Principles of energetics and stability in human locomotion

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People are skilled walkers and runners. We move with economy, agility and speed, and can do so even while we travel through our rough and variable world. Present-day humanoid robots are certainly much less capable than humans at accomplishing the same locomotor tasks (1). One potential path to improving the design and control of robots is to draw inspiration and guidance from biology. That is, we may be able to build more capable robots if we better understand how people move. One argument against this possibility is that humans and robots are comprised of fundamentally different components. Where robots are built using metals, encoders, wires, computers, magnetic motors, and batteries, humans have evolved to use bone, sensory cells, nerves, brains, muscles and food.

While humans and robots have quite different components, these components are assembled into a common system-level design. Both humans and humanoid robots employ a skeletal system comprised of relatively rigid segments connected by relatively low friction joints. Actuators power movements by applying forces between segments. Sensors make measurements that help estimate the configuration of the segments, the forces acting on them, where they are with respect to the outside world, and the state of the world itself. Control systems interpret the sensor signals and implement the policy that commands the actuators to move the body. And power systems supply energy to the working actuators, sensors, and computers.

Given that there are both similarities and differences, what types of insights into robot design should we expect to gain from studying humans? Here it is helpful to consider the overlap between robots and humans at three different levels of analysis (2). The highest level concerns their objectives, the middle level focuses on the principles employed to meet these objectives, and the lowest level concerns the physical implementation of these principles. Restricting our high-level analysis to locomotion, we suspect that humanoid robots either already share the same objectives as their human counterparts, or we might learn how to improve their design by studying objectives of human locomotion not currently embodied in robots. In contrast, and as we noted earlier, humans and robots use strikingly different hardware leaving perhaps little insight to be gained into improving robot design by mimicking component level physiology. Given these shared objectives and different underlying hardware, the most fruitful insights into robot locomotion are most likely reached with an analysis focused on the middle-level principles of human locomotion.

Our goal in this chapter is to identify and explain central principles underlying why people walk and run the way they do. We consider principles that span biomechanics, energetics and control. Despite our breadth of scope, or perhaps even because of it, we don't intend this chapter to be an exhaustive review. Instead, we focus on principles of energetics and stability that we suspect are most relevant for designing and controlling new humanoid robots, or aiding in the understanding of existing ones. But human locomotion is not just about energetics and stability. Stability, for example, is only one aspect of locomotor robustness, and principles of energetics and stability don't at all explain how humans achieve their locomotor agility. We nevertheless narrowly focus on energetics and stability as that is where our expertise lies. We endeavor to emphasize principles that are grounded in both theory and experimental evidence, as these principles have the strongest foundation. While there are many non-human animal studies that have greatly informed our understanding of human locomotion, here we focus on biped theory and human experiments to keep the chapter length manageable. In writing reviews such as these, one has to make choices about the intended readership: we have aimed this chapter at roboticists that haven't had much experience with the physiological sciences.

An important caveat: the principles of human locomotion that we are about to describe should be viewed as a guide more than a formula. It is unlikely that the solutions favoured in our human physiology are the only solutions, and alternatives may in fact be better for a robot, especially given its hardware differences. But guidance is perhaps more necessary than one might initially think because it is only possible for a roboticist to evaluate a very small part of their very large design and control spaces within realistic amounts of time. Studying evolution's solutions helps constrain the huge numbers of choices available to a roboticist to

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combinations that might actually work. After all, nature's exemplars are the only ideas that we have that aren't our own, and unlike our own ideas, we know Nature's solutions work (3).

Bipedal locomotion is a defining trait of humans

There was a time when our ancestors weren't bipedal. These animals—the common ancestor between humans and apes— primarily moved around by climbing between trees and when they moved overground, they employed all four limbs. The clearest evidence of the origin of bipedalism comes from hominid fossils that are about 4 million years old, although it possibly originated millions of years sooner (4). This bipedalism plays a central role in our human origins—evidence suggests that it only evolved once within what we now recognize as many hominid lineages, and it occurred millions of years before our ancestors acquired distinctly human traits like large brains, long life-spans, language, tool use, and fire (5, 6). These millions of years of natural selection have adapted the human locomotor system in many ways, including straightening leg posture, lengthening the legs, increasing energy storage capacity in the feet, and changing the relative sizes of muscle groups (7, 8).

Not only has human locomotion been shaped by evolution, but we also tune it over a lifetime of practice. The typical human baby takes its first steps around 1 year of age, and quickly ramps up to taking an average of about 14,000 steps per day while covering around 5 km of ground (9). At first, walking is at the boundary of infants' capabilities—they fall more than 100 times per day on average (9). But skill rapidly improves—walking kinematics resemble the adult form by about four years of age, and falls become very rare, even in older adults (10). The frequency of walking is maintained over much of the lifespan, with adults averaging about 6,000-10,000 steps per day (11). These daily step counts are not typically accomplished with a few periods of long walks, but instead are dominated by a large number of very short duration bouts (11-13). We are moving around—rather than standing, sitting, or lying down—for about 8 hours each day. And this movement demands about one-third of our daily energy requirements, and about 95% of the energy we use above that required to simply sustain life (14). While the amount of walking declines in older adults (15), we have logged about 300 million total steps by the time we take our last one.

A central objective for human locomotion is to minimize energetic cost

An important performance metric for walking and running is the rate at which the body, including all the active muscles, consumes chemical energy. This is referred to as metabolic energy expenditure, or simply energetic cost. While it is not technically possible to measure the energy consumed by each individual muscle, we can measure the total energy consumption in a few different ways (16). The most common method—termed indirect calorimetry for historical reasons—measures the air we breathe in and out to determine the volume of oxygen consumed by our body. Our bodies use this oxygen to liberate the energy stored in the chemical bonds of fat and other molecules, in the same way that a campfire uses oxygen to release the energy stored in wood. There is a fixed relationship between the number of oxygen molecules required to break each bond, and the amount of energy released with each break. So, we can simply count the difference between the number of oxygen molecules that go into the body and the number that leave to determine the body's chemical energy consumption. It is a little more complicated than conveyed in the previous few sentences because the body has different stored fuel types—fats, carbohydrates and proteins—and the energy liberated per oxygen molecule depends on the fuel type. Fortunately, the amount of carbon dioxide released differs for each fuel type, so we can increase our accuracy in estimating energetic cost by also measuring carbon dioxide production (17). Nevertheless, an accurate rule of thumb is that 21 Joules of chemical energy is liberated for each milliliter of oxygen consumed when the body metabolizes a typical mix of its fuels (17).

