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## Musculoskeletal Dynamics in Rhythmic Systems: A Comparative Approach to Legged Locomotion

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### 1 Introduction

#### 1.1 Advantage of Rhythmic Systems

The challenge to integrate neural control with musculoskeletal dynamics has and will continue to benefit from the study of rhythmic systems. Rhythmic systems offer at least two major advantages over systems that are episodic, discontinuous or ballistic. First, experiments on individual organisms which manipulate a single variable—*direct experiments*—can be more conclusive because differences in continuous, patterned outputs are often easier to discern (Figure 13.1). Second, rhythmic systems are ubiquitous in nature. Fliers, swimmers and runners cycle their bodies and appendages at frequencies that range from less than 1 cycle per second in the largest animals such as whales to as high as 1000 Hz in flying insects. The extraordinary pervasiveness of rhythmic systems allows us to conduct *natural experiments* on choice animals by using the comparative method (Figure 13.1). By choice animals, we mean the ones most amenable to a particular experimental procedure. The giant squid axon and the robust gastrocnemius muscle of frogs are notable examples. August Krogh said it best in 1929 at the 13th International Congress of Physiology in Boston: “For many problems there is an animal on which it can be most conveniently studied” (Krebs 1975). By the comparative method or natural experiment, we mean the process of inferring function by comparing two or preferably more species that differ in the variable of interest due to evolutionary history as opposed to an experimenter’s procedure.

#### 1.2 Advantage of the Comparative Method

The advantage of natural experiments is substantial. Comparing systems that have evolved over millions of years can result in enormous differences in variables of interest. Organismal diversity can enable discovery. Comparing systems which differ naturally can avoid the disruption in function to a finely integrated system that can result from direct experimental perturbations pushed too far in search of a significant difference. For example, the metabolic cost of locomotion often varies by much less than ten-fold when speed, stride frequency, inclines or added loads are altered in individuals, whereas cost naturally differs by over five orders of magnitude when all legged animals are compared. Large variation in dependent variables found in natural systems permits isolation and investigation of processes of interest in nearly an ideal setting—one of exaggerated function in a normally operating system. Large differences in function are associated with differences in body mass, environmental extremes, and lifestyles. Fortunately, variation in dependent variables shows remarkably general patterns and correlations which can be used to infer function and predict performance in animals not yet studied. Equally important, however, are those systems that demonstrate spectacular performance and deviate from the general pattern. Characterization of these specialized systems can allow extrapolation to other systems in which the properties of interest are not present in the extreme, but in which the principles of function are the same.

## Experimental Approaches

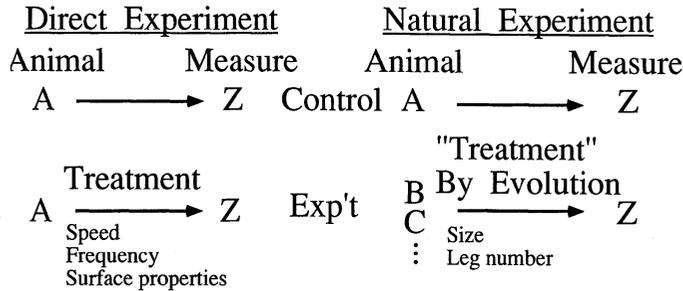


FIGURE 13.1. Comparative method. Direct experiments with imposed treatments and tight controls are most effective at establishing cause and effect. Natural experiments compare species that differ by the "treatment" variable because of evolution. With a comparative ap-

proach, large differences can be measured among species in a naturally operating system unperturbed by the investigator. Natural experiments may be less controlled because variables other than those of interest may also differ among species.

For example, hopping red kangaroos can increase speed without an increase in metabolic energy cost (Dawson and Taylor 1973). Further examination provided evidence of elastic strain energy storage in the tendons of kangaroo leg muscles (Alexander and Vernon 1975; Alexander 1988; Biewener and Baudinette 1995). It is reasonable to conclude, at least in large vertebrates such as humans, that tendons serve a similar role, albeit to a lesser extent than in specialized, bipedal hoppers.

