

CHAPTER ONE

Concepts Through Time: Historical Perspectives on Mammalian Locomotion

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1.1 INTRODUCTION

This chapter is meant only as a subjective description of some important landmarks along the route that has brought the field of terrestrial (primarily) mammalian locomotion to its current position. I have not been particularly interested in documenting the sequence of specific events, but have instead tried to follow the often circuitous path of ideas as they originate, are modified and are passed along to influence others.

In evaluating the current status of the field of terrestrial locomotion, I find that those of us working in this area are part of a long, and often very illustrious, community of individuals who seek out novel and creative methods of divining the constraints and opportunities exploited by animals in attaining movement within the physical world. The motivation for the development of this volume is to focus attention on the role of mechanics in understanding animal locomotion and, particularly, that of terrestrial mammals. The field is currently undergoing a substantive change in perspective, as new

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technologies allow the critical evaluation of dynamic features of gait, and novel conceptual approaches are being assessed (although as we will see, few ideas in a field with such a long history can be considered truly novel). Overall, this volume is designed to stimulate the discussion of these newly arising opportunities, and this chapter is designed to “set the stage” for such a discussion.

Historical evaluations relevant to the field of locomotion science appear with some regularity, either as a contribution designed to put the field in historical context (Cappozzo *et al.*, 1992; Medved, 2001; Ashley-Ross and Gillis, 2002) or integrated within a discussion of the state of the field at the time of writing a more comprehensive assemblage of knowledge on the topic (Howell, 1944; Gambaryan, 1974; Walker, 1972). My interest is in emphasizing the origin of unifying (or dividing?) concepts, rather than exhaustively mapping the history of the field. To this end, I will trace my personal impression of key conceptual breakthroughs, whether in the fields of animal or human biomechanics and physiology or, indeed, even if it strays into robotics or the fundamental mechanics that ultimately underlies our field. I will liberally add my “interpretation” of events and the stimulus that led to them. When doing so, I will provide the evidence as I see it, but in few cases will this be conclusive, so all such descriptions should be evaluated as only the personal opinion of an interested observer.

1.2 THE ANCIENTS AND THE CONTEMPLATION OF MOTION

Undoubtedly, prehistoric man observed and wondered at the remarkable abilities of animals to move, likely largely motivated by the elusiveness of the prey they pursued, but also by wonderment at the fleetness of some terrestrial runners. The cave paintings from Lascaux, France (approximately 15,000 BC) demonstrate that our distant ancestors were, indeed, keen observers of the form and movement of mammals, indicating a fundamental interest in understanding and interpreting animal motion (Figure 1.1).

The movement of animals and their relationship to the locomotion of humans also holds an inherent interest for those trying to understand the world they observe. Such was the case with Aristotle (384–322 BC), an individual who has had a great influence on philosophical thought and the foundations of modern science. Among Aristotle’s influential writings was *De motu Animalia* (On the Gait of Animals). Aristotle’s interest in locomotion derived from the fundamental question of the difference between passive matter and the activity of living things, placing questions of locomotion at the foundation of major philosophical issues regarding the makeup and function of the physical world.

Among other surprising observations listed in *De motu Animalia*, Aristotle noted vertical motion of the human when walking, by observing the “zig-zag” movement of the shadow against a flat wall (as translated by Farquharson, 2007). This was particularly in reference to how the swing limb must flex in order to pass under the individual, but the observation was astute and important in recognizing the complexity of motions required to produce effective locomotion, and that locomotion involved multidimensional movement of the body as well as the limbs.



FIGURE 1.1

The cave painting from Lascaux, France, known as the “Third Chinese Horse”. This painting depicts a galloping horse with arrows approaching its back, taken from the series referred to as the “Chinese horses”. The cave was discovered by adventurous boys in 1940. The painting likely dates from 15,000 BC.

Aristotle also described the limb motions of quadrupeds as they walked, but these “observations” seem to have come more from theoretical analyses than from direct observation. As will be described below, some two millennia later, Borelli revised some of these descriptions to reflect more accurately the actual movements of walking quadrupeds as a means to explain some of the reasons that motions occur as they do.

1.3 THE EUROPEAN RENAISSANCE AND FOUNDATIONS OF THE AGE OF DISCOVERY

Although it is well known that Leonardo da Vinci (1452–1519) studied fish swimming and bird flight, it is not so well known that he also studied human and animal terrestrial locomotion. His approach to the investigation of structure, including meticulous anatomical studies, paved the way for considering the mechanisms of movement. Indeed, his work, in many ways, heralded the beginning of the European Renaissance. He performed many artistic studies on the form of animals and people in motion. For many of these studies, it is difficult to tell whether the objective of the work was to understand the function of the system, or to observe the natural motions in order to improve his art – in many cases, for da Vinci, these seem to have been one and the same.

Of particular note are his drawings of individuals walking up and down stairs, standing from a seated position and stopping from a run, all of which represent the mechanical realities of each of these circumstances. His pen and ink studies of individuals and animals laboring, demonstrating a variety of positions, are reminiscent of Muybridge's photographic studies that followed nearly 500 years later. Da Vinci's notebooks indicate that he was collecting material for a never-completed work on mechanics, a work that would have given us a complete view of his understanding of motion, including that of animals and people.

As keen an observer as he was, however, he did make some errors. He clearly believed, as all of us do as children, that heavier objects fall more rapidly than lighter ones. Our modern perspective of the world benefits from the luxury of the accumulated understanding that we call knowledge, served to us in the form of education.

The extensive notebooks of da Vinci hold numerous examples of his understanding of locomotion mechanics, some of which have proven correct, while others were not so successful. Leonardo (more or less) correctly observed that, "*Man and every animal undergoes more fatigue in going upwards than downwards, for as he ascends he bears his weight with him and as he descends he simply lets it go.*" However, he profoundly misunderstood the role of impulse, and suggested, "*A man, in running, throws less of his weight on his legs than when he is standing still. In like manner the horse, when running, is less conscious of the weight of the man whom it is carrying; consequently many consider it marvelous that a horse in a race can support itself on one foot only. Therefore we may say regarding weight in transverse movement that the swifter the movement, the less the weight towards the centre of the earth.*" (p. 150, Richter and Wells, 2008).

It is now eminently clear that, provided we remain in the Newtonian realm, we weigh the same regardless of how fast we run. It is the subtle strategies employed to deal with this fact that make the understanding of running gaits, in people and other mammals, a challenge to understand.

A substantial influence on the origins of biomechanics were the works of Galileo Galilei (1564–1642), particularly *Discourses on Two New Sciences*. One of these "New Sciences" was the formal western origin of mechanics. The principles outlined formulated the basis of understanding the mechanics of biological movement. Indeed, many examples described in the *Discourses* are biological, indicating that, in Galileo's mind, there was no definitive difference between the mechanics of the organic world and that constructed by humans. TA McMahon (1975) referred to Galileo's analysis of scaling issues, noting ironically that a woodcut from *Discourses* (Drake, 1989, p. 127 and 128) differed somewhat from Galileo's own discussion and analysis of scaling mechanics, and appeared to represent a scaling relationship intermediate between constant shape geometric "isometry" and the changing proportions of "static stress similarity", which Galileo suggested was necessary to preserve mechanical support function over large size changes. From more thorough analyses, McMahon described the consequences of this alternative scaling model, which he termed "Elastic Similarity" (1973, 1975; see also Chapter 8).

