

COMMENTARY

Neglected losses and key costs: tracking the energetics of walking and running

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Summary

As one of the most energetically demanding daily activities, locomotion has attracted substantial investigative attention. Although legged locomotion has been well described, it is currently not well understood. Looking at energy accounting might be a good pathway with which to solve this problem. One relatively simple way of analyzing energy management is to look directly at the flow of mechanical energy into and out of the system, in terms of costs and losses (with some attention to the mechanisms responsible for this flow). In this commentary we argue that a key source of energetic loss has largely been neglected: the redirection of body motion from downward to upward at each step. We discuss the role of this loss and the compensating energetic costs, identifying some of the general features of the trade-offs that determine gait optimization strategies. We find that even at a conceptual level, a focus on the main mechanism of loss and the strategies available to the organism to effectively compensate for losses can yield substantial insight into observations as diverse as the functional limits of a playground swing through to the strikingly different effect of reduced gravity on human walking and running. Such insight changes the interpretation of fundamental features of leg function, such as push-off timing and the role of elastic deflection during stance.

Key words: collision, locomotion, optimality, reduced gravity, energy loss, pseudo-elasticity.

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Introduction

For decades, a prevailing assumption in comparative biomechanics has been that the coordination of walking gaits (whether bipedal, quadrupedal or multi-legged) should be considered in terms of an inverted pendulum motion during stance that maximizes the exchange between kinetic (E_k) and gravitational potential (E_p) energy. Exchange between energy forms, it was thought, meant that most of the available energy could be retained and re-used in the following stride. Likewise, the coordination of running gaits (whether the bipedal run, quadrupedal trot or multi-legged bouncing runs) appeared dependent on the recovery of elastic strain energy as the organism's center of mass (CoM) falls and loads the limb during the initial stages of foot contact, then is reaccelerated upward by elastic rebound during the latter half of stance. Again, the thought was that these bouncing gaits exist to facilitate exchange between energy forms, kinetic to strain energy and back again, so that energy could be 'recovered' within the stride cycle.

Of particular influence in establishing the focus on energy recovery within terrestrial forms was Cavagna et al. (Cavagna et al., 1977). This study measured the fluctuations in the terms that make up the total mechanical energy of the CoM in a wide variety of species, from bipeds such as humans and birds to quadrupeds such as rams and monkeys. The concepts applied by Cavagna and colleagues were originally developed in studies of human locomotion performed over several decades (Cavagna et al., 1963; Cavagna et al., 1964; Cavagna and Margaria, 1966; Cavagna and Kaneko, 1977). Because substantial exchanges of energy were demonstrated in all species analyzed, and because of the obvious value of making energy from one stride available to the next, the energy recovery ideas have been commonly embraced in comparative terrestrial locomotion literature.

Such exchanges between energy forms within the system do indeed occur. In addition, it is undeniable that they can be useful to gait energetics of animals. However, we do not agree that recovery *per se* best explains why animals move the way they do. Even though it has influenced locomotion research for several decades, the recovery perspective has not helped much with the ultimate goal of locomotion research: to understand how adaptations of form or behavior can influence legged locomotion performance.

To explain possible shortcomings in the recovery approach let us start with the common ground. It is indeed reasonable to think that management of energy is important in locomotion. And it is reasonable to think that large terms in energy accounting are associated with CoM potential and kinetic energy. So, it is also reasonable to hypothesize that the patterns and variations of CoM kinetic energy, and also of total potential energy (which only depends on the CoM motion), are related to energy economy.

The disagreement is about the best and simplest ways of looking at this CoM energy accounting. The 'recovery' approach looks at energy flows within a system whereas the approach we advocate focuses on the flow of mechanical energy into and out of the system, with some attention to mechanisms: how much energy flows, when does it flow, by what mechanism and for what purpose?