By using a phylogenetic approach with three or more species, the effects of history can be examined. Although powerful, the comparative method is best used in conjunction with a knowledge of evolutionary history or phylogeny (Huey 1987; Garland and Adolph 1994). The reason is simple. Natural experiments can be viewed as imperfect because they may lack an appropriate control. Seldom do the species being compared differ only by the variable of interest. The ideal comparison—very closely related species possessing a large difference in the process being studied—is rare. Fortunately, recently developed techniques in phylogenetic analysis (Felsenstein 1985; Garland et al. 1992) offer a tool to remove the effects of history or use them to hint at present function. If the process of interest has severe functional/structural constraints or complete adaptation has taken place, then the potentially confounding effects of historical differences may be of little consequence. If, however, functional constraint and adaptation have been less than com-

pletely dominant, then the most parsimonious assumption is that the process should operate as it did in the ancestor.

Adopting the comparative method has made it possible to use a three pronged approach toward integrating neural control with musculoskeletal dynamics. The *forward dynamics* approach has emphasized circuit breaking in animals such as arthropods (see Chapter 16), lamprey (Chapter 15), and annelids (see Chapter 14). Fundamental neural control principles, which include central pattern generation and parallel, distributed control, have been derived from animals that exhibit rhythmic behavior. Musculoskeletal *system identification* techniques are finally allowing the characterization of muscle function under stimulation and strain conditions actually found during rhythmic behavior. One such approach is termed musculoskeletal work-loop analyses (Josephson 1985). Lastly, the mechanical behavior of the complete rhythmic system can be characterized first by using an *inverse dynamics* approach. For each approach, we advocate both direct experimental manipulations in close coordination with modeling which employs extensive sensitivity analyses.

The present perspective focuses on an inverse dynamics approach for several reasons. First, it argues for a broader view of the plant—the musculoskeletal system. Second, it illustrates the utility of the comparative approach. Third, it demonstrates how a simple model of the musculoskeletal system can be used as a starting point to limit the possible ways in which legs function.

### 1.3 Control Offered by the Musculoskeletal System

The rigid characterization of the controller as the central and sensory neural networks and the plant as the musculoskeletal system is artificial and counterproductive for several reasons (Zajac and Gordon 1989). First, the information flow among neural and musculoskeletal units is closed loop, not unidirectional. Joint and muscle sensors feed back information about limb and body position, velocity and force. In a way, feedback makes the musculoskeletal system act as the controller and the neural system function as the plant. Second, feedback can occur within the musculoskeletal system itself where joint position and velocity can determine musculoskeletal dynamics (i.e., reflexes of Brown and Loeb in Chapter 10). Moreover, joint angle can affect joint geometry by altering moment arms which, in turn, affect joint dynamics through torque development.

The third and most important reason for not characterizing the musculoskeletal system as simply a plant is the increasing evidence that the mechanical system as a whole exerts a form of control. Raibert and Hodgins (1993) stated it this way, "Many researchers in neural motor control think of the nervous system as a source of commands that are issued to the body as direct orders. We believe that the mechanical system has a mind of its own, governed by the physical structure and laws of physics. Rather than issuing direct commands, the nervous system can only make suggestions which are reconciled with the physics of the system and task at hand." In this vein, Mochon and McMahon (1980, 1981) showed the importance of a passive leg swing in ballistic walking. Playter and Raibert (1994) demonstrated how movable arms attached by springs can stabilize rotation by passive dynamics. McGeer (1990a, 1990b) showed that completely passive, somewhat anthropomorphic 2D mechanisms, including kneed models, could walk stably down shallow slopes. Ruina and his students have built similar mechanisms and studied related 2D (Garcia et al. 1998) and 3D (Coleman and Ruina 1998) passive-dynamic models. These walking machines have no sensors or actuators and lack any computer control. For years, Raibert has devised spectacular hopping, running and trotting robots with only very simple control systems (Raibert and

Hodgins 1993). Perhaps it would be easier to identify active neural control if we adopted the view that the musculoskeletal or mechanical system functions also as a control system—a more passive, yet dynamic, control system. In passive dynamic control, the control algorithms are simply embedded in the form of the machine or animal itself. Control results from the properties of the parts and their morphological arrangement. Musculoskeletal units, leg segments, and legs do much of the computations on their own by using segment mass, length, inertia, elasticity, and dampening as "primitives." Nevertheless, passive dynamic control lacks the plasticity of active neural control, since suites of integrated structures which have evolved over millions of years take longer to modify. Passive dynamic controllers can respond, however, immediately (i.e., zero order) and effectively to a variety of perturbations.