Giovanni Borelli (1608–1679) is noted for applying Galileo's principles of mechanics to the action of the musculoskeletal system – "*Borelli then shows what the forces of various muscles must be: for example, the force exerted by the biceps when a weight of 28 lbs is being held by the hand with the arm extended horizontally is 560 lbs*"

(Des Chene, 2005). Borelli's major contribution, *De Motu Animalium* (On the movement of animals, published posthumously in two parts in 1680 and 1681), is full of examples that would not be out of place in a modern introductory university course on musculoskeletal mechanics. Borelli worked on numerous problems in parallel with Newton, whose career and influence was rising toward the end of Borelli's life.

Although he studied planetary movement and pendular motion, Borelli never arrived at the conceptual formulation of gravity or the laws of motion that were some of Newton's greatest contributions. One of his most profound errors was to assert that, in some cases, forces were not "equal and opposite" but that, within the body, they could be unequal. However, he was extremely influential in describing the function of muscles, and also in his description of locomotion, particularly quadrupedal walking. With meticulous illustrations and well-founded arguments, Borelli was able to dispense with Aristotle's contention of diagonal-only foot contacts in quadrupedal walking, and was able to describe the features of balance associated with a stability tripod, as later championed by Sir James Gray (1944, 1968). The arguments were apparently convincing enough that the depiction of animal walking in sculpture and painting began to change following the publication of Borelli's book.

Another 17th century luminary was Claude Perrault (1613–1688). Like Borelli, he was instrumental in applying mechanical concepts to the action and organization of the musculoskeletal system. He introduced some important concepts, such as the spring-like capacity of muscles and joint position, representing the equilibrium between protagonist and antagonist muscles. Perrault also astutely observed that muscles function through "introduction of the spirituous substance brought by the nerves from the brain" (Des Chene, 2005).

As da Vinci had influenced thought and helped to initiate the Renaissance, Isaac Newton's (1643–1727) formulation of the laws of mechanics and the explicit role of gravity initiated a new era of enlightened modern science. Newton provided the theoretical framework with which to evaluate the role of the organic components of animal and human function in the physical world, within which they operate and from which their motions are influenced. Newton's Laws of Mechanics form the foundation of all modern biomechanics and find their way, at least in implied assumptions, into basically all modern work in the field.

1.4 THE ERA OF TECHNOLOGICAL OBSERVATION

With the beginning of the modern era and the application of novel technological advancements came the possibility of observing and quantitatively measuring aspects of human and animal movement that had previously not been available. Goiffon and Vincent (1779) are widely acknowledged as an important early example of applying technical evaluation to gait studies. A bell system was attached to the front hooves of horses, and the difference in ring pattern for different gaits was evaluated. As da Vinci's studies of motion and Borelli's descriptions of quadrupedal walking influenced the interpretation of how motion is shown in art, one stated purpose of the Goiffon and Vincent evaluation of the equine gait was to inform artists with regard to how the gaits of horses should be depicted in order to properly represent their actual motion.

In a conceptually parallel but more sophisticated approach, Marey (1884) used pneumatic bulbs attached to the feet of horses that operated an armature recording pressure changes on a smoked drum carried by a rider. From this apparatus, fairly accurate determinations of the foot contacts were documented for all of the standard equine gaits. Marey also applied a similar approach to the study of human locomotion. His work overlapped with that of Muybridge, and in his later career, he adopted photographic approaches originated by Muybridge and added to these by developing several novel technological innovations of his own – for instance, the photographic “rifle” (1892) and the development of modern-style multiple-frame “movies” (1899).

The ability to technically observe locomotion achieved a watershed point with the work of Muybridge (1887). Through the use of a series of shuttered still cameras operated by trip wires, Muybridge was able to produce high-quality serial still image photographs through the range of motions of a wide variety of human and animal activities. The motivation for this innovative approach apparently derives from his involvement in a bet regarding whether a trotting horse has any portion of its stride without contact with the ground. Settling this bet to the satisfaction of all involved required clear demonstration of the gait cycle, with adequate time resolution to indicate how the motions were produced.

Muybridge recognized that his novel technique provided a totally new perception of (and perspective on) movement. He produced a remarkable data set of images from as wide a variety of animal and human motion as he could manage. Included in these were figures of humans doing everyday tasks that, though composed of evenly timed separate images, resemble the “snap-shot” views drawn by da Vinci centuries previously. It is likely that da Vinci would have liked to produce the series as Muybridge had, if the technology had been available to him. Muybridge’s original compilation (Muybridge, 1887), ten volumes in total, has been reproduced in a variety of abridged editions that remain remarkably useful through to the current day (Hildebrand, 1962, 1989; Bertram and Gutmann, 2008).

Imaging motion yields a range of information about the process of locomotion, but the analysis of much of the mechanics is facilitated by also measuring the forces involved. Amar (1916, cited in Jarrett *et al.*, 1980) developed a mechanical force-reactive platform that had a great deal of early influence on the analysis of human locomotion, particularly in adapting technology to the needs of amputees returning from World War I. Elftmann (1934) later developed a reliable mechanical force platform system for human locomotion. Manter (1938), working with Elftmann, devised a multiple mechanical force plate system (two platforms in series) appropriate for analysis of quadrupedal locomotion, and used these to analyze the locomotion of the cat.

Gray (1944) recognized that Manter’s results indicated that horizontal forces generated by the limbs of quadrupeds create turning moments around the animal’s center of mass, which can ultimately influence the measured vertical forces at each foot. Due to the complications arising from redistributed forces in quadrupeds moving at non-steady speeds, in his highly influential 1968 compendium of animal locomotion mechanics, Gray advised stringent control of horizontal accelerations for quadrupedal gait analyses. Unfortunately, the difficulty in controlling animal motion meant that this advice was not always followed appropriately, and the “stringent” limits on speed

variation and acceleration became relaxed, as force platform analysis became more common with the commercial availability of strain gauges and piezoelectric sensors that formed the basis of electronic force plates (Cavagna *et al.*, 1963; Heglund, 1981; Biewener *et al.*, 1988). Just as Muybridge set the groundwork for the eventual application of high-speed imaging and cinematography in the study of locomotion, Manter's force plates played a similar role for the electronic analysis of force in quadrupedal locomotion (Roberts, 2005).

For human locomotion studies, Elftmann's force plate analyses (1934) set the stage for all who followed – and there were many, once electronic force plates and, even later, microcomputers, made digital management of data and analysis possible. Elftmann's innovations in understanding gait continued through the late 1960s, when he created novel investigative approaches. In 1966 he was the first to consider the metabolic cost of locomotion as a “surface” within gait parametric space – a perspective on the interaction between the physical processes of locomotion and the metabolic consequences that was ahead of its time.