How can we best understand the body movement choices and functional consequences that animals face in trying to get from one place to another? One way, with which we are in total agreement, is by looking at the management of energy. In the energy recovery view, however, one assumes that when gravitational, strain or kinetic energy decreases it is lost unless 'recovered' into another form. The recovery view further implies that this loss is the main energetic cost of locomotion. Thus, in the recovery view it is then

necessary to track energy exchange in order to understand energetic effectiveness. In contrast, we argue here that it is better to assume all energy is available (recovered) unless lost. Understanding locomotion thus becomes an investigation of the amount of this loss, the mechanisms responsible for the loss, the strategies used to reduce such loss, and an analysis of the energy costs associated with various options for making up for losses.

Recent studies of simple walking and running machines (e.g. McGeer, 1990; Garcia et al., 1998) and the simple gait optimization calculations in the tradition of Alexander (Alexander, 1976; Alexander, 1980; Alexander, 1992; Minetti and Alexander, 1997; Srinivasan and Ruina, 2006; Srinivasan, 2011) demonstrate that numerous features of legged locomotion are explicable with no reference, even implicitly, to recovery concepts. This is not to mean that energy exchanges and recovery do not occur in walking and running – these exchanges unequivocally do occur – but the fractional ‘recovery’ is not particularly useful for understanding the coordination patterns observed in legged gaits.

When walking, people certainly appear to use an inverted pendulum-like exchange (Kuo et al., 2005). However, this exchange is not perfect, indicating that energy loss occurs. In a complex walking human there are a number of sources for energetic loss, but one of the key mechanisms of loss – abrupt dissipative (collisional) change in CoM motion – is not easily captured in the recovery analysis, and as a consequence has largely been neglected in the analysis of comparative locomotion mechanics. In contrast, the gaits preferred by terrestrial animals (as indicated by their use in normal locomotion) can be understood as a means to effectively manage the transition of the CoM between successive steps as its motion path changes from partially downward to partially upward; where we assert that this transition could, as a first approximation, be considered as a collision.

The amplitude limit of a playground swing: a collision-based phenomenon

The playground swing moves with a familiar cyclic pendulum-based motion. It provides a simple example of the energetic effects of collisions. An ideal pendulum exchanges potential and kinetic energy while the total mechanical energy of the system remains nearly constant. A child swinging on a playground swing is an active version of a pendulum. Children learn that they can distort their body one way or another to pump energy into the swinging system and thus increase swing amplitude. Now think of an ambitious child on a playground swing trying to swing as high as she can. On a typical playground swing she is supported by flexible cables or chains. When the child swings above the cable support point the cables will go slack. While the cables are slack the child falls ballistically until the cables suddenly go taut, at which point the radial component of the child’s velocity goes to zero (Fig. 1). This (near) discontinuity in velocity is felt as a small jolt that involves a loss of system energy (in dynamics a discontinuity in the velocity of a moving mass is defined as a collision). The height of the child’s swing cycle following this jolt is substantially lower than the previous cycle – indicating that energy has been lost. The higher the child’s swing cycle, the greater the slack, the bigger the jolt, and the greater the loss of energy. Energy input by pumping is lost by this collisional dissipation, and the amplitude of swinging is limited to not much more than the height of the support point.

Sometimes in a circus the flexible cables are replaced with stiff rods that do not go slack. These rods thus avoid collisions and the associated energy loss when the swing goes above the horizontal. With the collision loss inhibited, a circus performer can do a full

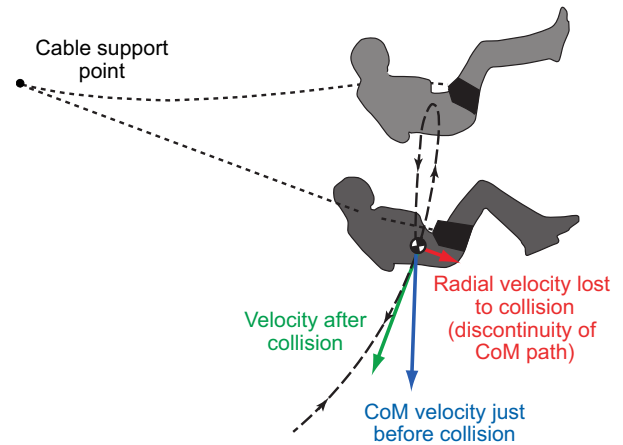


Fig. 1. Schematic of the amplitude limit of a playground swing (positions traced from video). If a person swings above the support point, the cables will go slack and the person will fall briefly. When the cables go taut again the person’s path is abruptly deflected and energy is lost. CoM, center of mass.