## 2 The Spring-Mass Model of Running

The purpose of this short perspective is to illustrate how a simple, passive dynamic model can be an effective starting point in attacking complex, indeterminate biological systems. We refer the reader to benchmark publications and insightful reviews of the history, development and characterization of the spring-mass model of running available (Cavagna et al. 1976, 1977, 1988; Heglund et al. 1982; McMahon 1985, 1990; Alexander 1988, 1992; Blickhan, 1989; Thompson and Raibert 1989; McMahon and Cheng 1990).

Terrestrial locomotion is accomplished by legged animals that could hardly be more diverse. Legged locomotors differ in leg number (from forty-four on a centipede to two on a human), body form (tall in bipedal birds, round in crabs, long in reptiles), skeletal type (exo- versus endoskeletons), body mass (from less than 1 g to hundreds of kg), and thermal strategy (warm- versus cold-blooded). With this degree of diversity, one reasonable assumption is that each taxa would have a unique set of kinematic and kinetic relationships which power their bodies forward. Abundant diversity does not suggest the possibility that simple rules for locomotion of legged animals would emerge when comparisons are made.

### 2.1 Comparable Ground Reaction Force Patterns

Surprisingly similar ground reaction forces are exerted by animals that do differ in leg number, body mass, body form and type of skeleton (Figure 13.2). Two-, four-, six- and eight-legged animals can produce similar force patterns during locomotion. They all can bounce as they run using two alternating sets of legs. One human leg works like two legs of a trotting dog, two legs of a trotting lizard, three legs of an insect and four legs of a crab.

Cavagna et al. (1977) provided the first evidence that the musculoskeletal system behaves like a sin-

gle linear spring in running, hopping and trotting gaits in mammals. These data led to the development of a spring-mass model, consisting of a single linear massless “leg spring” and a mass (Figure 13.3). The “leg spring” represents the spring-like characteristics of the overall integrated musculo-skeletal system during locomotion. The mass is equivalent to the mass of the animal. This spring-mass model has been shown to describe and predict the mechanics of running gaits remarkably well (Ito et al. 1983; Alexander 1988; Blickhan 1989; Thompson and Raibert 1989; McGeer 1990a; McMahon 1990; McMahon and Cheng 1990; Farley et al. 1991, 1993; He et al. 1991; Blickhan and