The energy required for walking and running depends upon how the task is accomplished. At faster speeds, for example, walking or running demands a higher rate of energetic cost (measured in energy (J) per unit time (s) and per unit mass (kg)) than when moving more slowly (Figure 1). For walking, the rate of energetic cost increases monotonically and is roughly proportional to the square of speed (18, 19). For running, it increases linearly with speed (20). Rather than express the energetic cost as energy used per unit time, it is often preferred to express it as energy used per unit distance. This is probably a more relevant metric for human behaviour because we usually have to get from one place to another rather than simply walk or run for a certain period of time. In walking, the energetic cost per unit distance—termed cost of transport—is bowl-shaped with the minimum cost at an intermediate walking speed. This cost bowl is quite flat around the minimum—for changes in speed of 10% we expect that people, on average, pay an energetic penalty of only about 1.5% (21). The minimum has a dimensionless value of approximately 0.3, when the measured energy is normalized for the distance travelled and the body weight of the individual. This economy is about equal to that measured for a similar-size quadruped moving at the same speed (22) and around 10 times lower than that

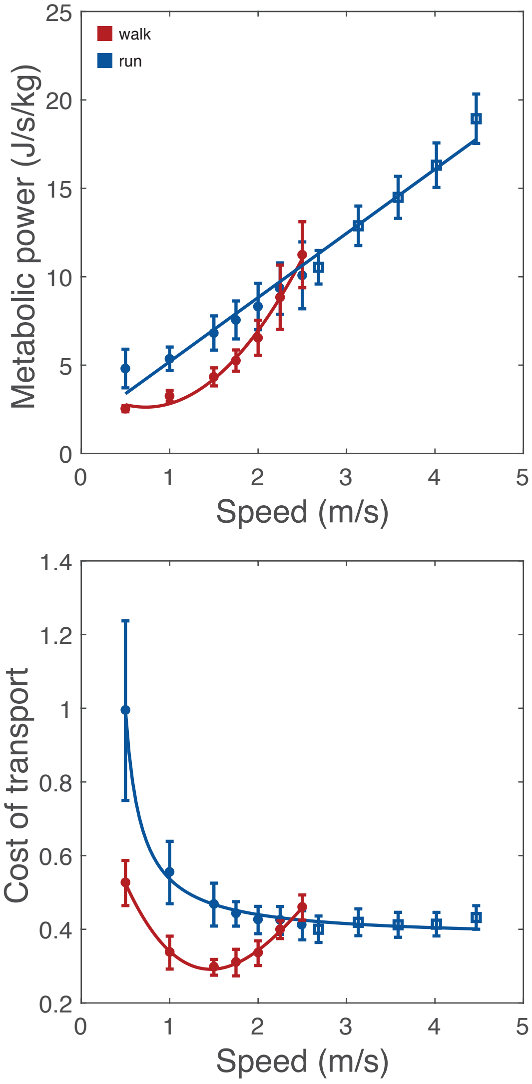

Figure 1. Metabolic data for walking and running. (A) Metabolic power of walking and running. For running, the metabolic power is linearly related to speed (blue). The metabolic power of walking increases non-linearly with walking speed. (B) The cost of transport of running and walking. Cost of transport is made dimensionless by dividing energetic cost (J) by the distance travelled and body weight. For running it decreases rapidly below speeds of 2 m/s, and remains roughly independent of speed thereafter. The cost of transport for walking has a minimum near the preferred walking speed (~ 1.5 m/s), and exceeds the cost of running at ~2.3 m/s. The walking data and slow running data (< 3 m/s, filled circles) are data from unpublished experiments at University of California, Berkeley. The high-speed running data (open squares) are from Mayhew et al. (60). Error bars denote standard deviations. The polynomial fit lines are for illustrative purposes only.

estimated for Honda's Asimo humanoid robot (23). In running, the cost of transport is nearly independent of speed (19) (Figure 1). This surprising result means that while the rate of energy expenditure is much higher at fast speeds, it is nearly exactly balanced by shorter total time the muscles have to be actively consuming energy—the same amount of energy is needed to cover a given distance no matter if it is run fast or slow. Importantly, energetic cost doesn't just depend on speed. It is strongly affected by step frequency, step width, degree of knee flexion, and injury, to name just a few (24-26). Indeed, almost any change to how a person walks or runs will change the way muscles are used and thus have an effect on the resulting energetic cost.

People prefer to walk and run in ways that minimize their energetic cost (Figure 2). For example, we tend to move at a speed that minimizes our cost of transport (27-30). And at a given speed, we select the best gait—be it walking or running—to approximately minimize energetic cost (31-33). People also consistently select the appropriate step frequency, step length and step width that keeps cost minimized (25, 34, 35).This is not to say that there aren't other goals during locomotion. A particular speed may be required if one is trying to catch a bus, for example, while stability is necessary to avoid falls. Yet, within these constraints, energy minimization appears to be paramount. Indeed, there are no known elective changes that we can make to our locomotion biomechanics that will decrease our energy expenditure relative to their preferred gait (36).

Our ability to find economical gaits reflects processes operating on different timescales. On the longest timescale, evolution appears to have favoured morphologies that made our ancestors more economical (37). Movement comprises a substantial fraction of our daily energy needs (38, 39), and adaptions for more economical movements would have meant less time required to search for food, leaving more time available for other factors that affect evolutionary fitness such as hiding from predators, reproduction, and raising offspring (40). Over shorter timescales, our economical gait might also be the product of the tuning of our neuromuscular physiology over developmental time. Indeed, our gait biomechanics mature over the course of childhood (12), and are mirrored by systematic decreases in the cost of transport (41). On the shortest timescales, our nervous systems employ real-time optimization to find energetically optimal control strategies. We think the clearest evidence of this comes from our own studies that have used exoskeletons to reshape energy cost as a function of a person's gait (42). After the exoskeletons present the wearer with new relationships between walking movements and energy expenditure, people rapidly adjust their movements to converge on the new energetically optimal gait, and do