360 deg loop around the swing axis. We do not recommend you try this at home, but an internet search will provide videos of numerous home-built examples of such devices.

What is the difference between the swing in the playground and that in the circus? In the former, the amplitude is limited by collision losses. Paying attention to the source of this dissipation pretty directly points to why a change in ‘morphology’, replacing flexible supports with rigid ones, makes such a difference to overall performance. Perhaps we can also gain insight into key aspects of the energetics of walking and running by watching directly how and when mechanical energy leaves and enters the system. Note that in a ‘recovery’ analysis one would see essentially the same exchanges of potential and kinetic energies in both the playground and circus swings, perhaps missing the key loss that determines the difference in the motion.

Energetics of transitioning from one limb to the next in walking

Consider a simple model of a bipedal gait in which a person’s mass is supported by two strut-like limbs (Fig. 2A). As the CoM falls forward from the previous stance, the next stance limb makes contact with the substrate. This contact constrains the motion of the CoM, and changes its path, just as the support cables do in the playground swing (this time as a compression collision instead of a tension collision). The action of the legs, along with the heel-strike collision, redirects the CoM velocity from downward to upward (while also moving forward). Some kinetic energy is lost at the collision (energy associated with the CoM velocity change along path ‘a’ in Fig. 2A, parallel with the leading limb, because this is the component of the CoM velocity affected by the collision). Before the entire velocity component along the new stance leg is lost, the trailing leg could make up the lost kinetic energy with an impulsive push-off (path ‘b’ in Fig. 2A, parallel with the effective trailing limb, the path of the impulse it applies to the CoM). In this case the ‘step-to-step’, or CoM ‘down-to-up’, transition is modeled as a heel-strike followed by a push-off. Halfway through the process kinetic energy has been lost and then it is made up by push-off work.

Now consider an alternative way to manage the step-to-step transition. This time the impulse from the trailing limb is applied