1.5 PHYSIOLOGY AND MECHANICS OF TERRESTRIAL LOCOMOTION – COST AND CONSEQUENCES

Ancient man surely recognized that locomotion requires the investment of metabolic energy, and that this was the case even for constant speed movement on level ground. The reason that such motion is metabolically expensive is not obvious, though. Like a wheel moving across an even substrate, the motion of any mass perpendicular to the action of gravity should require very little energy to maintain motion once it has been established. Identifying the source of the cost of locomotion, however, is key in understanding what must be accomplished in order to produce locomotion. As Borelli famously observed, “*A perpetual law of nature consists of acting with the smallest work...*”. This statement implies that, if walking costs energy, the cost must be unavoidable. The question of “what about walking determines that it must cost?” formed the focus of much work in the early part of the 20th century.

A.V. Hill is renowned for his work on muscle mechanics and the formulation of a robust model describing the mechanical behavior of muscle (see Chapter 3). Hill (1927) originally assumed that the cost of locomotion came largely from the viscosity of muscular movement (this was known as the “viscoelastic” model of muscle; see Gasser and Hill, 1924). Hill's research group attempted to apply the results of their groundbreaking muscle experiments to whole-body behavior. Hill's group observed that walking and running on level ground appeared to require little mechanical work (although it did require substantial metabolic energy), “save that of air resistance” (Furusawa *et al.*, 1927). As a result, they suggested that, “*The whole of the mechanical energy liberated is used in overcoming the frictional resistance of the body itself, particularly the “viscosity” of the muscles*” (p. 32–33).

These ideas were very influential at the time and, in spite of much contrary evidence, they remained influential for decades following. For instance, Rashevsky mentions muscular viscosity in his analyses in 1948, “*Hence the inertial forces are not the limiting factor in determining ϕ* (where ϕ is the angle between limb axis and the substrate at

initial contact – editor’s comment), *and we must conclude, in agreement with A.V. Hill, that the viscous forces are the main source of resistance in continuous running.*” (Rashevsky, 1948, p. 20).

Early on, however, Fenn contended that Hill’s results did not entail a complete accounting of the mechanical work accomplished during walking and running. He explains the purpose of an important pair of papers on running: “*Hill, 1927, who has discussed in many valuable papers the problems connected with rapid movements of muscles has regarded frictional loss as the limiting factor in a fast run and as in fact the only item of considerable importance.*” (Fenn, 1930a, p. 584). Fenn’s conclusion was that a complete accounting of mechanical cost was necessary in order to determine how much metabolic “cost” remained to be explained by muscle “viscosity”.

Fenn and colleagues performed some meticulous studies of kinematics and kinetics that rival modern attempts, albeit with substantially less sophisticated (but nevertheless cleverly utilized) equipment. Working with CA Morrison of the Eastman Kodak Company, they performed kinematic analysis on human runners using images taken from the newly emerging technology of cine film. At that time, such cameras were driven by hand crank, which resulted in variable framing rates. Frame rate was precisely calculated from measurements of a falling croquet ball (consequently a known acceleration) included in the view. Kinematic measurements were taken from images at intervals of approximately 0.016 sec, or just over 60 Hz. Kinetic measurements were derived from a mechanical force platform styled after that developed by Amar (1916, 1919, 1920).

From these studies, Fenn (1930a) organized the mechanical work of locomotion into two measurable categories: “*The external work of running may be divided into two parts – 1, the movements of the limbs in relation to the center of gravity of the whole body and 2, movements of the whole body as represented by the movements of its center of gravity.*” (p. 433, Fenn, 1930b). These “movements of its center of gravity” are, of course, the subtle variations in height and forward speed that occur over the course of a normal stride – the “zig-zag” pattern recognized by Aristotle. Fenn also calculated that work against the drag of the air was not necessarily negligible, particularly for running. He concluded, however, that the production of what we now refer to as “internal” and “external” work (Cavagna and Kaneko, 1977) were responsible for the vast majority of mechanical “cost” incurred in locomotion.

Fenn’s early work was technically sound, but appears to have been ahead of its time, and the approach was really only explored fully beginning in the late 1950s. Some other early workers took a similar technical approach to make some valuable breakthroughs in understanding. Much like Hill and Fenn, Margaria was at the forefront of investigations into the function of muscle (Margaria *et al.*, 1933; Margaria and Edwards, 1934) that led to an interest in how those muscles functioned in locomotion. His monograph on investigations of locomotion cost (1938) stands as an example of considerable conceptual insight, but it was largely neglected by the English-speaking scientific world until the work was reviewed by Margaria himself in book form some decades later (Margaria, 1976).

With the advent of electronic, rather than mechanical, force plates (Cavagna *et al.*, 1963) and, following this, the development of computer-based analysis techniques, the types of analyses originated by Fenn could be done effectively for a wide variety of species (Jayes and Alexander, 1978; Heglund *et al.*, 1982; Biewener, 1983). Ultimately,

this led to the proposal that two fundamental mechanisms were responsible for limiting the cost of locomotion in animals that use legs to move across a substrate – namely, pendulum-like exchange of gravitational potential energy and kinetic energy of motion, and spring-like storage and return of kinetic energy through elastic strain energy in muscles and tendons (Cavagna *et al.*, 1977).

The approach formulated by Cavagna and colleagues has grown to be remarkably influential over the last four and a half decades, and forms the basis of much of the approach to the mechanics of animal locomotion currently in use. Due to this perspective, however, the field was turned toward an emphasis on the mechanisms available for energy *recovery*, and this came at the expense of clearly identifying the source of energy loss. It was, after all, the identification of the source of loss that motivated Fenn's original locomotion studies.

The determination of the mechanical work of locomotion for most of these studies is based on the assumption that mechanical work can be estimated as a function of the positive increases in total energy over an integral number of strides (complete gait cycles) – basically the approach utilized by Fenn. Blickhan and Full (1992) discuss some of the complexities involved with the assumptions on which such analyses are based. Donelan *et al.* (2002a) demonstrate that the standard use of the force plate to monitor center of mass motion underestimates the mechanical work done in human walking, because substantial work is done by one limb on the other during the transition between foot contacts. It is certain that a similar situation occurs for quadrupedal walking, albeit in an even more complicated manner, due to the potential for multiple interactions between limbs.

As influential as the internal and external work approach has been, there are some nagging inconsistencies generated from it and apparent paradoxes exposed. Human walking emerges with one of the greatest recovery levels measured (bested only by penguins – Griffin and Kram, 2000), and yet only reaches approximately 60–70% of the energy available to recover. This seems remarkably high to those who assume all kinetic energy must be lost, if not recovered, while others wonder why not higher? Quadrupeds universally appear rather poor at recovery, in the order of 35–50% (Cavagna *et al.*, 1977).

This type of analysis also appears to grossly underestimate the cost for larger mammals. For instance, “*The mechanical work rate of the horse exceeds the rate at which its muscles consume energy over its entire range of speeds, indicating that springs must supply the difference between energetic input and output.*” (Taylor, 1994). Producing more apparent mechanical work than metabolic energy consumed should raise concerns about breaching the Laws of Thermodynamics. As Taylor implies, however, it is routine to invoke elastic energy recovery to replace the unexplained mechanical cost with minimal metabolic investment. Elastically acting structures had been assumed for an extended period, and work such as the Camp and Smith (1942) treatise on the digital ligaments of the horse specifically characterized the properties of these structures in the context of the animal's locomotory capabilities.