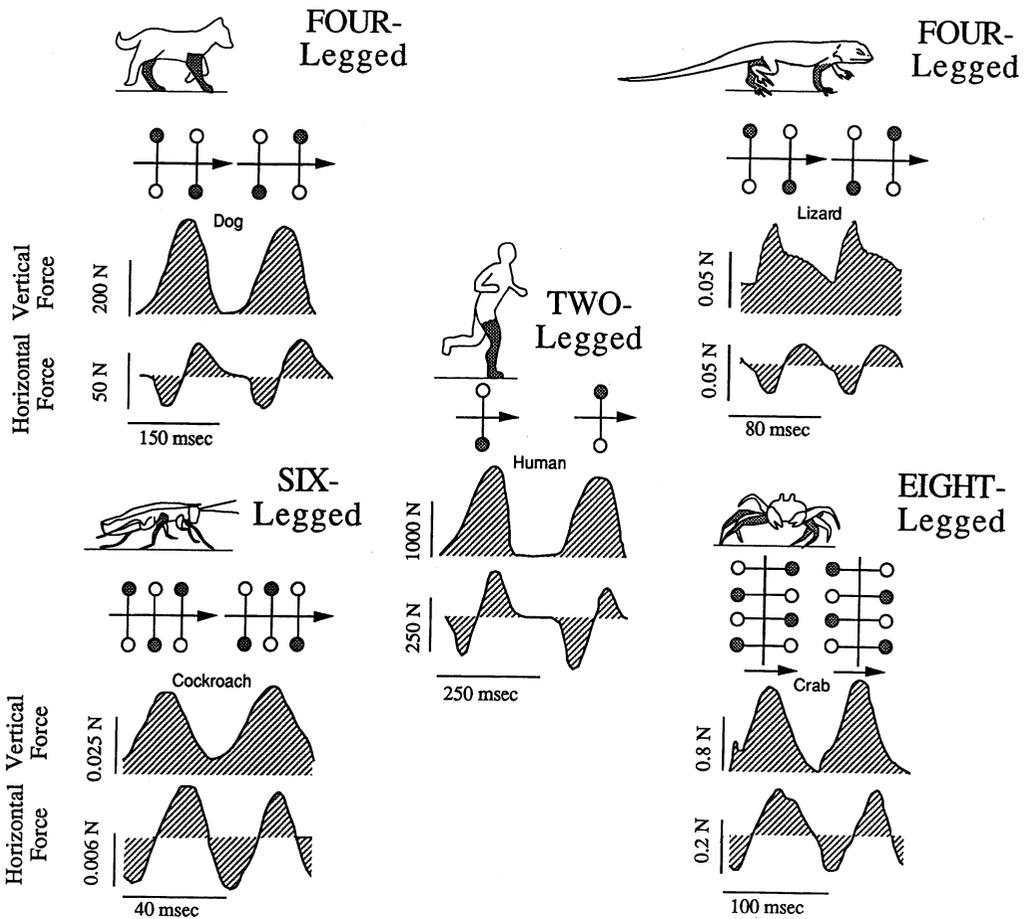


FIGURE 13.2. Comparable ground reaction forces in diverse animals. Each legged animals generates a similar pattern of forces as they bounce along like a pogo stick or spring-mass system. In each case two sets of propulsors operate as leg springs to slow down and then speed up the animal.

The leg spring is composed of one leg in a human, two legs in a trotting dog, three legs in a cockroach and four legs in a trotting crab. Closed circles in gait diagrams represent legs contacting the ground. (Modified from Full 1989; data on lizard is from Farley and Ko, 1997.)

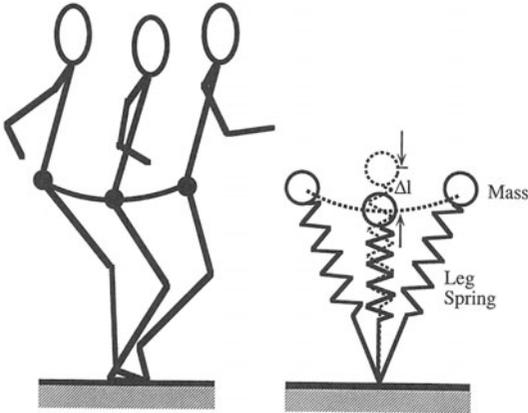


FIGURE 13.3. Trotting, hopping, and running animals are modeled as simple spring-mass systems bouncing along the ground. The model consists of a single linear leg spring and a point mass, equivalent to the mass of the animal. This figure depicts the model at the beginning of the stance phase (left-most position), at the middle of the stance phase (leg spring is oriented vertically) and at the end of the stance phase (right-most position). The arc shows the movement of the mass during the stance phase. The leg spring is maximally compressed at the middle of the stance phase. The dashed spring-mass model shows the length of the uncompressed leg spring. Thus, the difference between the length of the dashed leg spring and the maximally compressed leg spring represents the maximum compression of the leg spring ( $\Delta l$ ). (Modified from Farley et al. 1993.)

Full 1993; Farley and Gonzalez 1996). The stiffness of the leg spring is defined as the ratio of the ground reaction force to the compression of the leg spring at the instant at midstance when the leg is maximally compressed (Figure 13.3). If  $F$  is the ground reaction force and  $\Delta l$  is the compression of the leg spring, the leg stiffness ( $k$ ) can be calculated from Equation 13.1.

$$k = F \Delta l^{-1} \tag{13.1}$$

### 2.2 Leg Spring Stiffness Scales with Body Size

The spring-mass model for bouncing gaits describes the mechanics of locomotion in animals ranging in body size from a cockroach (0.001 kg) to a horse (135 kg). Force platform studies of locomotion have revealed that larger animals have stiffer leg springs (Figure 13.4). For example, a trotting horse has a leg spring stiffness 100-fold