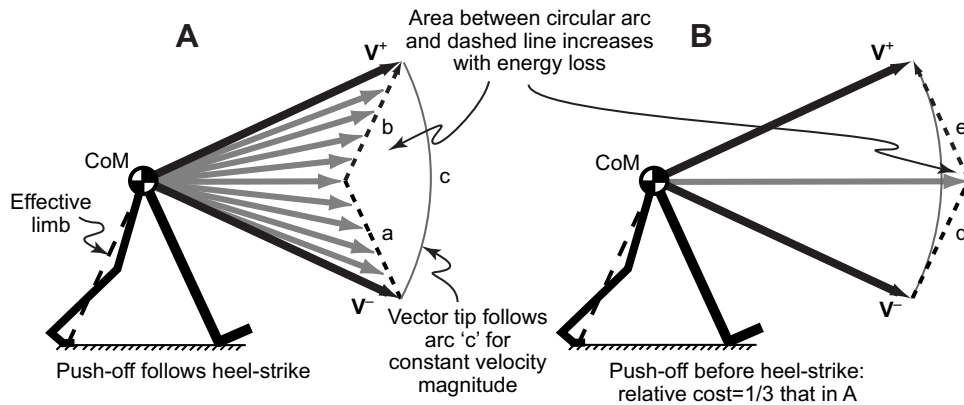


Fig. 2. Energy changes in a simple model of walking. In A, the new (lead) stance limb makes contact and constrains the CoM path prior to push-off by the previous stance limb. Kinetic energy is lost, as indicated by the decrease in the CoM speed where velocity decreases from V^- (just before contact) along line 'a' (parallel to the limb strut). Before the entire velocity along the new stance limb is lost, the previous stance limb applies an impulse via the effective limb (path between foot contact and CoM). Kinetic energy increases as the velocity vector grows along path 'b' until it becomes equal to its original magnitude. The curve 'c' follows the loci of velocity vector tips for constant velocity magnitude. The system is identical in B, but now the impulse from the previous stance limb is generated just before the next contact. This impulse increases the energy (velocity magnitude increases) along line 'd' (parallel to the effective limb). When the new stance limb makes contact, the velocity vector shrinks along line 'e' (parallel to the new stance limb). The energy loss in this transition is larger when the area between the circular arc and the dashed lines is greater. Simply by reversing the order of the action of the two limbs, much less energy is lost because the geometric relationship between the velocity vector and the limbs is more favorable in B (modified from Ruina et al., 2005; following Donelan et al., 2002a).

just before the next stance limb makes contact. The CoM velocity is redirected and increases in parallel with the thrust of the trailing leg (path 'd' in Fig. 2B). The positive work associated with the trailing limb thrust increases the system kinetic energy, and the CoM moves faster at mid-transition between contacts than it did as it fell forward. At heel-strike the CoM velocity component along the new stance leg is lost (path 'e' in Fig. 2B), and the speed and energy return to the value they had before the start of the transition.

In both cases the simple model has the same mass, limb dimensions and step length, as well as CoM speed at the beginning and end of the transition. The trailing and leading limb orientations are also equivalent in both cases, as well as the impulses associated with the legs. However, and here is the value of directly considering the mechanism of loss in the transition between support limbs in walking, the second sequence (push-off then heel-strike) requires only one-third the mechanical work as that of the first [heel-strike then push-off (Kuo, 2002)]. In other words, the ultimate dissipation of heel-strike (loss) in the second case is reduced by 66% using the pre-emptive push-off. The trailing leg push-off has this effect by altering the direction of the CoM velocity vector during the transition between stance limbs so that less energy is lost in the collision at contact of the new stance leg. In reality, negative muscle work and energy loss due to deformations of other tissues contribute to energy loss at the step-to-step transition. All of these identifiable losses are simply specific mechanisms through which mechanical energy is lost, but they originate with the limb-substrate contact dynamics, and so can more generally be considered as a subset of the collisional loss described above.

Running: the same problem with a different solution

At first sight, walking and running appear fundamentally different. In human running, for instance, there is a flight phase between foot contacts that does not occur in walking. In walking, the CoM is at its highest point when it is directly over the supporting limb (the mass of the body vaults over the supporting limb, which is held relatively straight), while in running the CoM is at its lowest point in the stride cycle when it is directly over the support limb (in

running the support leg deflects, effectively shortening, as the body passes over the foot). The CoM path in walking resembles an inverted pendulum arc, while in running it looks like the path of a bouncing mass-spring. But these differences mask some key similarities in the function of the limbs in these two gaits. Note that both running and walking involve a portion of the gait that is relatively cost-free. For walking the low-cost portion is during single-limb contact when the mass of the body spontaneously vaults over the stance limb (in an inverted pendulum motion where E_k and E_p are exchanged), and during running the low-cost portion of the stride cycle occurs when both feet are in the air and the body mass moves ballistically (and where E_k and E_p are also exchanged). Both of these low-cost portions of the stride cycle occur while the CoM passively transitions from upward to downward motion because of the action of gravity.

For both walking and running, these low-cost (passive and smooth) portions of the stride are interspersed between the (less smooth) high-cost portions during which the CoM transitions from going down to going up (stance in running and support transfer between legs in walking). For both walking and running this is when the CoM is at its lowest point in the cycle. In both cases this down-to-up transition must be actively mediated by action of the limbs, and this involves 'costs' associated with energy loss and work expended.

In walking the energy loss at the down-to-up transition can to some extent be mitigated by careful relative timing of the push-off and heel-strike, as explained above. However, for running this sequence strategy for reducing collision loss is not available because only one foot is in contact with the ground at a time (Lee et al., 2011). Often we think that for running to be effective the kinetic energy loss of landing must be 'recovered', at least in part, by tendon elasticity. But a careful tracking of the work and dissipation shows that features other than elastic recoil are also important in the transition of CoM direction.