Although elastic-like structures exist and have been shown to act as energy recovery systems (Thys *et al.*, 1972), it does not appear to be easy to identify structures in which the required quantity of energy storage and return is accomplished during locomotion. For instance, although substantial elastic energy storage has been anticipated in horse galloping, it has been remarkably difficult to identify elastic components operating in such a way in either the back (Alexander, 1988) or the distal limbs (Pfau *et al.*, 2006).

More recently, the concept of compliance as an integral feature of stability has also drawn substantial attention (McMahon, 1985; Geyer *et al.*, 2006; and see Chapter 7), where combined elastic-like and pendular features operate together to produce the mechanical features of even highly “pendular” gaits, such as that of the human walk.

1.6 COMPARATIVE STUDIES OF GAIT

Much of Gray’s analyses of mammalian locomotion utilized a variety of species as examples for fundamental mechanical concepts he meant to illustrate. His work, however, did not involve an attempt to classify mammalian locomotion comprehensively, but worked toward distinguishing the mechanisms that affected how general categories of animal types function. Gray had a great talent for cutting past the details of complex morphology to identify the mechanical factors that underlay the detailed design of an animal but, in order to accomplish this, it was necessary for him to neglect much of the anatomical detail of any given species.

The alternative approach is to organize the details of animal motion and, from the result, to identify the factors responsible for affecting the opportunities and limitations of each form. Howell (1944) produced one of the most complete early treatises on specializations of animals for speed. Within this work, Howell systematically described the gaits of mammals, with particular interest in what makes them move fast, or fast for long distances. An ultimate goal of this work was to determine the phylogenetic relationship of locomotion types and, to this end, the work was ahead of its time. Unfortunately, key analytic techniques were not available at that time, so much of the classification depended on subjective determinations. The wealth of information in Howell’s work, however, has meant that it receives continued reference (Biewener, 1983; Gatesy and Middleton, 1997; Griffin *et al.*, 2004).

Hildebrand (1965, 1977) revolutionized gait studies by developing a systematic classification of gaits that quantified not only foot placement, as had been done previously (Marey, 1873; Howell, 1944), but also phase relationships and contact timing features between limbs. His most useful formulation of this defined the gait of mammals on the basis of two independent features – the percentage of the complete stride that a selected foot is in contact with the ground, and the interval that a forelimb follows the hind limb placement. In this way, fundamental gaits emerged from the gait formula (Figure 1.2), and it was possible to easily compare the gaits of many different quadrupedal species (see Chapter 2). Although this classification has been instrumental in comparing gaits of different forms, it does not involve any functional or mechanical explanations for the patterns observed.

Gambaryan (1974) collected a substantial amount of material available from comparative biomechanical and anatomical analyses, and organized it according to phylogenetic relationships. This monograph represented a compilation of both understanding that had been generated in the English-speaking literature, of which Gambaryan was aware, and a large and independent Russian-speaking literature, of which the English speaking scientific world appeared largely unaware. Although many of the gait classifications have been regarded as somewhat arcane (does anyone refer to a dorsostable dilocomotory gait?), the work remains one of the most comprehensive collections of detailed morphology related to mammalian locomotion.

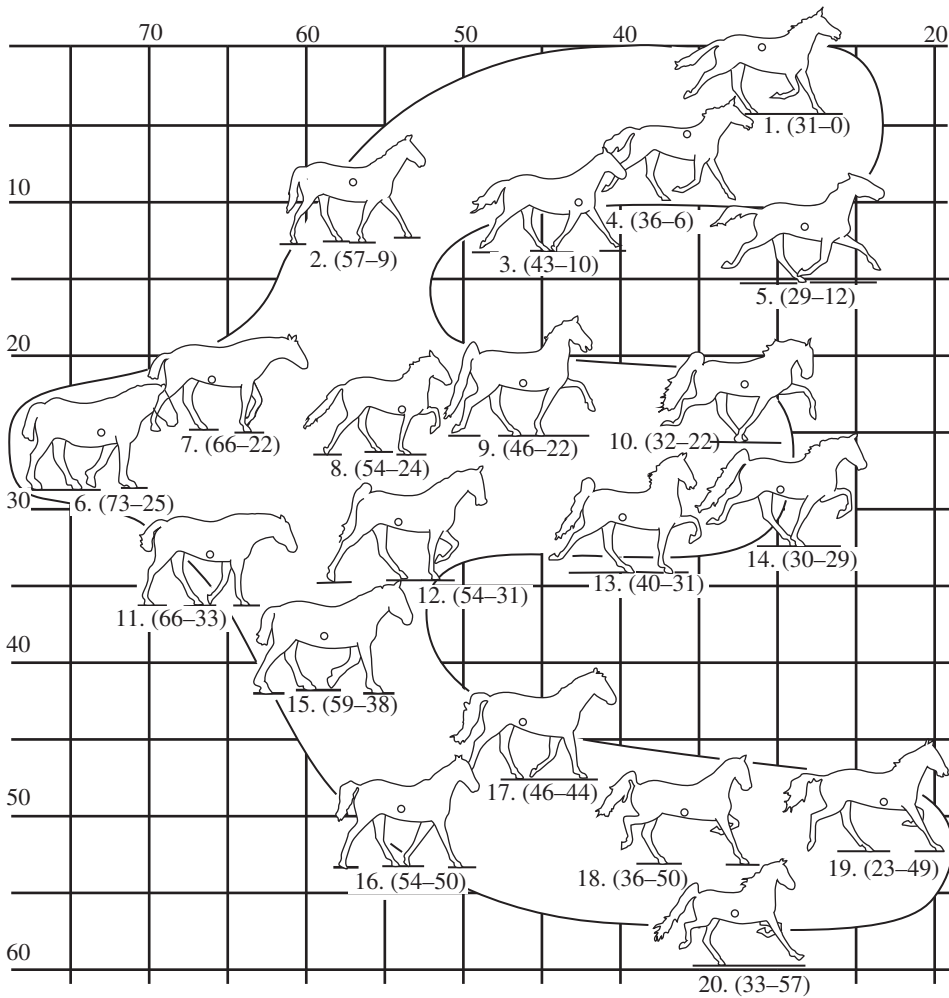


FIGURE 1.2

A “Hildebrand plot” of the symmetrical gaits utilized by horses (Hildebrand, 1965). By comparing the proportion of the stride that each hind foot was on the ground (x axis) with the proportion of the stride interval that the forefoot contact followed hind foot contact on that side (y axis) a distinct pattern of gait forms emerged. In this plot, the gait formulae, as determined by these two proportions, are listed for each of the small circles. The silhouette of the animal representing each gait form at the time of rear foot contact is also shown.