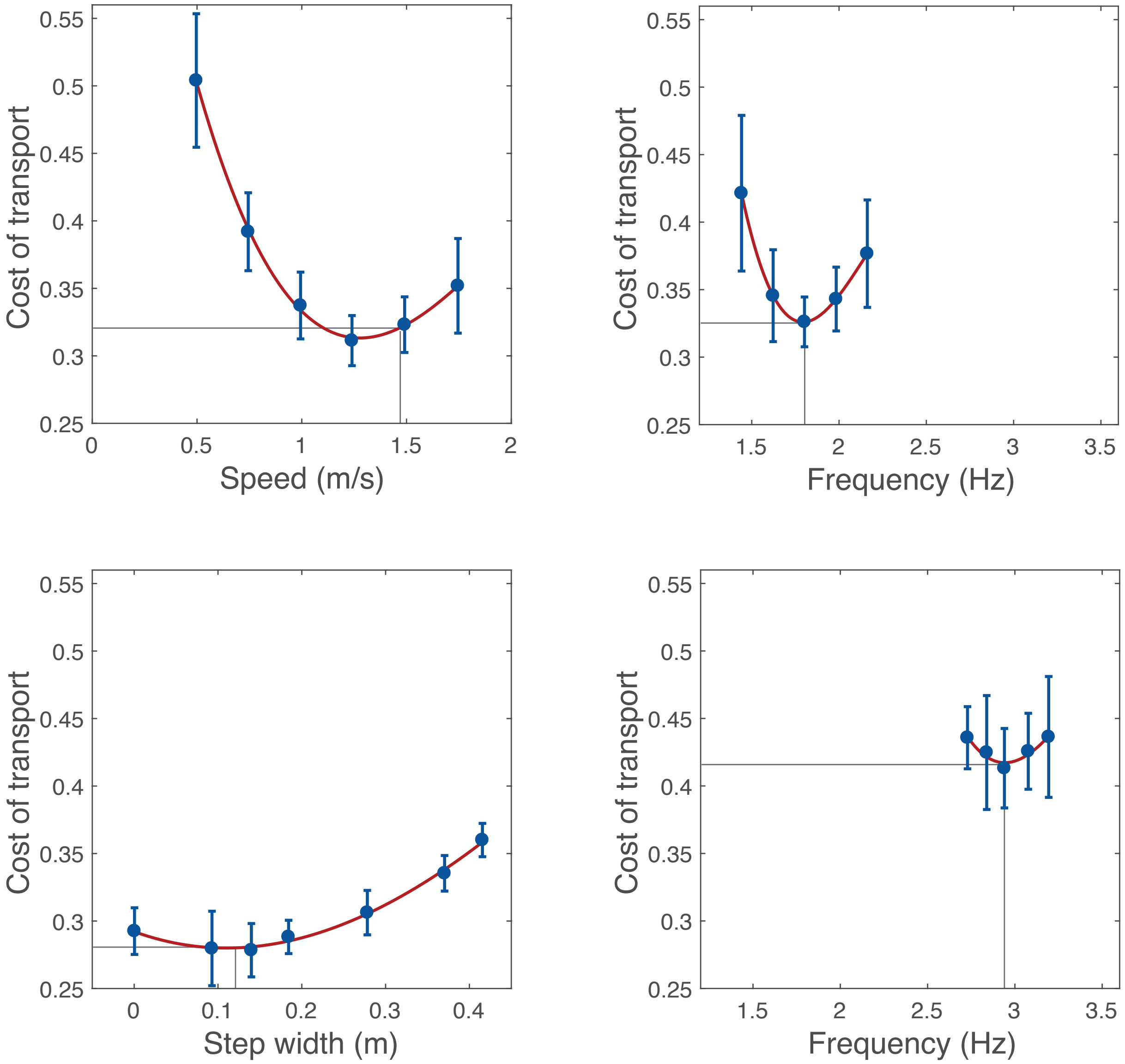

Figure 2. Humans prefer to move in ways that minimize energetic cost. The grey lines in each figure denote the energetic cost at the preferred (A) speed of walking (21), (B) step frequency of walking (24), (C) step width of walking (25), and (D) step frequency of running (59). Error bars denote standard deviations. The polynomial fit lines are for illustrative purposes only.

so for remarkably small savings. The nervous system is both rapid and frugal in its desire to minimize energetic cost.

Walking and running employ distinct underlying mechanisms

Almost no net mechanical work is required when walking or running over level ground at a constant speed. This is because if the ground is hard—like packed dirt rather than sand—the legs need to perform very little mechanical work on the environment. And the body doesn't need to perform net mechanical work on itself because its average potential and kinetic energy are not changing. This is not to say that the gravitational and potential energy of the body don't fluctuate within a stride cycle—they do (Figure 3). But, these fluctuations need not be entirely due to muscle and other tissue dissipating energy by performing negative mechanical work on the body, and then muscle restoring it using metabolically expensive positive mechanical work. Instead, in both walking and running, these energy fluctuations could be due to passive mechanisms that

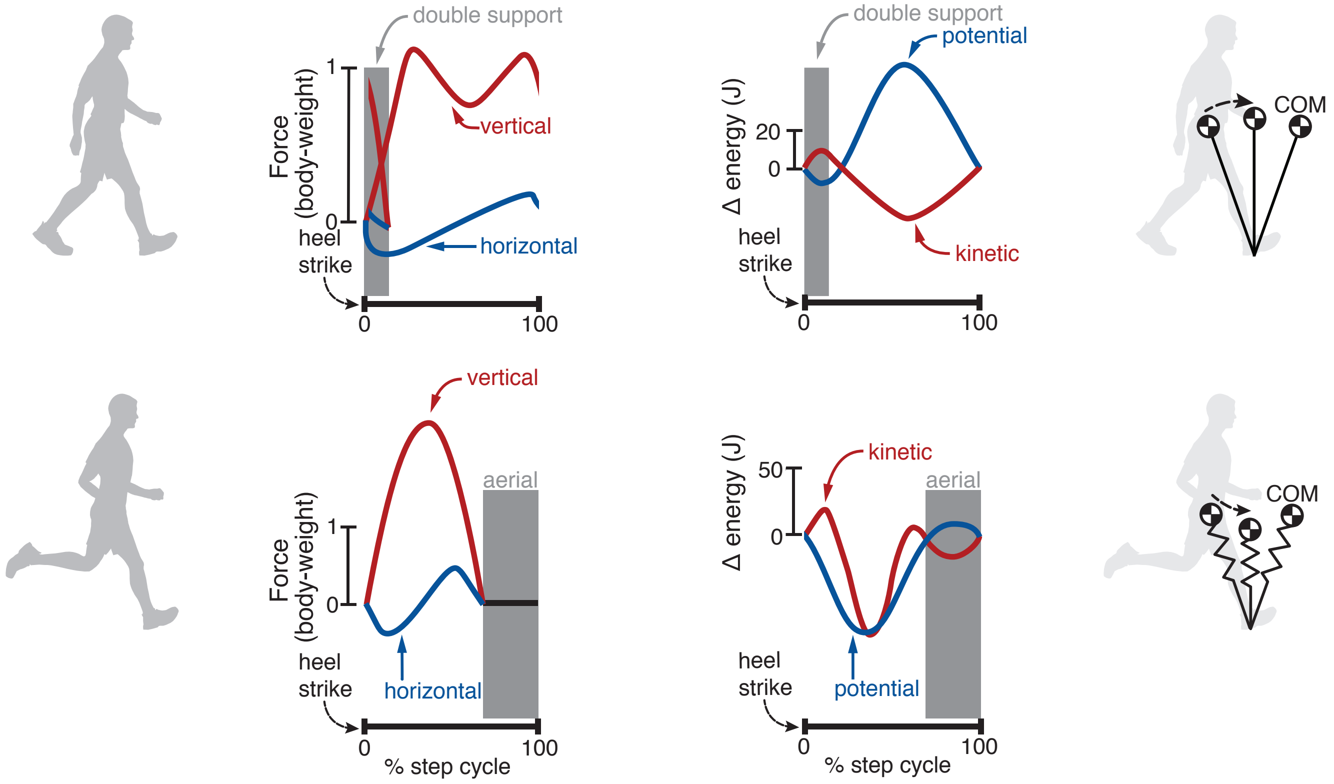

Figure 3. Dynamic walking models. TOP: (A) At slow speeds, humans move by walking. (B) Here we show the vertical and horizontal ground reaction forces on the stance foot during one gait cycle, beginning at heel strike and ending with push-off. (C) These input forces result in changes in the center of mass kinetic and potential energy (gravity), which oscillate out of phase with each other. (D) The simple model of walking represents the motion of the center of mass as an inverted pendulum – a point mass (COM) located on a massless, rigid leg. Not shown is the swing-leg, which is also modelled as a pendulum. BOTTOM: (A) At faster speeds, humans move by running. (B) The ground reaction forces on a leg during stance are shown (no forces act on the feet during the aerial phase). (C) During contact with the ground the center of mass kinetic and potential energy fluctuate in phase. After push-off, the center of mass enters an aerial phase, before returning to the ground. (D) The spring-mass model approximates the centre of mass (COM) behaviour. Here the swing leg is omitted. Data adapted from Farley & Ferris 1998 (144).

enable the storage and return of mechanical energy within a stride cycle. While walking and running may share this common feature of energy conservation, the consensus is that they differ in the mechanisms they employ to execute it (43).