Srinivasan and Ruina (Srinivasan and Ruina, 2006) showed that when moving adequately fast bounce-like running, in which the downward deceleration phase mirrors the subsequent upward

acceleration phase, is energetically better than other ways of using the legs – even if there is no elasticity in the system. That is, the forces chosen during the down-to-up transition following the aerial phase can be energetically favorable even if all the rebound work is active muscle work and not at all from stored elastic energy [this ‘pseudo-elasticity’ concept is also discussed in Ruina et al. (Ruina et al., 2005) and Alexander (Alexander, 1997)]. Consequently, at adequately high speeds running requires less work than walking even with no elastic ‘recovery’. Elastic recoil can enhance the economy of running, but the energy effectiveness (and indeed, the optimality) of running does not depend on it.

The recognition that elastic recovery is unnecessary to either understand or produce running and other bouncing gaits might appear counter-intuitive. For instance, it might seem that the elegant and effective (at least at higher speeds) bouncing gait of the macropod marsupials is dependent on the elastic behavior of the muscle–tendon complexes of their hind limbs. However, minimizing energy cost in mechanically simple models suggests that kangaroos would benefit from a gait that appears to bounce even if they did not have elastic elements; just like many small mammals use a bouncing salutatory gait even though their tendons do not provide appreciable elastic return (Biewener and Blickhan, 1988). Of course, passive elastic return reduces the energetic cost of locomotion even more, and can be particularly effective for organisms with moderately large body mass. The energetic benefits of the pseudo-elastic leg behavior during stance (active bouncing) and strain energy return from real elastic structures (passive bouncing) are complementary. Thus, bouncing is mechanically (and presumably metabolically) cost effective even without passive elasticity, but passive elasticity can operate in concert with the advantageous motion-path to increase the economy of the gait even more. This insight solves an evolutionary pathway problem. If running gaits were primarily dependent on effective elastic recoil, how could elastic structures be developed prior to the gait that

exploits them? Instead, by minding the costs and losses we see the benefits of running even without springs. Following the development of running (and trotting or bouncing) without springs, the adaptation of appropriate tendons that can return elastically stored energy to make locomotion even more effective would be expected.

Optimization strategies in walking and running: an example

As strongly argued by Alexander (Alexander, 2001), if management of energy is crucial for animals, evolutionary adaptation and learning may be thought of as, in part, energy-use optimizers. What do we learn from this viewpoint? One simple bipedal model demonstrates that walking and running are the dynamically optimal gaits for slow and fast legged motion, respectively (Srinivasan and Ruina, 2006). This is an informative result in its own right, but the optimization approach to energy management shows even more promise in understanding legged locomotion. For example, two decades ago Farley and McMahon (Farley and McMahon, 1992) described human walking and running in simulated reduced gravity. They found that the metabolic cost of running decreased with a reduction in effective gravity, while the cost of walking was, surprisingly, much less sensitive to gravity level (Fig. 3A). We have looked at an optimization model for explaining this difference. We use a bipedal model that is conceptually similar to that in Srinivasan and Ruina (Srinivasan and Ruina, 2006), but is slightly more complex: it includes realistic mass distribution and proportions and the potential for active torques at the ankles and between an upper body and legs. The biped model is still quite simple compared with other more complex models of humans (e.g. Ackermann and van den Bogert, 2010; Anderson and Pandy, 2001). Optimization of movement in this model with no springs indicates that the adjustments made to altered gravity by the subjects in the Farley and McMahon study coincide with those expected of a biped