Although CJ Pennycuick has been better known for his work with bird flight, he also made important contributions to the documenting and analysis of ungulate gait. In the inimitable manner of those leaders in the field, such as Gray, Hildebrand and Alexander, Pennycuick (1975) was able to simplify the analysis of complex gait patterns to focus on functional features that had key importance in the production of effective locomotion.

He suggested that only three fundamental gaits should be recognized: walk, trot, and canter (where the gallop is simply a fast form of canter, and bounds and half-bounds are canter-like gaits with one or both limb pairs contacting together, rather than distributed in time). It was suggested that these gaits should be distinguished on the basis of:

- a. the symmetry or otherwise of the stepping pattern;
- b. the range of average foot contact over the gait; and
- c. the nature of the energy transformations which occur at each step.

This latter was a departure from gait classifications that had predominated previously, where the motions were described but the mechanics, and energetics, were left largely unexplained. The work of Cavagna and others that followed, such as that of Gray, Alexander and Pennycuik, set the stage for returning to the rigorous mechanical analyses originated by Fenn some 50 years earlier.

Although the locomotion of small mammals was treated in the major monographs such as those of Howell and Gambaryan, most research attention has been paid to gaits of the larger mammals. To some extent, this can be attributed to attention garnered by the impressive abilities in terms of speed or endurance of these animals, or because key domestic species, such as the dog and horse, are readily trainable. The horse, in particular, has long been integrated in human civilization and important to commerce. When considering mammalian locomotion, it is natural to turn to models that are convenient and familiar and, thus, a great deal is known about canine, feline and equine locomotion. However, the vast majority of mammals are small and are more or less adapted to locomotion that does not necessarily involve high speed (see Chapter 10), or even steady speed running (see Chapter 11).

After establishing a dependable method for documenting and distinguishing limb motion in the various gaits, Hildebrand recognized that the dynamics of the swing limb could be a major influence on stride frequency. Stride frequency and its relationship to limb length was recognized as an important component of the gait diagrams he had developed. Thus, swing limb dynamics were one way of adding mechanical explanations to the gait descriptions (quantified via the diagrams) that he had developed. He also recognized that to drive the limb at frequencies that differed substantially from their natural swing period could require large and undesirable energetic expense. From there, he hypothesized that this may be influential in morphological differences in distal limb form (Hildebrand, 1985).

Although these theories are basically sound, the predictions met with some problems when tested specifically. Taylor *et al.* (1974) compared cheetahs, gazelles and goats and found that the metabolic cost of locomotion did not match the expectations of reduced moment of inertia in the distal limb. This is most likely because swing limb mechanics are only one portion of the energetic determinants in locomotion. However, the idea of integrating motion with the passive mechanical swing of the limb did point to a perspective of optimizing swing limb dynamics. This, ultimately, led to the ballistic model of human leg swing (Mochon and McMahon, 1980a, 1980b (again challenged experimentally; Mena *et al.*, 1981; Selles *et al.*, 2001) and has found its way into aspects of numerous mechanical models of bipedal (McGeer, 1990a; Garcia *et al.*, 1998; Collins *et al.*, 2001) and quadrupedal locomotion (Herr and McMahon, 2000, 2001).

1.6 RE-INTERPRETING THE MECHANICS: A FORK IN THE ROAD, OR SIMPLY SEEING THE OTHER SIDE OF THE COIN?

I pointed out above that much of the focus of comparative locomotion mechanics and energetics has been drawn to the consideration of mechanisms for passive and near-passive *energy recovery*. This is accomplished either through the exchange of gravitational potential energy with kinetic energy, emulating pendulum-like exchange, or through strain energy exchange with kinetic energy, as in the bouncing of a spring-mass system. In contrast, the investigation of bird flight energetics progressed in a substantially different conceptual direction, and one that might provide an interesting alternative for terrestrial locomotion.

Although comparable fluctuations in the vertical position of the center of mass (CoM) and multidirectional velocities occur during flapping flight, the consideration of energy recovery was not emphasized in the analysis of flight (although some exchange occurs). Instead, the focus remained, as it had started in legged locomotion with Hill and Fenn, on identifying the source of the *energetic costs* involved, as determined by the dissipative mechanisms responsible for energy loss to the environment in which the organism functions (Raspel, 1960). The analysis of flight then progressed to determining what features of the morphology and activity replaced the associated losses (Tucker, 1973). In the case of flight, the basic dissipative mechanisms can be readily identified as the modes of drag that result from the dynamic interaction of the organism with its aerial environment, and those actively generated by the production of lift. One possible reason that the analysis of terrestrial locomotion did not progress along the same lines as that of flight might be that identifying the source of cost is not necessarily as intuitive for legged locomotion (Bertram *et al.*, 2006; Kuo, 2007).

As mentioned above, Hill's original viscous muscular loss was replaced by mechanical considerations related to inertial motions of the body and its components. However, these, in turn, led to conclusions that required remarkably effective energy exchange mechanisms, particularly for larger running mammals. Is effective recovery the key to understanding the mechanical consequences of adaptive form and behavior in locomotion? Has the source of cost, the fundamental dissipative mechanism, been identified for terrestrial locomotion? There are currently two main factors that are viewed as the "source" of cost in legged locomotion. That is, two mechanisms are identified as the cause of the main dissipation when moving on limbs – one biological, and the other physical. As will be seen, both have long histories in locomotion analysis, and ultimately they may well be intimately related.

1.7 THE BIOLOGICAL SOURCE OF COST

It has long been recognized that positive work had to be produced by the musculature to raise the body against gravity and to accelerate the limbs, and also that the momentum of the body and its components could do work "on" the muscles through stretching them while they actively attempted to contract. This latter reversed, or negative, work could be demonstrated, but was essentially lost because, except for stretching elastic elements, it could not be utilized further in locomotion. That is, it could only be

converted to heat and lost from the system. Thus, the biological cost of locomotion, the route through which metabolic resources were converted to active locomotion, had two main components: the generation of positive work within the muscles in the process of accelerating the body and its parts; and the negative work involved with decelerating those components.

Although positive and negative work, and their relative metabolic cost, had been recognized at the level of the muscle fiber (Fenn, 1924), Margaria was one of the first to demonstrate that such cellular mechanisms had a direct influence on whole-body metabolic cost in locomotion, by showing that the apparent efficiency of uphill and downhill walking and running asymptote to the same efficiency limits as single muscle fibers (0.25 for positive and -1.2 for negative work; Margaria, 1938, 1963). Margaria (1976) recognized the value of passive energy exchange, whether the gravitational E_p-E_k exchange in walking or the strain E_p-E_k exchange in running.

However, he also recognized that these models did not fully account for the losses involved in locomotion – what Margaria termed “wasted” mechanical work (p. 103): *“The resistance to progression can therefore be considered as substantially due to the negative work that is performed at each step in walking and running; to maintain a constant speed of progression this must be compensated by an equal amount of positive work.”* (p. 101); *“... the “resistance” met by the subject when walking or running on the level appears to be essentially met by the negative work that is performed at each step which must be compensated by an equal amount of positive work in the first phase of the following step: practically all the energy spent in walking and running on the level is utilized to meet this resistance.”* (p. 105). He also concluded that, at specific slopes, little negative work is actually performed (p. 104).