Walking employs pendular mechanisms that conserve mechanical energy (43-45). During the single support phase of walking, the stance leg is relatively stiff (46). Consequently, the rest of the body first moves upwards and then downwards as it translates forwards. This behaviour is well described by an inverted pendulum that models the stance leg as a massless rigid strut, and the rest of the body as a point mass located at the center of mass (COM; Figure 3). A pendular mechanism enables forward motion of the body without requiring muscles to perform mechanical work, by exchanging translational kinetic energy for gravitational potential energy. Measurements of the mechanical energy of people's COM during this period indicate that the translational kinetic energy and gravitational potential energy indeed fluctuate out of phase (43)(Figure 3). The swing leg dynamics also take advantage of pendular motion—the leg swings passively for much of its swing phase, converting gravitational potential energy into kinetic energy in the first half of swing and then reversing that process in the second half (47). However, the entire motion isn't passive—brief periods of muscle activity at the beginning and end of swing force the leg to accelerate and decelerate quickly (48).

Running employs spring-like mechanisms, which may help conserve mechanical energy. During the ground contact phase of running, the stance leg is relatively compliant—it flexes during the first half of stance, and extends during the second half. This has led to a simple model of running that, like the inverted pendulum model of walking, models the body as a point mass. But unlike walking, the leg is approximated as a massless spring rather than a rigid strut (Figure 3). This mechanism, which is sometimes called a spring-mass model and sometimes called a spring-loaded inverted pendulum, conserves mechanical energy by storing it as elastic potential energy during the first half of stance phase and then returning it during the second half. Indeed, human experiments demonstrate that the COM is at its lowest during mid stance in running, but at its highest during mid stance in walking (46). Furthermore, measurements of the mechanical energy of the body's COM during stance indicate that the translational kinetic energy and gravitational potential energy fluctuate in phase with each other, but out of phase with the elastic potential energy of the leg (18, 49, 50). Perhaps most remarkably, human experiments demonstrate that the entire leg behaves like a single spring during ground contact, delivering force to the ground in proportion to its compression. This leg stiffness is remarkably linear, and exhibits very little hysteresis (51).

The inverted pendulum and spring-mass model described above are more conceptual and descriptive than predictive. They do describe the measured COM trajectory during walking and running, and have played an important role in conceptualizing the utility of mechanical energy conservation in moving the body forward economically. They also demonstrate that there are multiple candidate mechanisms for useful energy conservation. However, humans and human locomotion don't strictly conform to these models. For example, our bodies aren't point masses and our legs aren't massless. And during walking, our legs are more compliant than implied by a strut-like inverted pendulum (46). Indeed, models with springy legs can reproduce human ground reaction forces and COM trajectories not only for running, but also for walking (52). And in running, our spring-like leg behaviour may be less related to conservation of elastic energy in structures like tendons, and more related to how our nervous system controls our muscles and joints. Importantly, the original inverted-pendulum and spring-mass models don't make predictions about our locomotor behaviour, such as our energetic cost, our preferred biomechanics, and our stability. Despite this major explanatory shortcoming, these models have nevertheless been central to our understanding of locomotion primarily by influencing the direction of more predictive models. For example, the idea of pendular walking has been taken to the under-actuated extreme in the seminal work of Tad McGeer (1990)(53). Inspired by the original work of Cavagna and McMahon, McGeer showed that simulated and physical models of straight-legged and kneed robots are capable of generating dynamic walking gaits in the absence of any actuation, save for that provided by gravity. The original McGeer models, and extensions of them that we collectively refer to as dynamic walking models, do make predictions about why walking requires energy and control, and how much energy and control it requires under different circumstances. The spring-mass model has similarly spawned useful predictive models that harness spring-mass mechanics (54-57). We further describe many of these walking and running models within this chapter, and do so when they become useful for explaining locomotion's underlying principles.

We walk at slow speeds and run at fast speeds because it is most economical to do so

The ways we normally walk and run are not the only ways of using our legs to get around. For example, we might skip, hold our centre of mass (COM) completely level, or land with stiff legs when we run, but we seldom do so. To understand why we walk and run the way that we do, Srinivasan and Ruina (2005)(58) developed a simple model of bipedal locomotion that could perform virtually any type of gait. They used numerical optimization to discover which types of gait would minimize muscle mechanical work at each speed. Unbiased by an expectation of what the optimal gaits may be, the optimization algorithm converged on the classic gaits of inverted-pendulum walking at slow speeds and spring-like running at fast speeds. Note that in the case of running, this behaviour was observed despite the fact that the biped did not store and return elastic energy, indicating that the spring-like behaviour of the human leg has energetic benefits beyond the conservation of mechanical energy. These optimization results suggest that we walk the way we do at slow speeds, and run the way we do at fast speeds, because they minimize energetic cost. Experimentally, it is impossible to compare all possible gaits. Because it is possible to run at all walking speeds, and walk at many running speeds, a logical comparison is between these two gaits at the same speeds. Measurements of the energetic cost of walking and running (Figure 1) show that it is more expensive to run than walk at slow speeds, while at fast speeds it is more expensive to walk than run (21, 24, 25, 59, 60). And, people prefer to switch between the two gaits at about the speed where it becomes cheaper to use the other gait (32). A second logical comparison is to gaits where the center of mass trajectory is kept flat and moving at a constant speed, like the center of mass motion in a rolling wheel. This is similar to the gaits made famous by the unlikely duo of Groucho Marx, the actor, and Asimo, the robot. Such a gait can be used at both walking and running speeds, but in either case, there is a very large energetic penalty relative to typical walking and running gaits (61, 62). These results demonstrate that it is energetically disadvantageous to eliminate the mechanical energy fluctuations that normally occur within a gait cycle.

Energetic cost of walking is dominated by transition costs and leg swing costs

Our movements are powered by muscles. Our muscles can behave like motors, generating forces while shortening by converting stored chemical energy into positive mechanical work that lifts and accelerates our bodies. This chemical energy originates from the food we consume, and is often referred to as metabolic energy. When performing positive work, the muscle's maximum efficiency – the ratio between mechanical work performed to the chemical energy consumed – is approximately 25% (20). That is, for every 1 J of positive mechanical work performed by muscle, it requires at least 4 J of chemical energy. This is the maximum efficiency—it can be much less than 25% under less favourable conditions. Behaving like a motor is perhaps the most intuitive role for muscle, particularly if one is used to thinking about robot actuators. But muscle has two other mechanical roles in human movement (55). First, it can behave like a brake, generating forces while it is lengthening and converting mechanical energy that was stored in the motion of our bodies into heat. Unlike magnetic motors that act as generators when braking, muscles consume, rather the produce, chemical energy when performing negative mechanical work. The energetic efficiency of such negative work conditions is approximately -120%. That is, when a muscle takes 1 J of mechanical energy from the body and turns it into heat through braking, it consumes 0.83 J of chemical energy to do so (20, 63). The final mechanical role of a muscle is that of a strut or a cable, where it generates forces while keeping its length constant. This active muscle still consumes chemical energy even though its mechanical work is zero, resulting in an efficiency of 0%. As we will describe in detail later, a benefit of this role is that it can allow tendons and other elastic tissues to store and return elastic energy while avoiding having to perform costly positive mechanical work. Thus, muscle force is most costly during shortening contractions when delivering positive mechanical work, and less costly under isometric or negative work conditions (55, 64). But no matter how the muscle is being used, an active muscle always consumes chemical energy.