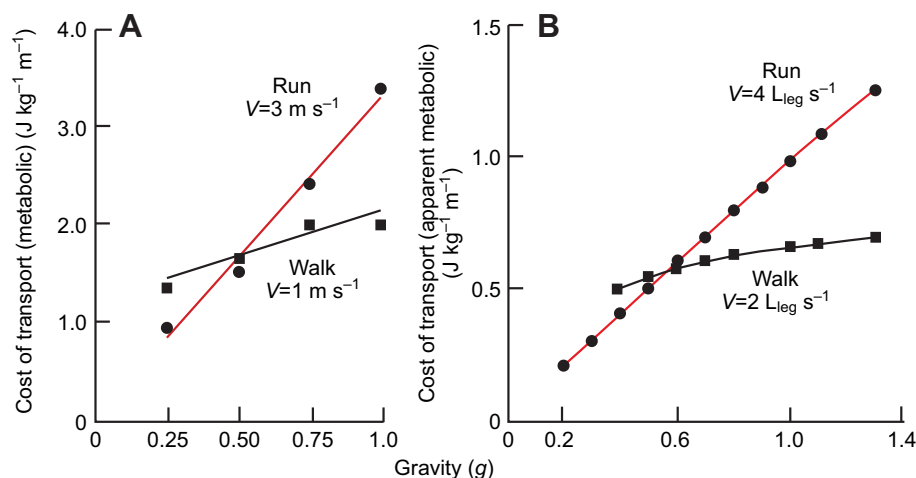


Fig. 3. (A) The metabolic cost of transport (metabolic cost per unit mass and distance traveled) of human walking and running in simulated reduced gravity (after Farley and McMahon, 1992). The cost of running declines steeply with gravity while that of walking is much less sensitive to gravity reduction. Below $\sim 0.5g$ it becomes less costly to run than to walk. (B) The apparent metabolic cost of transport [apparent metabolic cost (as defined below) per unit body mass and distance traveled] for optimal (cost minimizing) gaits of a seven-link model (torso and two-link legs, each with feet) with human-like mass distribution, extensible legs and hip and ankle torque capability (Hasaneini et al., 2013). The model is free to select the actuation profiles, step length and frequency that minimize cost of transport. A gait response and a cost pattern are generated that parallel those of human subjects when gravity level is reduced (Hasaneini et al., 2011). The optimization generated for any set of conditions results primarily from a trade-off between collision loss, support limb work controlling the movement of the center of mass, and swing limb cost. The y -axis values differ between the plots: those in A use direct metabolic cost in human subjects while those in B are calculated using apparent metabolic cost from the model. Apparent metabolic cost is calculated assuming 20% combined efficiency for positive and negative work performed by the actuators (Ruina et al., 2005). The cost values change slightly with the discretization scheme used in optimization, but the cost trends remain the same.

moving in such a way as to minimize the mechanical cost of transport (Hasaneini et al., 2011; Hasaneini et al., 2013) (Fig. 3B).

The relative simplicity of the model (in comparison to a biological system) allows a direct interpretation of the optimized behavior. There appear to be three main factors that interplay to determine the most cost-effective movement pattern. One is the energy loss associated with deflecting the CoM motion from down to up with each step (Donelan et al., 2002b), which we refer to as ‘collision’ energy loss. This can be considered the key ‘original’ loss, because without this there would be little or no cost to locomotion (as in the collisionless rolling of a wheel).

Collision energy loss could be eliminated completely by, say, moving the CoM in a horizontal path, where the limbs bend and extend as the body moves smoothly across the substrate. Unfortunately, such motion requires more work from the limbs, flexing and extending, than is saved in reducing energy loss at collisions (Srinivasan and Ruina, 2006). Direct measurements of energy cost using such a flat gait verify the inefficiency of this mechanism of collision avoidance (Ortega and Farley, 2005; Gordon et al., 2009). Thus, the second factor involved in the optimization of gait is the cost of leg work required to control and redirect the CoM to first help reduce collision loss and then replace the loss that remains (appropriately timed thrust that reduces energy loss and replaces any that remains). For a walking system with biological actuators, somewhere between leg work mediated exclusion of collision loss and a simplistic strategy that does nothing to decrease collisional energy loss is a compromise that involves the least net work, and this is the strategy employed by terrestrial animals.