However, if one important driving force in the “design” of natural systems is limiting metabolic energy expenditure, as the energy recovery models suggest and as Borelli anticipated nearly 400 years ago, we have to wonder at the required “cost” of negative work. Is this a limitation (or flaw in the design) of the muscular system, or something physically required for legged locomotion? That muscles should use metabolic energy to absorb mechanical work was taken as a given until very recently.

1.8 THE PHYSICAL SOURCE OF COST [WITH BIOLOGICAL CONSEQUENCES] — THE ROAD LESS TRAVELED

It appears to have come as some surprise to early investigators, utilizing force plates to study the physical interaction of the limb with the ground during locomotion, that contact involved a horizontal deceleration in the first half of contact, followed by a re-acceleration in the following portion of the contact. However, we now know that this is a necessary consequence of transferring contact between limbs for steps of functional length. In other words, steps of a reasonable length will require that the falling mass of the individual be redirected by the next contact limb, and this requires an impulse with a component in the rearward direction that allows the body mass to “vault” over the limb. The deceleration that occurs in the first half of contact is where negative work is almost exclusively performed. If such forces are “required”, then what are the consequences and, if there are consequences, how can such a contact be “optimized”?

Nicolas Rashevsky is well known as a key figure in developing mathematical biology – the application of mathematical modeling to a diverse range of questions in biology. Although his interests ventured into most areas of biology, he appeared intrigued by the mechanics of locomotion, publishing a number of papers on the topic (Rashevsky, 1944, 1946, 1948). Rashevsky was a physicist with an interest in applications to biology, and his work is renowned for being both insightful and almost entirely theoretical. This may explain why his locomotion analyses were met with some resistance (or neglect) by experimental biologists. He remained convinced that Hill's viscous muscle cost was an important consideration and, following Fenn's approach, he attempted to calculate what viscous damping "must" be by estimating the other important mechanical costs associated with locomotion. He concluded that only the hind limbs were really necessary for locomotion (possibly as a precursor to arguments he intended regarding the processes through which humans developed bipedalism). He concluded that quadrupedalism must exist for alternative reasons (what these might be he did not specify, but he implied that they would not be for generating thrust).

Rashevsky's analysis of limbed locomotion is best known from discussions published in the first part of his two-volume treatise on mathematical biology (Rashevsky, 1960, 1961). Although this work has been highly influential in many areas of biology, the implications of his ideas on limb function appear to have had marginal influence on thinking regarding animal locomotion. His discussions of running and jumping evolved over time. His 1948 analysis, largely reiterated in the 1960 volume, included a novel cost that did not appear in his very early models. This newly considered "cost" was the loss of momentum and, consequently, energy that results from the deflection of the animal's center of mass trajectory when the limb makes contact with the substrate (p. 266, 1960).

The first statement of this approach to the problem appears as, "*Running is essentially a series of consecutive jumps. During each jump the animal is for a while completely without contact with the ground, its center of gravity describing a parabola during the 'flight' phase. If at the end of each jump the total kinetic energy of the animal were completely lost, then the mechanism of running would be identical with the mechanism of jumping. Actually only a fraction of the total kinetic energy is lost at the end of each 'flight' phase. Therefore the theory of continuous running is somewhat different from the theory of jumping.*" (p. 12, 1948).

This conclusion followed from the dynamics of interacting bodies, and indicates that Rashevsky treated the contact of the limbs and their influence on the center of mass trajectory as a rigid body collision (since this particular analysis did not include spring-like strain energy storage and return). Rashevsky simplified his model by having the limb make contact directly under the center of mass, thus limiting the collision loss to the vertical direction: "*During the 'flight' stage either the extremity which caused the propulsion or another one swings forward, hitting the ground when the body falls downward at the end of the parabolic flight phase. For simplicity let us consider the case in which the extremity hits the ground in such a position that (a line between the foot contact and the animal's center of mass – editor's comment) is vertical at the moment of impact. In this case only the vertical component of the velocity is lost or, at any rate, affected.*" (for a more complete explanation of collision dynamics in the context of legged locomotion see Chapter 5).

It was possibly this simplifying assumption restricting the effect to vertical motion, and the unrealistic contact configuration, that caused this feature of the mechanics of limb locomotion to be neglected by the biological field – or possibly it was that Rashevsky did not explicitly describe this feature of the model, or discuss its importance for locomotion energetics (instead, he went on to discuss its implication to the form of limbs and the calculation of ultimate running speed). In any case, the vertical loss Rashevsky alluded to results from momentum and energy loss associated with deflecting the center of mass trajectory as a result of limb contact. It is determined by the physical interactions of the body with its substrate, and does not depend on functional properties of the musculoskeletal system, such as the metabolic cost of negative work (although negative work is one mechanism through which this loss can occur).

MG Bekker's 1956 book *The Theory of Land Locomotion* has had a great deal of influence on vehicular design, particularly for battlefield military transport, but also for vehicles as far afield and specialized as the "lunar rover" moon transport vehicle (Bekker, 1985). The first chapter of his 1956 book, however, is dedicated to discussing general features of legged locomotion, with particular reference to the principles affecting animal locomotion. Bekker followed Rashevsky's general approach, albeit in a more realistic formulation, and utilized a momentum-balance, collision-based approach to determine where the physical loss in the system originated. Although his work has been influential in vehicular design, this approach has largely gone neglected in the biological consideration of the mechanics of locomotion until quite recently.

VA Tucker, more renowned for contributions to flight physiology than terrestrial locomotion, recognized that walking and running were apparently highly inefficient modes of transportation, compared to swimming or flying. Having dealt effectively with the physiology of flying (Tucker, 1973), he recognized that substantially different constraints accounted for the "costs" associated with legged locomotion. Identifying logically that the metabolic cost of negative work in the muscles accounts for much of this apparent inefficiency, Tucker (1975) proposed that a system that eliminated the motivation to have the limb deflect the CoM at contact would avoid this important source of locomotion cost.

Tucker proposed that, to avoid such loss, the system, "...*applies force to the center of mass at right angles to its direction of motion. No work is done to change the velocity, for work is the product of a force and a displacement that are parallel to one another. When the force is at right angles to the displacement, the muscles that supply the force can neither do work nor have work done on them. The result is that the body is accelerated – that is, its velocity is changed to a new direction – at no expense for muscular work.*" (Tucker, 1975 p. 418). This perspective led him to suggest some interesting devices that would not have this loss, and to propose that bouncing was quite possible without the assistance of strain energy storage and return.

Just as Gray had begun with an analysis of fish form and locomotion, R McNeill Alexander acquired his initial interest in comparative morphology from working on a variety of aquatic forms. This changed during the 1960s to a more and more terrestrial perspective, and his work eventually became remarkably influential in modern human, animal and even legged robot research. This can be attributed largely to his approach which, again much like Gray, sought to find the fundamental mechanical factors that

influenced form and performance. Alexander's work is characterized by relatively simple experiments that validate propositions based on stringent theoretical foundations, and is directed more to opening entire new directions of investigation, rather than meticulously documenting all aspects of each such system.