Since walking uses pendular mechanisms to conserve mechanical energy, why does it exact an energetic cost? The answer appears to be that there are energetic consequences to behaving like an inverted pendulum. During single support, when the body is swinging upward like a pendulum, the leg is behaving like a rigid strut. When a leg isn't changing length, then there is no component of the center of mass velocity that acts along the leg—instead it is directed perpendicular to the leg. At each new step, the body must transition from a trailing leg inverted pendulum to a leading leg inverted pendulum (53, 65, 66). Thus, the center of mass velocity must be redirected from being perpendicular to the trailing leg to being perpendicular to the leading leg. People accomplish this redirection partially by performing positive mechanical work by pushing off with the trailing leg, and partially by performing negative mechanical work by the leading leg. The period over which the redirection occurs is called the step-to-step transition (67). This period is modeled as an instantaneous event in most dynamic walking models, and the leading leg negative mechanical work is modeled as an inelastic collision. But in humans, the step-to-step transition is stretched out over the double support period and sometimes longer (68). Experiments designed to tease apart the work at the step-to-step transition from other contributors to the energetic cost of walking have demonstrated that transition work is responsible for about two-thirds of the cost of walking under normal conditions (66, 69).

In principle, COM velocity redirection could be accomplished entirely with leading leg negative mechanical work. But to prevent slowing down, this negative work has to be replaced by an equal amount of positive work. As long as it is in the right amount, this positive work could be performed at any time during the gait cycle. But, there is an energetic advantage to performing it during push-off—it helps redirect the COM velocity so that less negative work is required of the leading leg, and thus less positive work is required to replace it. Models analyzing the sequencing of positive work suggest that the energy lost at the transition with an appropriately timed push-off can be as little as one quarter of that lost if the replacement work is performed with other strategies (65). In line with this prediction, humans do perform most of the positive work in walking during the trailing leg push off, and most of the negative work during the leading leg collision (68). And if push-off is impaired, the negative mechanical work of the leading leg increases, therefore requiring more positive work during the rest of the gait cycle and increasing the energetic cost of movement (70, 71, 72). One application for this theory is gait assistance for amputees, by replacing the lost push-off work in the amputated limb with an actuated prosthetic. However, the effect of added push-off work has produced results that are a challenge to explain with existing theory. In a recent study the addition of positive push-off work with an ankle prosthetic reduced energetic cost but not by reducing negative work by the leading leg. Instead, the positive work seems to help reduce the costs of swinging the leg (73). at this time, it is unclear whether these results are caused by particulars of amputee gait, limited time spent learning to use the actuated prosthetic, or rather represent a shortcoming in current theory.

People actively swing their legs to reduce the step-to-step transition cost. Were transition cost the only cost to walking, it would favour walking with very short steps. This is because, at the extreme step length of zero, the walking motion becomes that of a wheel and no work is required to redirect the COM velocity. For a given walking speed, short step lengths require high step frequencies. This can be accomplished with periodic hip torques to entrain the leg to swing with frequencies higher than its natural frequency. But actively swinging the leg is not free—it is estimated to contribute about one-third of the total cost of walking (36). Experiments on human participants indicate that the cost of leg swing increases steeply with increases in swing frequency, when amplitude is kept fixed. This pattern is opposite to the step-to-step transition cost, placing the two in tension—people should avoid long steps to avoid high transition work and avoid short steps to avoid high leg swing cost. Indeed, minimizing the sum of the two costs across a range of walking speeds well predicts the preferred relationship between walking speed, step length and step frequency (65). And summing their independent energetic costs yields a value close to the total measured energetic cost—transition and leg swing costs are the primary contributors to walking's energetic cost in healthy adults (36).

Energetic cost of running is dominated by the cost of producing isometric force

As with the pendular mechanisms in walking, there are energetic consequences for the spring-like behaviour of the stance leg during running. Anatomically, the primary springs within our legs are our tendons. These tissues are quite effective at storing and returning energy, and do so without any energetic cost (74). However, they don't independently cross human leg joints and directly attach bone to bone. Instead, they attach in series with muscle as a muscle-tendon unit. Consequently, muscles must generate force to allow the tendons to lengthen under load and store mechanical energy. As described earlier, this muscle force generation comes with an energetic cost. The muscle need not perform expensive mechanical work, however, if energy can be recycled in a passive tendon. Instead, it can generate force and keep its length constant. This still exacts an energetic cost, but less so than if the muscle had to perform new positive mechanical work (75). It is technically difficult to measure muscle and tendon lengths and forces in running humans. The data we do have in humans and other running animals demonstrate that important muscles in running generate large forces while indeed keeping their length constant (76-78). This enables the in-series tendons to lengthen and then shorten, first storing mechanical energy and then returning it into the running gait cycle. Moreover, muscles benefit from operating at the length for which their force is maximal. At this length, the fewest number of muscle fibres need to be active to generate a given force. At shorter and longer lengths, the same total muscle force requires more active muscle fibres, and active muscle fibres consume chemical energy to generate force. Thus producing isometric force at or near the muscle's optimum fibre length further improves running economy (77-79).

The energetic cost of isometric force generation depends on both the magnitude of force and the time available to generate the force. If the average force is kept constant, it is also more expensive to generate a short burst of force followed by a long period of inactivity, rather than to generate a long burst followed by a short period of no force (80). This time dependence is attributed to a number of factors that include an added cost to turning a muscle on and off, and a greater rate of consuming chemical energy in faster muscle fibres (80-83). The dependence on magnitude of force and burst duration are collectively referred to as the cost of generating force, and they explain much of the energetic cost of human running at different speeds (19). That is, running at faster speeds results in a higher rate of energy consumption due, in part, to the shorter durations of ground contact, resulting in shorter, and more expensive, bursts of muscle activity.

How much does it cost to swing the legs during running? While spring-mass models of running often ignore the dynamics of leg swing, or assume a massless leg, running has been studied experimentally in guinea fowl who conveniently have muscles partitioned into those used for leg swing and those used for leg stance. Blood flow estimates in these animals suggest swinging the leg costs roughly 25% of the total energy during running (84). This is in line with estimates from human running experiments where leg swing is assisted with external springs (85). Given that both leg swing cost and the cost of generating force appear to penalize shorter step periods, why don't people adopt longer step periods for a given running speed? The answer appears to be that, like when walking, people prefer to minimize energetic cost during running, and step periods that are longer than preferred come with an energetic penalty(35, 59). But unlike walking, where we have a good mechanistic understanding of the determinants of energetic cost, the source of this long step period penalty is unknown. One candidate explanation is that longer steps require increased leg compliance and thus perhaps increased muscle forces to support a more bent leg posture (86).