The energy loss at each step also depends on step length. If steps are very small, then the downward CoM velocity is small, so the energy absorbing collisions are small. In a simple model, cutting the step length in half cuts the collisional energy loss per step by four, and the energy loss per unit distance in half (Kuo, 2002). If steps were small enough, the CoM would travel nearly in parallel with the substrate, and collisional losses would nearly vanish. However, to travel with such short steps at any reasonable forward speed would require substantial effort to swing the legs so rapidly (Doke and Kuo, 2007). Thus, the third main factor involved in the optimization of gait is the cost of swinging the limbs. The computer optimizations discover this trade-off, and choose an intermediate step length somewhere between a long step length that involves large CoM velocity redirections with energy absorbing transitions and a minute step length that requires too much effort to swing the leg so rapidly (Kuo, 2001).

The three factors that largely determine the best coordination strategy for legged locomotion are inter-related: the initial dissipation associated with the step-to-step CoM transition from downward to upward (a loss determined by collision events) is modified and compensated for by two main costs – mechanical, and consequently metabolic, investment involved with support leg work and swing leg work. Numerous other lesser costs also impact locomotion strategy (those related to stability, for instance), but under steady-state conditions the major determinants of an effective movement strategy will arise from managing and repaying loss incurred from the interaction of the organism’s mass with its supporting substrate.

The energy recovery perspective was solidified by the paper entitled, ‘Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure’ (Cavagna et al., 1977). Those exchange mechanisms observed in walking and running were the inverted pendulum and the mass bouncing on a

spring. Applying this perspective to the analysis of human and animal locomotion, however, has not resulted in substantial improvement of our understanding of why these systems move as they do, or why some systems appear better than others. In order to interpret the locomotion strategies available to animals and the consequences of variations in these strategies, we have found a losses-and-costs-based approach more fruitful. Specifically, two basic costs more directly determine energy expenditure, and these costs are intimately related with a fundamental loss arising from the interaction of the movement of mass across the substrate. Although patterns of potential and kinetic energy variation may serve as signatures of some gaits (just as some gaits can be distinguished by noting the presence or absence of overlapping stance), identification of the consequences, in terms of losses and costs, of the motions possible provides a valuable route to understanding locomotion and interpreting the strategic options exploited by the animal world.

Glossary

Center of mass (CoM)

The point where the weighted relative position of a distributed mass sums to zero. The distribution of mass is balanced around the center of mass.

Collision

The sudden change in relative motion between two solid objects, associated with large, brief contact-interaction forces and change in energy level.

CoM kinetic energy (E_k)

$1/2$ total body mass \times (CoM speed)².

CoM potential energy (E_p)

Total body mass \times gravity acceleration \times CoM height from the reference.

Elastic energy

Energy stored in a spring or spring-like materials or tissues, e.g. tendons.

Impulse

The time integral of a force over a period of time, equal to the change in the momentum of the CoM of the system experiencing the corresponding force.

Mechanical energy

The sum of potential energy and kinetic energy of a system.

Negative work

Negative mechanical work calculated from integrating the negative part of the mechanical power over a period of time. It is the dissipative part of the work.

Positive work

Positive mechanical work calculated from integrating the positive part of the mechanical power over a period of time. It is the generative part of the work.

Pseudo-elastic

Motions that are equivalent to those of an elastic system, but with no passive storage and return of energy; all work is actively generated or dissipated.

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References

- Ackermann, M. and van den Bogert, A. J. (2010). Optimality principles for model-based prediction of human gait. *J. Biomech.* **43**, 1055-1060.
 Alexander, R. McN. (1976) Mechanics of bipedal locomotion. In *Perspectives in Experimental Biology 1* (ed. P. S. Davis), pp. 493-504. Oxford: Pergamon Press.

