. Physiol.* 93, 433–462.
- Garcia, M., Chatterjee, A., Ruina, A., Coleman, M., 1998. The simplest walking model: stability, complexity and scaling. *J. Biomech. Eng.* 120, 281–288.
- Garcia, M., Chatterjee, A., Ruina, A., 2000. Efficiency, speed, and scaling of two-dimensional passive-dynamic walking. *Dyn. Stab. Syst.* 15, 75–99.
- Gellman, K.S., Bertram, J.E.A., 2002. The equine nuchal ligament 2: The role of the head and neck in locomotion. *Vet. Comp. Orthoped. Traumat.* 15, 7–14.
- Gomes, M., Ruina, A., 2005. A five-link 2D brachiating ape model with life-like zero-energy-cost motions. *J. Theor. Biol.*, in press, doi:10.1016/j.jtbi.2005.04.014.
- Gordon, K., Ferris, D., Kuo, A., 2003. Reducing vertical center of mass movement during human walking does not necessarily reduce metabolic cost. *Proceedings of the 27th Annual Meeting of the American Society of Biomechanics*.
- Haggerty, P., 2001. Radiation-induced instability. Ph.D. Thesis, University of Michigan, Ann Arbor.
- Hoyt, D.F., Taylor, C.R., 1981. Gait and the energetics of locomotion in horses. *Nature* 292, 239–240.
- Kram, R., Taylor, C.R., 1990. Energetics of running: a new perspective. *Nature* 346, 265–267.

- Kuo, A.D., 2001. A simple model of bipedal walking predicts the speed-step length relationship. *J. Biomech. Eng.* 123, 264–269.
- Kuo, A.D., 2002. Energetics of actively powered locomotion using the simplest walking model. *J. Biomech. Eng.* 124, 113–120.
- Kuo, A.D., Donelan, J.M., Ruina, A., 2005. Energetic consequences of walking like an inverted pendulum: step-to-step transitions. *Exercise Sport Sci. Rev.* 33, 88–97.
- Langsetmo, I., Weigle, G.E., Fedde, M.R., Erickson, H.H., Barstow, T.J., Poole, D.C., 1997. VO₂ kinetics in the horse during moderate and heavy exercise. *J. Appl. Physiol.* 83, 1235–1241.
- Marey, E.J., 1874. *Animal Mechanism. A Treatise on Terrestrial and Aerial Locomotion*, second ed., Henry S. King & Co., London.
- Margaria, R., 1976. *Biomechanics and Energetics of Muscular Exercise*. Clarendon Press, Oxford, UK.
- McGeer, T., 1990a. Passive dynamic walking. *Int. J. Robot. Res.* 9, 68–82.
- McGeer, T., 1990b. Passive dynamic running. *Proc. R. Soc. London B.* 240, 107–134.
- McGeer, T., 1992. Principles of walking and running. *Adv. Comp. Environ. Physiol.* 11, 113–139.
- McGeer, T., 1993. Dynamics and control of bipedal locomotion. *J. Theor. Biol.* 163, 277–314.
- McMahon, T.A., 1985. The role of compliance in mammalian running gaits. *J. Exp. Biol.* 115, 263–282.
- Merkens, H.W., Schamhardt, H.C., van Osch, G.J., Hartman, W., 1993. Ground reaction force patterns of Dutch warmbloods at the canter. *Am. J. Vet. Res.* 54, 670–674.
- Minetti, A.E., 1998. The biomechanics of skipping gaits: a third locomotor paradigm? *Proc. R. Soc. London B* 265, 1227–1235.
- Minetti, A.E., Alexander, R.Mc.N., 1997. A Theory of Metabolic Costs for Bipedal Gaits. *J. Theor. Biol.* 186, 467–476.
- Minetti, A.E., Ardigó, L.P., Reinach, E., Saibene, F., 1999. The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* 202, 2329–2338.
- Muybridge, E., 1887. *Animals in Motion*. Dover, New York, reprint (1957).
- Potard, U.S., Leith, D.E., Fedde, M.R., 1998. Force, speed and oxygen consumption in thoroughbred and draft horses. *J. Appl. Physiol.* 84, 2052–2059.
- Raibert, M.H., 1986. *Legged Robots that Balance*. MIT Press, Cambridge.
- Raibert, M.H., 1990. Legged robots. In: Winston, P.H., Shellard, S.A. (Eds.), *Artificial Intelligence at MIT*. MIT Press, Cambridge, pp. 149–179.
- Raibert, M.H., Cheppouis, M., Brown Jr., H.B., 1986. Running on four legs as though they were one. *J. Robot. Autom.* 2, 70–82.
- Rashevsky, N., 1944. Studies in the physicomathematical theory of organic form. *Bull. Math. Biophys.* 6, 1–59.
- Rashevsky, N., 1948. On the locomotion of Mammals. *Bull. Math. Biophys.* 10, 11–23.
- Rubanovich, E.M., Formalskii, A.M. (1981). Some aspects of the dynamics of multiple-element associated with impact phenomena. *Izv. AN SSSR Mechanica Tverdogo Tela* 16(2), 166–174.
- Tucker, V.A., 1975. The energetic cost of moving about. *Am. Sci.* 63, 413–419.
- Wagner, P.D., Gillespie, J.R., Landgren, G.L., Fedde, M.R., Jones, B.W., Debowes, R.M., Pieschl, R.L., Erikson, H.H., 1989. Mechanisms of exercise-induced hypoxemia in horses. *J. Appl. Physiol.* 66, 1227–1233.
- Wright, S., Weyand, P.G., 2001. The application of ground force explains the energetic cost of running backward and forward. *J. Exp. Biol.* 204, 1805–1816.