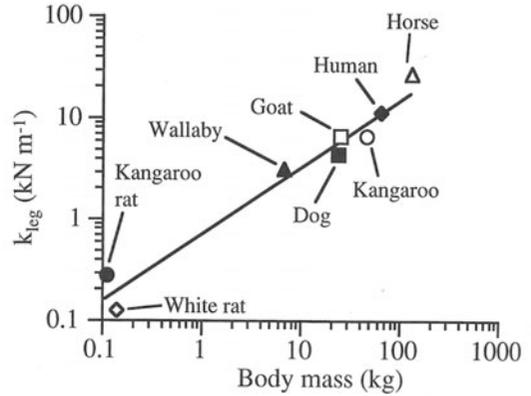


FIGURE 13.4. The stiffness of the leg spring ( $k_{leg}$ ), calculated from the ratio  $F/\Delta l$ , increases with body mass ( $k_{leg} \propto M^{0.67}$ ). This comparison was made at moderate trotting, running, or hopping speeds where the duty factor (0.4) and the Froude number (1.5) were similar in all of the animals. (Modified from Farley et al. 1993.)

higher than a trotting white rat. Comparison of mammals with a 1000-fold range of body masses has revealed that the stiffness of the leg spring increases in proportion to  $M^{0.67}$  ( $M$  = body mass). As a result, the resonant period of vibration of the spring-mass system increases in larger animals ( $M^{0.19}$ ), exactly paralleling the observed increase in the time of foot-ground contact with increasing body mass (Farley et al. 1993).

### 2.3 Similarity in Relative Individual Leg Spring Stiffness

The number of legs used to support the weight of the body during the ground contact phase of bouncing gaits varies from one to four among the legged animals studied thus far (Blickhan and Full 1993). A relative leg stiffness of all limbs in contact with the surface can be calculated by dividing the relative force of the spring (normalized for body weight) by the relative compression (normalized by leg length), and we can calculate the relative stiffness of the leg spring ( $k_{rel}$ ) as

$$k_{rel} = \frac{\frac{F}{mg}}{\frac{\Delta l}{l}} \tag{13.2}$$

where  $m$  is body mass,  $g$  acceleration due to gravity and  $l$  is the "hip" height. Six-legged trotters (in-

TABLE 13.1. Legged animals as spring-mass systems.

Gait	Legs used per step	Steps per cycle	Relative force	Relative compression	Relative stiffness (sum of legs used per step)	Relative force per leg	Relative stiffness per leg
Trotters (dog)	2	2	F/mg	1/2 $\Delta l/l$	2k	1/2 F/mg	$k_{rel,leg}$
Trotters (cockroach)	3	2	F/mg	1/3 $\Delta l/l$	3k	1/3 F/mg	$k_{rel,leg}$
Runners (human)	1	2	F/mg	$\Delta l/l$	k	F/mg	$k_{rel,leg}$
Hoppers (kangaroo)	2	1	2F/mg	$\Delta l/l$	2k	F/mg	$k_{rel,leg}$

Each column labelled relative represents the relative magnitude of a dimensionless ratio. For example, the relative force of hoppers (2F/mg) is twice that of trotters and runners (F/mg). Blickhan and Full (1993).

sects using 3 legs on the ground at once) compress their virtual leg spring by only a small amount (1/3) relative to runners and hoppers (Table 13.1). Because the relative force is the same as in runners, the whole body stiffness of the insect’s virtual leg spring is 3-fold greater than for runners. Since the stiffness of the virtual leg spring is determined by the number of legs that hit the ground, the relative individual leg stiffness can be estimated by dividing the relative whole body stiffness of the insect’s virtual leg spring by the number of legs (e.g., for insect  $3k / 3$ ). Given this reasoning, the relative leg stiffness is surprisingly similar in trotters, runners and hoppers using 1 to 3 legs per step (Figure 13.5). Relative force is about 10-fold greater than relative compression in 6-legged trotters (cockroaches), 4-legged trotters (dogs, horses), 2-legged runners (humans, birds) and 2-legged hoppers (kangaroos; Table 13.1).