- Alexander, R. McN.** (1980). Optimum walking techniques for quadrupeds and bipeds. *J. Zool.* **192**, 97-117.
- Alexander, R. McN.** (1992). A model of bipedal locomotion on compliant legs. *Philos. Trans. R. Soc. Lond. B* **29**, 189-198.
- Alexander, R. McN.** (1997). Invited editorial on 'interaction of leg stiffness and surface stiffness during human hopping'. *J. Appl. Physiol.* **82**, 13-14.
- Alexander, R. McN.** (2001). Design by numbers. *Nature* **412**, 591.
- Anderson, F. C. and Pandy, M. G.** (2001). Dynamic optimization of human walking. *J. Biomech. Eng.* **123**, 381-390.
- Biewener, A. A. and Blickhan, R.** (1988). Kangaroo rat locomotion: design for elastic energy storage or acceleration? *J. Exp. Biol.* **140**, 243-255.
- Cavagna, G. A. and Kaneko, M.** (1977). Mechanical work and efficiency in level walking and running. *J. Physiol.* **268**, 467-481.
- Cavagna, G. A. and Margaria, R.** (1966). Mechanics of walking. *J. Appl. Physiol.* **21**, 271-278.
- Cavagna, G. A., Saibene, F. P. and Margaria, R.** (1963). External work in walking. *J. Appl. Physiol.* **18**, 1-9.
- Cavagna, G. A., Saibene, F. P. and Margaria, R.** (1964). Mechanical work in running. *J. Appl. Physiol.* **19**, 249-256.
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R.** (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243-R261.
- Doke, J. and Kuo, A. D.** (2007). Energetic cost of producing cyclic muscle force, rather than work, to swing the human leg. *J. Exp. Biol.* **210**, 2390-2398.
- Donelan, J. M., Kram, R. and Kuo, A. D.** (2002a). Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* **35**, 117-124.
- Donelan, J. M., Kram, R. and Kuo, A. D.** (2002b). Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *J. Exp. Biol.* **205**, 3717-3727.
- Farley, C. T. and McMahon, T. A.** (1992). Energetics of walking and running: insights from simulated reduced-gravity experiments. *J. Appl. Physiol.* **73**, 2709-2712.
- Garcia, M., Chatterjee, A., Ruina, A. and Coleman, M.** (1998). The simplest walking model: stability, complexity, and scaling. *J. Biomech. Eng.* **120**, 281-288.
- Gordon, K. E., Ferris, D. P. and Kuo, A. D.** (2009). Metabolic and mechanical energy costs of reducing vertical center of mass movement during gait. *Arch. Phys. Med. Rehabil.* **90**, 136-144.
- Hasaneini, S. J., Macnab, C. J. B., Bertram, J. E. A. and Leung, H.** (2011). Gravity effects on energetics and kinematics of walking and running using dynamic optimization. In *Proceedings of Dynamic Walking Conference July 2011*, pp. 101-102. Jena, Germany: Friedrich Schiller University of Jena.
- Hasaneini, S. J., Macnab, C. J. B., Bertram, J. E. A. and Leung, H.** (2013). The dynamic optimization approach to locomotion dynamics: human-like gaits from a minimally-constrained biped model. *Adv. Robot.* (in press).
- Kuo, A. D.** (2001). A simple model of bipedal walking predicts the preferred 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. and Ruina, A.** (2005). Energetic consequences of walking like an inverted pendulum: step-to-step transitions. *Exerc. Sport Sci. Rev.* **33**, 88-97.
- Lee, D. V., Bertram, J. E. A., Anttonen, J. T., Ros, I. G., Harris, S. L. and Biewener, A. A.** (2011). A collisional perspective on quadrupedal gait dynamics. *J. R. Soc. Interface* **8**, 1480-1486.
- McGeer, T.** (1990). Passive dynamic walking. *Int. J. Robot. Res.* **9**, 62-82.
- Minetti, A. E. and Alexander, R. McN.** (1997). A theory of metabolic costs for bipedal gaits. *J. Theor. Biol.* **186**, 467-476.
- Ortega, J. D. and Farley, C. T.** (2005). Minimizing center of mass vertical movement increases metabolic cost in walking. *J. Appl. Physiol.* **99**, 2099-2107.
- Ruina, A., Bertram, J. E. A. and Srinivasan, M.** (2005). 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. *J. Theor. Biol.* **237**, 170-192.
- Srinivasan, M.** (2011). Fifteen observations on the structure of energy-minimizing gaits in many simple biped models. *J. R. Soc. Interface* **8**, 74-98.
- Srinivasan, M. and Ruina, A.** (2006). Computer optimization of a minimal biped model discovers walking and running. *Nature* **439**, 72-75.