The foot can act like a spring and a wheel

Human feet are complex. They contain one quarter of the bones in the human body, more than 100 muscles, and an astonishing 33 joints (87). Our foot design is almost certainly not optimal—our ancestors' feet were likely prehensile and evolution has adapted this morphology to be used as our primary interface with the ground. The function of the foot depends on whether a person is walking or running. In walking, it appears that the foot helps to minimize step-to-step transition work. This was studied first in dynamic walking models by using feet shaped like circular arcs (53). It was found that the work required of each transition decreases with increases in the radius of curvature of the feet. This is because the point of application of the ground reaction force translates along the foot, reducing the angle over which the COM needs to be redirected. Indeed, for foot curvatures equal to leg length, and foot lengths equal to step length, the redirection angle goes to zero requiring no transition work and the COM travels in a straight line without change in speed, like the hub of a wheel. Measurements on humans indicate that the motion of the point of ground reaction force application along the foot of a walking person is well predicted by a circular arc shape, and that the arc has a radius of 0.3 times leg length. Why is this value optimal? Dynamic walking models show that larger curvatures than 0.3 with our forward-facing and human-length feet have increased energy losses during step-to-step transitions. These losses are due to the unfavourable position of the leg mass relative to the point of collision with the ground. While longer feet (at the same curvature) can decrease redirection cost further, long feet have additional costs. They are heavier and thus have greater swing cost, and the added mass makes them less maneuverable. Experiments that varied artificial foot shape while measuring energetic cost have demonstrated that arced feet with curvature and lengths similar to human feet provide measurable energetic savings over point contact with the ground (88).

Several elastic storage mechanisms distributed across the entire leg allow humans to store energy during running in a manner similar to the carbon fiber lower limbs of modern Paralympians. As the foot hits the ground and initiates a stance period for a particular leg, the foot itself acts as an elastic energy mechanism as it stores energy during collision with the ground and releases it during push-off. The forces that a single foot applies to the ground are large—often more than three times body weight at fast running speeds (89). Measurements of the strain energy stored and released under compression estimate that the ligaments and other soft tissue in the human feet store and return 17 J per step (90). An analogous storage and return cycle acts about the ankle joint, as forces on the forefoot during collision dorsiflex the ankle and store energy in the Achilles tendon. This mechanism is thought to store and return 35 J per step, slightly more than double that of the foot (90). Taken together, this represents a substantial fraction of the 100 J increment in the mechanical energy of the body during stance. Given the large contribution of these elastic storage mechanisms, variations in their effectiveness between individuals could have significant consequences on individual running economy. For example, all else being equal, the amount of strain energy that is stored in the Achilles tendon is inversely proportional to its moment arm, and measured moment arms turn out to be a strong predictor of running economy (91, 92).

Another central objective for human locomotion is to remain stable

While we refine our gaits to minimize energetic cost, it is paramount that these gaits are stable. After all, if you are too unstable to get to where you want to go, how important is it that your attempted gait minimized cost? It is reasonable to assume that one of the strongest evolutionary pressures on our ancestors' locomotion was placed on adaptations that stabilized gait—falling during locomotion would have increased vulnerability to injury or predation, and decreased the chance of catching prey when hunting. While toddlers fall frequently when learning how to walk, we almost never fall during locomotion as healthy adults (10). But this changes as we continue to age—older adults are typically less stable, walking is a major cause of falling, and the consequences for falling are severe. Hip fractures are among the most serious consequences, with more than one million falls per year causing hip fractures in older adults, 90% of which happen during walking (93). Twenty percent of all hip fractures lead to death within 1 year (93). Clearly, stability has been important in human evolution and development and continues to be important in our daily lives.

Researchers typically use three types of experiments to study gait stability. First, they measure actual falls that take place in the real word. This natural experiment is in many ways the most desirable, but the data are the most difficult to acquire given the infrequency of falls and their occurrence outside of the well-controlled lab environment (93, 94). More common is the use of experimental paradigms that perturb walking and running to understand the causes of falling. In such experiments, researchers can probe stability using both physical and sensory perturbations. That is, they can apply external forces to the system, or they can alter sensory information to test the neural systems underlying the control of stability. One complication of these experiments is that it can be difficult to ensure people don't adopt a different stabilizing strategy than they would have used outside of the experimental paradigm. People tend to only respond naturally to the first unanticipated perturbation, and then adopt a different and more stable strategy for subsequent perturbations (95). Finally, rather than use an experimental perturbation, researchers have attempted to analyze normal walking data to determine characteristics that may correlate with instability or falls, such as step width variability. But, this correlational approach is hard to validate given how infrequently falls occur. Moreover, since these observed characteristics of movement are affected by feedback, they may not even reflect a cause of instability. For example, is step variability indicative of decreased stability or of increased active control via foot placement?

Physiological feedback control is relatively slow

One way to stabilize a system is with feedback control, but feedback delays in human locomotion are remarkably long. Physiological feedback control involves sensing changes to the body's state, and then making adjustments to the control of muscle based on this sensory feedback. One of the fastest neural response in humans is a mono-synaptic stretch reflex (Figure 4). This is the fastest feedback response because it uses the fastest nerve and muscle fibres and the signal only has to pass through a single synapse. However, nerves and muscles are quite slow—the maximum conduction velocity along a human nerve fibre is only about 65 m/s (96, 97), and it takes about 65 ms from the time a signal arrives at a muscle until it can generate its peak force (98). Consequently, the shortest total time between stimulus and response is remarkably long—about 120 ms from stimulus to peak force for the muscles that extend the human ankle (98). This is about equal to the total time that the foot spends in contact with the ground during sprinting (89, 98). At these speeds, a stimulus occurring at the beginning of ground contact may be able to contribute to the response at the end of ground contact, but it would be impossible to implement multiple cycles of closed-loop feedback control (99). The latencies are even more extreme in other feedback pathways—signals from our touch receptors travel slower than from stretch receptors, and signals from pain and temperature receptors travel slower still (100). There are major additional delays if commands require computation by the brain, due to both the added distance over which the signal is conducted and the additional synapses involved in the computation. Taken together, these delays make it difficult for our nervous system to use rapid feedback control to stabilize fast locomotion in response to unanticipated perturbations (101, 102).

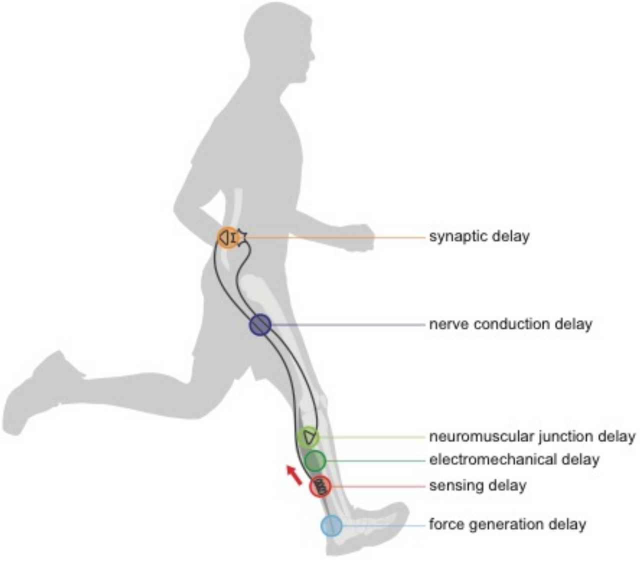

Figure 4. Delays Neuromuscular delays in biological locomotion. Here we depict the delays that result from a single-synaptic reflex, which includes 6 principle delays: 1) transduction of sensory stimuli into a neural signal; 2) transmission of the neural signal along a nerve returning to the spinal cord; 3) synaptic transmission of the neural signal from one neuron, across a synapse, to another; 4) transmission of the neural signal toward the muscle; 5) transduction of the neural signal arriving at the neuromuscular junction into muscle activity; 6) the change in muscle activation that produces a change in force delivered by the muscle.