Although Alexander worked on a myriad of questions and structures in biology, his contributions to locomotion are defined by two basic directions of inquiry. The first is the analysis of form in (largely) musculoskeletal structures, including skeletal proportions (Alexander *et al.*, 1979), and the role of elastically behaving structures in locomotion (Alexander and Bennet-Clark, 1977). He also developed models of walking and running, working from basic mechanical principles. To both of these areas, a key feature of his approach was to develop optimization models through the identification of the key competing factors affecting the performance of the system.

Of particular importance in the consideration of the mechanics governing legged locomotion is a set of models of bipedal walking and running that were able to predict many aspects of human locomotion performance (Alexander, 1976). One main feature of these models was the consideration of kinetic energy loss associated with diverting the center of mass velocity vector at foot contact: "*The part $1/2mu_b^2$ of the kinetic energy* (referring to the horizontal component of the kinetic energy – editor's comment) *is carried over to the next step but the part $1/2mv_b^2$* (referring to the vertical kinetic energy – editor's comment) *is absorbed by the muscles as the descent is halted, and has to be replaced by work done by the muscles which give the center of mass the vertical component of velocity + v_b needed to start the next step.*" (Alexander, 1976, p. 494).

In this analysis, Alexander assumed that the angles with which the limb moved while on the ground were conveniently small, so the characterization of the loss as basically vertical, and the remaining kinetic energy as horizontal, are reasonably close. However, the component of the kinetic energy lost would actually be that in line with the axis of the new stance limb, having both horizontal and vertical components, and what remains would be the component perpendicular to the new stance limb (Garcia *et al.*, 1998; Donelan *et al.*, 2002b; Ruina *et al.*, 2005). In the model, Alexander associated the energy loss with the momentum of the body doing negative work on the muscles of the limb. This was in spite of the fact that the simple model in which this concept was introduced did not have a jointed limb in which negative work could be absorbed. Rather, the model identified this loss as a consequence of the geometry involved in diverting the travel of the center of mass. Although muscular absorption of work is a realistic mechanism, the loss dictated by the model originates with the dynamics of the supporting limb's deflection of the center of mass of the organism (see also Chapters 5 and 6).

As discussed above, Margaria (1976) attributed the cyclical losses involved in locomotion to negative work within the muscles. However, he also noted that force applied down the axis of the limb is the ultimate source of the work that must be actively absorbed by the muscles, and that such forces come from the geometry of the limb contact and the center of mass (as also described by Rashevsky, 1948, 1960; Bekker, 1956; Alexander, 1976). Margaria recognized that the horizontal component of the contact is involved with generating the horizontal deceleration, and that this would decrease the horizontal kinetic energy of the moving body. Likewise, the vertical component of the contact indicated loss in the vertical direction.

However, he did not expressly state that this implied that the component perpendicular to the contact strut (at right angles to the limb, as described by Tucker, 1975) was unaffected by the contact and would remain (leaving some portion of both vertically and horizontally oriented momentum to assist in the re-lifting the body in the next step): “*The negative work performed at each step is substantially that caused by the deceleration of the body when the forward foot strikes the ground.*” (p. 105). Margaria, as Rashevsky had done previously, discussed the consequences of quadrupedal gait, suggesting that quadrupedalism had substantial disadvantages (p. 108). However, this conclusion depends on assumptions about the distribution of the body mass between limbs and the costs of other factors, such as stability.

Although Cavagna and colleagues (1976, 1977) influenced the direction of the field toward a focus on the mechanisms of energy recovery, they were aware of the mechanical energy loss that results from contact of the new stance limb and its redirection of the center of mass path. Citing Alexander’s 1976 bipedal model, this group noted, “*In the simplest inverted pendulum system which has been used to characterize walking – the stiff-legged walk of Alexander (1) – E_{kv} (where E_{kv} is the vertical kinetic energy – editor’s comment) would be lost from the system in each step when the front foot hits the ground and the transfer of kinetic energy into gravitational potential energy could only take place between E_{kf} (referring to kinetic energy of forward motion – editor’s comment) and E_p (referring to potential energy – editor’s comment).*” (Cavagna *et al.*, 1977, pp. R245 and 246).

Thus, Cavagna *et al.* (1977) recognized that it was likely that energetic complexities existed during the transition between supporting limbs. However, they elected to focus on the novel and physically compelling recovery mechanisms that they had identified. Due to this logically reasoned and extremely influential paper, the entire field was drawn away from the concept of energy loss at the transition, and drawn to the concept of identifying the proportion of mechanical energy recovered within the stride cycle. From this, the focus turned toward analyzing the morphological and behavioral adaptations available to allow for optimum recovery. Implicit in this approach, however, is the assumption that all available energy would be lost if specific strategies for recovery were not implemented – contrary to the implications of Alexander’s analysis (or Bekker or Rashevsky).

Cavagna *et al.* (1977) was remarkably influential in the area of comparative mechanics of legged locomotion. Originating largely from the influence of this one paper, the concept of physically determined dissipative loss seems to have been neglected following its publication. Many factors combine to influence the focus of a field, but it is interesting to note that the key acknowledgement of the geometry associated with determining this aspect of loss (the relationship between ground reaction force generated by limb contact and the path of the CoM), as described by Alexander’s model (and quoted above), comes in a sentence that is split between pages, with a large, important and complex figure intervening between the two halves of the sentence.

Is it possible that such a distracting presentation of a key sentence in an influential paper, due only to the serendipity of typesetting limitations, could have contributed to downplaying the importance of the concept and led to its neglect by almost the entire field? Certainly, it did not help to direct attention to this potentially important, but admittedly unintuitive, alternate perspective. On the other hand, it may have been inevitable that the field was drawn in different directions by the complexity of the

issue of loss and recovery. The potential confusion is apparent if one considers a wheel: is the wheel a mechanically effective system because it has near perfect recovery or inconsequential loss?

McGeer (1990a, 1990b) recognized that inverted-pendular motion of a mass on a supporting limb could be added to McMahon's ballistic swing limb model (Mochon and McMahon, 1980a, 1980b). By further recognizing that the main source of loss in this system comes from the inevitable mechanical energy losses that occur when the center of mass path is diverted from one support limb to the next, McGeer was able to optimize the system to minimize this loss. Thus, he created a passive dynamic "pseudo-bipedal" walking machine with knees and feet. Note that this was by no means the first passive dynamic walking machine, as there had been such toys available for over 100 years (Fallis, 1888). However, none of these had knees, and none depended on dynamic stability (i.e., the McGeer walker was only stable while moving, and it was essentially unable to stand when not moving).

The original McGeer walker was dynamically stable only in the forward-rearward direction. Lateral stabilization was artificially engineered by having laterally paired legs that provided a wide base of support to prevent sideways pitching. Although it only had two "feet", it was a functional "biped" in only two dimensions. However, this did demonstrate that forward-rearward passive stabilization was not particularly difficult in motion.