### 2.4 Constant Leg Spring Stiffness Versus Speed

Studies have shown that the stiffness of the leg spring remains nearly the same at all forward speeds in a variety of running, hopping, and trotting mammals including humans (Figure 13.6A) (He et al. 1991; Farley et al. 1993). As animals run faster, the body’s spring system is adjusted to bounce off the ground more quickly by increasing the angle swept by the leg spring during the ground contact phase rather than by increasing the stiffness of the leg spring (Figure 13.6B). By increasing the angle swept by the leg spring at higher speeds, the vertical excursion of the center of mass ( $\Delta y$ ) is reduced without changing the leg stiffness (Figure 13.7). This method of adjusting the spring-mass system for different speeds is the same in all of the mammals studied to date (He et

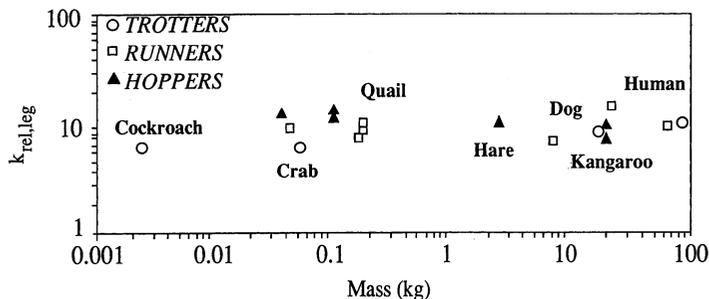


FIGURE 13.5. Relative individual leg stiffness as a function of body mass. Relative leg stiffness was determined by normalizing peak vertical ground reaction force by body weight and virtual leg spring compression by hip

height. To determine relative individual leg stiffness, relative leg stiffness was simply divided by the number of legs used in a step. See relative magnitudes in Table 13.1. (Blickhan and Full 1993.)

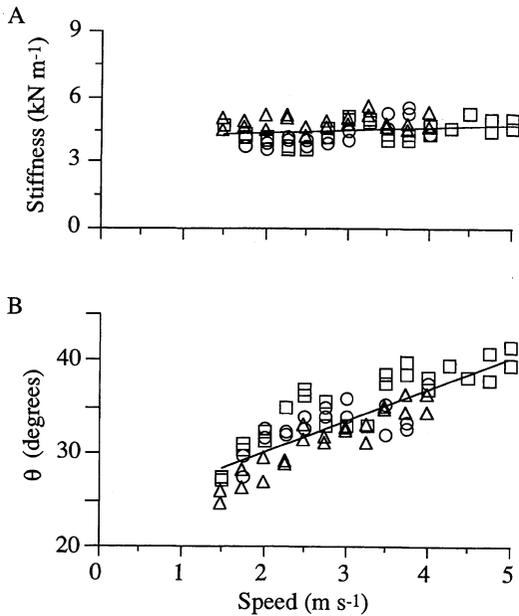


FIGURE 13.6. Leg spring stiffness and landing angle as a function of speed for trotting dogs. (A) The stiffness of the leg spring is independent of speed (Farley et al. 1993). (B) Half the angle swept by the leg spring ( $\theta$ ; Figure 13.7) increases at higher speeds. This adjustment to the geometry of the spring-mass system reduces the vertical displacement of the center of mass during the stance phase at higher speeds. Different symbols are used for each of the trotting dogs in the study ( $n = 3$ ). A similar pattern has been observed for trotting goats and horses, hopping kangaroos, and running humans. (He et al. 1991; Farley et al. 1993.)

al. 1991; Farley et al. 1993). Interestingly, it is also the method used to change the forward speed of running robots with spring-based legs (Raibert and Hodgins 1993).

## 2.5 Leg Spring Stiffness Is Adjustable to Bouncing Frequency

Although the stiffness of the leg spring remains the same at all locomotor speeds in mammals, experimental evidence shows that it is possible for humans to alter the stiffness of their leg spring. The first evidence comes from a study of humans hopping in place, an ideal experimental system for examining leg stiffness adjustment because it follows the same basic mechanics and spring-mass model as forward running yet has simpler kinematics. When humans hop in place at a range of frequencies, the stiffness of the leg can be more than doubled to accommodate increases in hopping frequency or to accommodate increases in hopping height at a given frequency (Figure 13.8) (Farley et al. 1991). Similarly, when humans run at a given speed using a range of stride frequencies, they more than double their leg stiffness between the lowest and highest possible stride frequencies (Figure 13.9) (Farley and Gonzalez 1996). A similar range of possible leg stiffnesses was observed in an earlier study that showed that when humans bounce vertically on a compliant board, the stiffness of the leg spring can change by as much as two-fold in response to changes in knee angle (Greene and McMahon 1979).