Reflexes help stabilize slow locomotion

Walking or slow running may allow time for reflexes to contribute to gait stability throughout the gait cycle. These reflex responses used to be thought of as fixed motor commands that were tailored to specific and sudden sensed events. For example, if cutaneous receptors in our skin detect a sharp object underneath one's foot, this signal is relayed to motor neurons that initiate flexion of the injured leg to remove it from harm and simultaneous extension of the other leg so that it can bear the body's weight (103). We now know that these reflexes are functionally tuned for the behavioural context (104, 105). This means that the same signals from cutaneous receptors on the foot elicit different muscular responses, depending on whether the person is walking, standing or lying down (106). Moreover, the magnitude, timing, and even direction of responses are tuned within different phases of the gait cycle. In stance for example, sensors that detect an increase in loading of the stance leg can signal the muscles of that leg to increase output force (107). Similarly, a sudden extension of the stance ankle beyond its normal angular deflection can trigger feedback inhibition of extensor muscles (108). To stabilize transitions between stance and swing, sensors that measure hip joint angle can trigger when a step should begin (109). To measure when a swing phase has ended, cutaneous receptors signal heel contact (110). And to stabilize walking gait using swing leg retraction, reflexes in the hamstring are upregulated at the end of swing (111). In principle, a set of reflexes could stabilize an entire gait cycle by integrating signals from many different afferent sensory pathways.

Physics-based models of walking demonstrate that locomotion is possible even when driven exclusively by these kinds of reflexes (112, 113). In the absence of descending commands, active stability relies solely on the comparatively simple nature of reflexes to adapt gait. These models are stable in the face of considerable changes in surface height and sloped terrain, without requiring any adjustment in reflex gains for the different surfaces. Of course, a model containing a very large number of reflexes might achieve stability by brute force—each unique state in a gait cycle could have a reflex-driven muscle command, and each of these commands could even be optimized for stability. In that case the resulting model would achieve stable gait but would also no longer reflect simple or necessary properties of biological gait. Since the models noted above have used a relatively small number of reflexes, they do serve as impressive tests of the benefits of reflexes for stabilizing gait.

Muscle properties help stabilize human locomotion

Rather than rely entirely on neural feedback control, our gaits also take advantage of biomechanical mechanisms for self-stabilization. One such mechanism concerns the visco-elastic properties of active muscle—they rapidly generate more force when stretched. This zero-delay intrinsic muscle response to perturbations is referred to as a preflex, as it occurs before even the fastest neural reflex (114). Some simulations suggest that preflexes endow human movement with additional intrinsic stability. In simulations of jumping, for example, when the commands to muscle were under open-loop control the jumps were remarkably stable to initial-state perturbations, with the muscle forces adjusting appropriately (115). In contrast, models that were under open-loop control of joint torques failed in response to even small perturbations. In simulations of hopping, which is often viewed as zero-speed running, unpredictable changes to surface stiffness were stabilized by the passive mechanical properties of muscle—leg stiffness was adapted in a stable manner without any change in the neural command (116). These simulations accurately predict the self-stabilizing behavior of humans when hopping during the same unexpected changes to surface stiffness—researchers measured appropriate adjustments to leg stiffness that were too rapid to be neural in origin (117). And, in response to anticipated changes to surface stiffness, researchers found increases in the commanded muscle activity that preceded ground contact, resulting in a feedforward adjustment to leg stiffness (118-120). That is, the nervous system doesn't benefit from preflexive mechanisms only when they happen to arise, but instead actively adopts control strategies to purposefully benefit from their rapid responses.

Passive dynamics also help stabilize human locomotion

Passive dynamics refers to motion that is generated by the body without the use of active control by the nervous system. Whenever a system is perturbed, there is a passive dynamic response. Remarkably, this response sometimes acts to reject the perturbation, endowing the system with passive dynamic stability. In walking, this is perhaps most clearly seen in dynamic walking models that are constrained to two-dimensional sagittal plane motion. For some set of speeds, these models are passively stable—they do not require a controller to actively adjust the limbs to prevent falling over when given a small push. The dynamics are such that a push that increases the energy of the walker causes it to take a longer step. The longer step elicits greater negative work by the leading leg at heel-strike than the nominal cyclic gait, thus dissipating a portion of the energy added from the push (53, 121). In this way, the passive dynamics continues to adjust step length with each new step, monotonically reducing the added energy of the push, and causing the walker to converge to its original gait cycle. A perturbation that slows the walker has the opposite effect: it acts to decrease step length, thereby reducing dissipation and allowing the walker to regain energy and return to its original gait cycle. That these walkers are passively stable to small perturbations doesn't mean that they are stable to all perturbations. Like real systems, if the push is hard enough, it will fall over. Still, the regions of stability are large enough that passive dynamic stability is of practical importance for human gaits (122).

Human walking appears to harness passive dynamic stability to assist with the control of locomotion. It is experimentally challenging to assign responsibility for stability to either active control or passive dynamics because, unlike in passive dynamic walking models, they are both always at work in human locomotion. One experimental trick mentioned previously is to study the short interval after a perturbation, within which neural control is too slow to have an effect. Studies that employ this approach demonstrate that passive dynamics plays an important role for the adjustment of leg stiffness during running (116, 117). Bauby and Kuo (2000)(123) employed a different approach—they contaminated the sensory feedback of participants walking over ground by having them close their eyes. The authors reasoned that this would negatively impact the stability of aspects of gait under active feedback control, while leaving those that benefit from passive dynamic stability relatively unaffected. As predicted by dynamic walking models, the researchers found that variability in step length was relatively unaffected by the added sensory noise—these adjustments appear to be primarily driven by passive dynamics. In a related experiment, O'Connor and Kuo (2009)(124) used virtual reality to apply visual perturbations and again found that step length was insensitive to the sensory disturbances. It appears that people harness passive dynamic stability to help stabilize their motion in the sagittal plane.

The stability of human walking can't be accomplished purely by passive dynamics. Three-dimensional dynamic walking models demonstrate that passive dynamic adjustments to step length that compensate for perturbations to system energy don't apply to step width—lateral motion in bipedal walking is passively unstable (125). Consequently, virtually any push to these walkers will cause them to topple over sideways. This suggests that lateral motion in human walking requires active control (125).

Walking uses active control of foot placement to achieve stability

In principle, passively unstable lateral motion can be stabilized with active control in a number of ways (125). One approach is to lean back toward the midline, opposite the tipping direction. Another approach is to rotate or pinwheel the arms to control the body's rotation, since the total angular momentum of the system (the body and the arms) is constant, thus moving the body towards the middle(126, 127). Another approach is to generate ankle torque to rotate the body about the ankles. A final approach is to adjust the foot placement for the swing leg, thereby moving the center of mass back between the base of support. Models suggest that this foot placement strategy achieves the largest region of stability (125), and is the most economical choice, primarily because the control of step location takes place over the entire swing phase, thus reducing energetic costs related to generating rapid and large forces. It also reduces the computational cost of stability, since the long duration over which the response is executed leaves ample opportunity for feedback corrections to compensate for any imprecision.