Ruina and colleagues refined the McGeer walker to become a truly passive dynamic biped (Figure 1.3; Collins *et al.*, 2001). They then added simple actuators to demonstrate that powered walking with a minimal system was possible (Collins *et al.*, 2005).

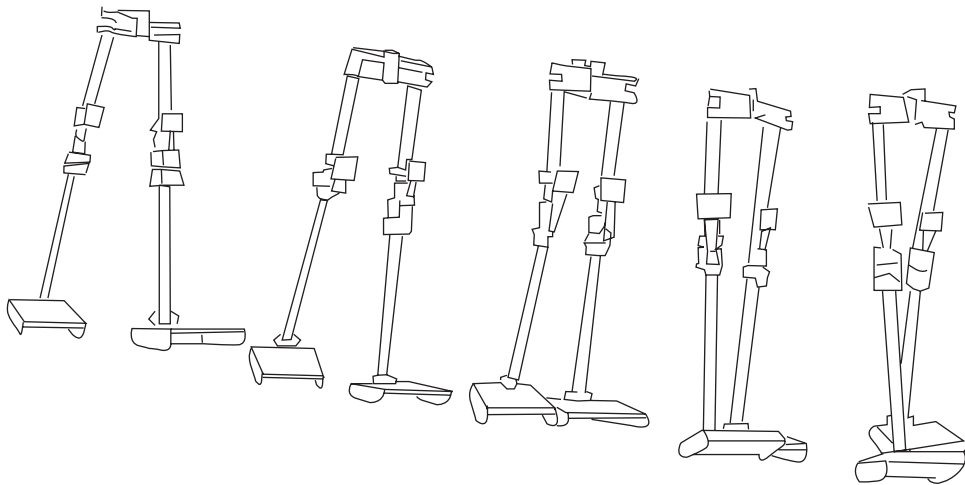


FIGURE 1.3

Tracing of a passive dynamic walking robot. This machine is composed of two legs, each with knees and a shaped foot. It has no motors or control, but "walks" down a shallow slope powered by gravity. Many characteristics of human walking are spontaneously generated by this machine, including pelvic tilt and rotation and the turning motion of the stance foot during mid to late stance (from a video supplied by A. Ruina).

Interestingly, the proportions that make the system work well are eerily similar to those of a bipedal human (McGeer, 1993). This observation raises the question of whether human proportions might be fundamentally based on exploiting subtle mechanical opportunities for energy conservation and control that had not previously been appreciated.

Smith and Berkemeier (1997) applied a similar passive dynamic approach to quadrupedal locomotion, using a very simple model, with some interesting and unexpected results (see discussion of this model in Chapter 6). For instance, their analysis suggests that many aspects of bipedal and quadrupedal walking are similar, though quadrupedal walking should be *more* efficient than bipedal (contrary to Margaria’s expectation). However, the quadrupedal system appears naturally unstable with respect to the phase relationship between limbs. If verified, we might anticipate that such phase instability would have to be actively determined – for instance, through a neural cycling system like the central pattern generator. At this time, quadrupedal passive dynamics has not been thoroughly or explicitly analyzed, largely because the addition of a second pair of limbs substantially increases the complexity of dynamic interactions of the components of the system (trunk, limbs, etc.) and the substrate. However, this remains one of the more compelling current questions in mammalian locomotion.

The successive contacts of the limbs are analogous to the contact of spokes of a rimless wheel (McGeer, 1993, p. 280). Even though passive dynamic walking machines are fairly recent in origin, the analogy of the rimless wheel has quite a long history. Although not explicitly described, the “zig-zag” motion of Aristotle derives from the limbs acting as spokes of a wheel. This analogy was explicitly indicated by Gray (1959), Margaria (1976) and McGeer (1993) (Figure 1.4). The rimless wheel is the simplest depiction of the substrate interactions of the contacting support limb, while neglecting any aspects of swing limb mechanics. Though simple, it has formed the

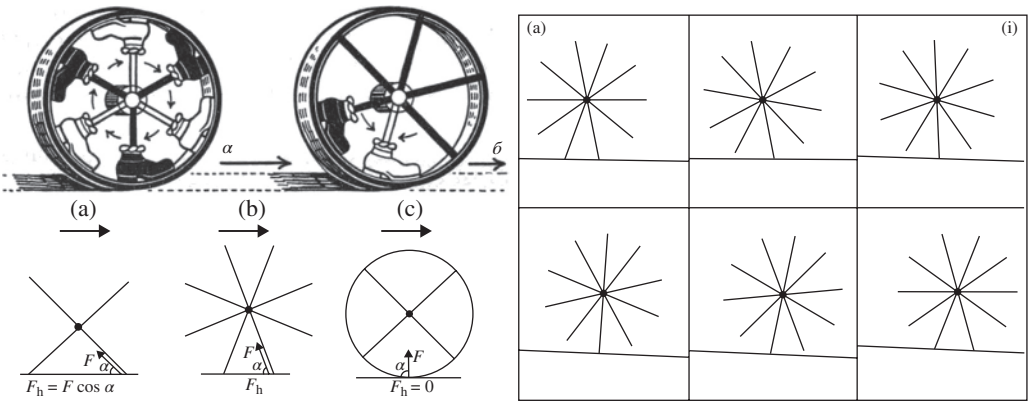


FIGURE 1.4

Some examples of using the rimless wheel as a starting point for analyzing the dynamics of bipedal locomotion. Above left: illustration from Gray (1959, p. 19). Bottom left: illustration from Margaria (1976, p. 106). Right: a portion of an illustration from McGeer (1993, p. 280).

starting point of a new set of analytic models of limbed locomotion (Alexander, 1976; Garcia *et al.*, 1998; Smith and Berkemeier, 1997). Implicit in these models is the assertion that the contact dynamics makes up an important (critical?) component of the mechanical interaction of legged locomotion. Unfortunately, this aspect of the mechanics appears to have been largely neglected until recently, and we currently await explicit application of these ideas to the analysis of limb function and the consequences of their form on determining animal performance and energetics.

1.9 CONCLUSIONS

It is likely that transfer between energy types – be it pendular, elastic, or the relatively under-investigated rotational kinetic energy – plays a substantial role in the economical production of locomotion and the provision of stability. However, it is also likely that dissipative effects of contact dynamics also play a role in determining how mammalian systems best utilize their opportunities for moving in the terrestrial environment. Yet to be determined are the relative contributions of dissipative and recovery components, and how these opportunities are provided for by specific behavioral and morphological “strategies”. Currently, the implications of each are not well understood, largely because most analyses have not recognized that loss and recovery might be integrated in non-intuitive ways.

In briefly reviewing the history of animal locomotion studies, I have neglected a great deal of very important and insightful work that has been done on specific features of the musculoskeletal system, including such issues as muscle chains of the limbs or trunk, connective tissues and their properties, joint function and the relationships between all of these. However, such detailed information only leads to general understanding of the organism, its functional abilities and constraints, when it is appropriately placed within the context of an understanding of the system of which it is a part. At this juncture, it is not certain that the system as a whole, even modeled at a simplistic level, is properly understood. It is hoped that the chapters of this volume will help to stimulate the discussion that will put such information in the context it deserves.

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