## 2.6 Leg Spring Stiffness Is Adjustable to Surface Stiffness

Almost all of the research to date on the mechanics and control of legged locomotion has focused on walking and running on hard and smooth laboratory floors. However, when legged animals run in the natural world, they encounter a variety of surfaces that have a range of mechanical proper-

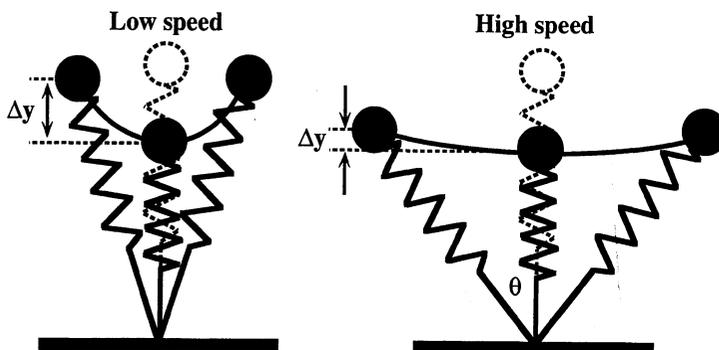


FIGURE 13.7. At higher speeds, the angle swept by the leg spring during the stance phase increases, and as a result, the vertical displacement of the center of mass ( $\Delta y$ ) decreases. In both examples, the displacement of the leg spring ( $\Delta l$ ) is the same.

ties. Clearly, the properties of the surface will have substantial effects on the mechanics of locomotion, if the mechanical behavior of the legs is not adjusted to accommodate changes in surface properties. For example, when lead weights are dropped onto a variety of surfaces, the impact force varies by much as 400% depending on the properties of the surface (Bodmer and Herzog 1980). This observation clearly indicates that if the mechanical properties of the legs are not adjusted to accommodate changes in surface properties, the mechanics of locomotion will be greatly affected.

Research has examined the mechanical behavior of the human leg during hopping in place on surfaces with a range of stiffnesses (Ferris and Farley 1997). The findings show that the stiffness of the leg is increased by as much as 3-fold to accommodate decreases in surface stiffness (Figure 13.10A) (Ferris and Farley 1997). The increased stiffness of the leg during hopping on surfaces of lower stiffness is reflected in reduced leg compression (Figure 13.10B). As a result of the in-

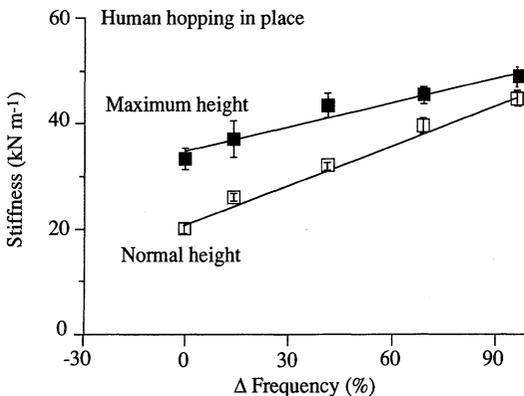


FIGURE 13.8. When humans hop in place, they can more than double the stiffness of the leg spring to increase hopping frequency. In addition, they increase the stiffness of the leg spring to hop higher at a given frequency. In both cases, the higher leg spring stiffness allows the hopper to have a shorter ground contact time. The open symbols represent data in which the subjects were simply instructed to hop at a given frequency set by a metronome; the closed symbols represent data in which the subjects were instructed to hop as high as possible at a given frequency set by a metronome. “ $\Delta$  Frequency” represents the percentage difference between the hopping frequency and the preferred frequency of 2.2 Hz. The error bars are the standard errors of the means. (Modified from Farley et al. 1991.)