Human experiments support the model predictions—people appear to use active control of foot placement to stabilize lateral motion. The previously mentioned experiments that tested for active control by perturbing sensory feedback may not have observed large effects on step length, but did find major increases in step width variability (123, 128). This suggests that the side-to-side placement of the feet is under active control that employs sensory feedback. Rather than making it more difficult for people to stabilize walking, it is instead possible to assist active control by using springs to apply stabilizing lateral forces (25, 129). This added stability decreased step width variability in both young and older participants, indicating a reduced need for active control of foot placement. A further indication that lateral foot placement is under active control is that decreases in step width variability were paralleled by decreases in energetic cost (25, 129). In healthy young people, stabilization appears to be the third main contributor to energetic cost (after step-to-step transition and swing leg costs), accounting for 5-10% of the total energetic cost (25, 130). And the elevated energetic cost of walking in older adults appears to be entirely explained by the additional active control that they require to stabilize their lateral motion (129).

Converging evidence supports the idea that stabilizing behaviours occur within just one or two steps after a perturbation. Dynamic walking models have been used to investigate the *controllability* of walking – the ability of a system to achieve a target state, typically a target velocity (131). It turns out that if the system can reach the target at all—say, to regain a steady-state speed after being pushed a little bit—it can almost always do so within two steps. What could have been a very computationally expensive task to plan many future steps therefore collapses into a very manageable one. The effects of lateral perturbations on normal human walking are also typically eliminated by the second step after the perturbation (132, 133). When planning future foot placements, people typically look only two steps ahead (134), and when planning steps over obstacles people use most of their eye movements to explore the next two step lengths of visual space(135). Thus the number of steps that achieve controllability as predicted by models matches the number of steps that people use to both stabilize their gait, and gather visual information to plan their upcoming steps.

Running stability is partially determined by swing-leg retraction

To study the stability of running, researchers have extended spring-mass models of the stance leg to include the swing leg. There are a variety of these models, but they generally have a stance leg that behaves like a spring, and a swing leg that repositions for the next stance phase. Some are fully dynamic models that accomplish repositioning using a hip spring (56), while others are quasi-dynamic and assume that the swing leg can be made to reach a specified state at ground contact. Unlike walking models, the dynamic running models are passively unstable in the sagittal plane at realistic running speeds and cadences (56, 136). McGeer's elegant analysis of dynamic running models demonstrates that they can be readily stabilized with once-per-step feedback control, similar to the use of foot placement to stabilize walking (56). The feasibility of intermittent feedback control such as this is important given the relatively lengthy delays in human nervous systems at fast running speeds. Also useful in the face of long feedback delays is feedforward control, which can stabilize these sorts of models with a mechanism referred to as swing leg retraction (137). In swing leg retraction, a burst of hip torque actively reverses the forward direction of the swing leg prior to ground contact. The swing leg is often modelled as moving at constant velocity during the flight phase. Since the leg retracts without feedback, the backwards angle swept before contact is defined by flight time. Longer flight times than the nominal trajectory make the leg swing further backward, so that the angle of the leg with the ground is more vertical when the foot contacts the ground. When the model leaves the ground after this contact phase its exit velocity is more parallel to the ground. Thus the center of mass achieves a lower height on the next stride, thereby providing negative feedback about the nominal running trajectory.

Swing leg retraction offers several benefits, including providing asymptotic stability, peak disturbance rejection, and improved foot placement stability (138-140). In this area, there is much more theoretical work than experimental tests (141). But the few controlled experiments designed to test whether humans employ swing leg retraction as a stabilization mechanism support it. For example, when runners are presented with changes to surface height, retraction angle at ground contact varies in proportion to the change in height, and in the direction predicted by theory (142).

Runners adjust leg stiffness to remain stable

Models of running suggest that stable running is achievable without changing leg stiffness. As described earlier, various control schemes can stabilize passively unstable running gaits even in models with a constant leg stiffness (56, 137). Furthermore, models with a constant leg stiffness can run across a wide range of speeds (143). Yet experiments show that people do adjust their leg stiffness in response to perturbations, and can do so over quite a large range (120). And these leg stiffness adjustments result in a conservation of running kinematics, preserving characteristics of gait such as contact duration, step frequency, and COM motion (144). For example, when transitioning from a stiff ground surface to a compliant one, people increase leg stiffness in such a way that the COM motion is essentially unchanged. It is an open question as to why the nervous system appears to conserve kinematics. One possibility is that maintaining a nominal motion of the center of mass reflects a feedback control strategy by the nervous system to preserve the motion itself (120). Another possibility is that reflex control strategies that stabilize gait operate about this nominal movement (144). Yet another possibility is that a known nominal motion of the center of mass could allow sensory systems such as the vestibular and visual systems to operate effectively. A further, and, in our opinion, unlikely, possibility is that this adaptation is made strictly to minimize energetic cost, since it seems unlikely that the minimum cost gait on both stiff and compliant gaits would share the same kinematics of the center of mass.

Concluding Remarks

Our goal in this chapter was to identify and explain central principles underlying why people walk and run the way they do. We focused on principles because humans and robots are comprised of very different hardware, but both may benefit from using similar algorithms to solve the common problem of locomotion. In brief, people quickly learn how to stabilize themselves early in development and rarely fall as adults. This stability is especially remarkable because physiological feedback delays are relatively long. Humans overcome these long delays using a combination of preflexes, passive stability, feedforward strategies, intermittent feedback control and, when time allows, continuous feedback control. While people need to be sufficiently stable to walk and run, they don't need to maximize stability for most situations. This leaves considerable flexibility in how people achieve their locomotor goals. The solution for most circumstances is to minimize energetic cost. This emphasis on energy optimization is evident in our anatomy, through the use of mechanisms like energy storage and return in tendons, and in our control, through the use of control policies that conserve mechanical energy. The energetics and stability mechanisms employed by humans have arisen over evolutionary, developmental and real-time learning time scales. That is, adaptations for economical movements and rapid stabilization are evident in human anatomy, and people learn over time to leverage their inherent body dynamics to improve economy and stability.

Although we are far from experts on the engineering of humanoid robots, it seems to us that many of the principles of human locomotion that we have described here are implementable in robots. Indeed, some roboticists are already actively employing similar approaches (145-147). Importantly, the principles we describe here should be used as inspiration, rather than be blindly copied, as some of them may be a consequence of human limitations with which robots need not suffer. For example, human adaptations to compensate for long feedback delays may not be characteristics that should be implemented in humanoid robots unless these robots also suffer from long delays. On the other hand, the fact that human control is so relatively good in the presence of these delays suggests that such delays are not in themselves an obstacle to control, and that high frequency control is not a necessary feature of stable and economical movement. We suspect that there is nothing particularly special about human hardware that can't be matched or exceeded by engineered components. If true, human locomotion capabilities are not only achievable by humanoid robots, but possibly exceedable. Such robots, we suspect, will employ some of the human locomotion principles that we have described here to be both stable and economical.

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