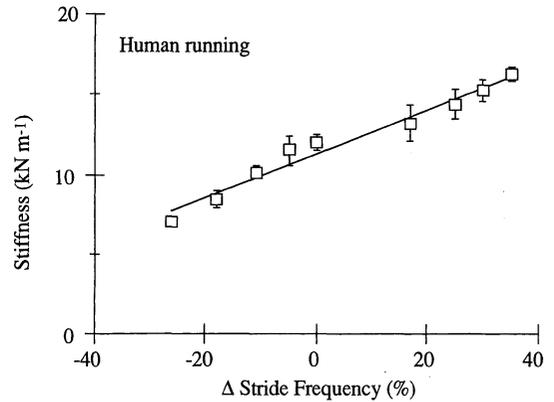


FIGURE 13.9. When humans run at a moderate speed, they can use stride frequencies other than their preferred stride frequency by changing leg spring stiffness. “ $\Delta$  Stride Frequency” is the percentage difference between the stride frequency used and the preferred stride frequency for that speed (speed = 2.5 m/s; preferred stride frequency = 1.3 Hz). The error bars are the standard errors of the means. (From Farley and Gonzalez 1996.)

creased leg stiffness on more compliant surfaces, the total stiffness of the series combination of the leg spring and the surface is independent of surface stiffness at the preferred hopping frequency (Figure 13.10A). This allows the peak ground reaction force, the ground contact time, and the vertical displacement of the center of mass to be nearly the same over a 1000-fold range in surface stiffness. Based on these recent studies of the interaction of leg stiffness and surface stiffness during human hopping in place, we hypothesize that the stiffness of the leg is increased to accommodate running on compliant surfaces. Although they did not examine submaximal sustainable speeds, McMahon and Greene (1979) did show that track stiffness influences the maximum speed that runners can attain.

### 3 Future Directions

#### 3.1 Increase Awareness of the Comparative Approach

Greater interaction between comparative biomechanists and those more interested in the human condition would benefit both groups. Realizing that the comparative method can be more than simply the study of one species as a model animal for humans

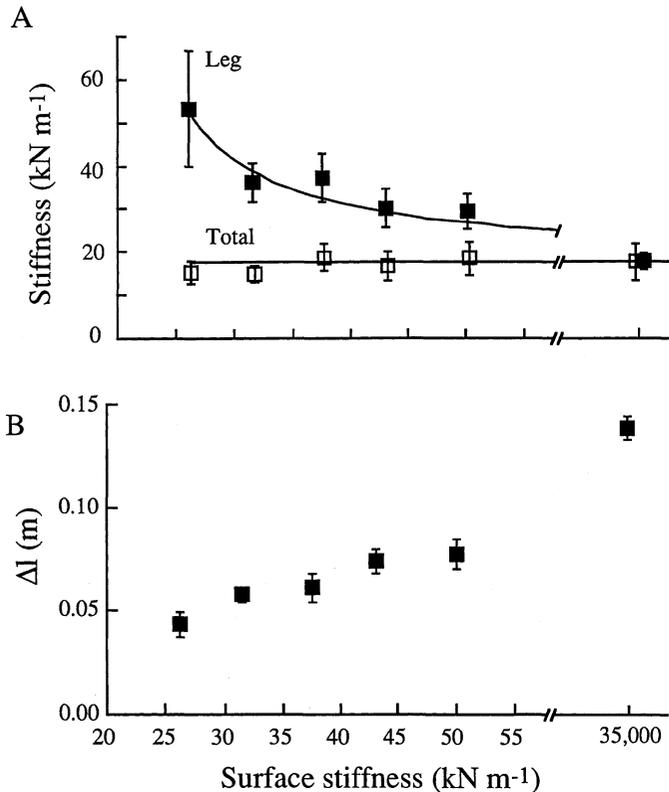


FIGURE 13.10. Leg spring stiffness and displacement of the leg spring as a function of surface stiffness. (A) The leg spring stiffness ( $k_{leg}$ ) is higher during hopping on less stiff surfaces (closed symbols). However, the stiffness of the series combination of the surface and the leg spring ( $k_{tot}$ ) is independent of surface stiffness (open symbols). The error bars are the standard errors of the means. (Modified from Ferris and Farley 1997) (B) When humans hop on surfaces with a range of stiffnesses, the displacement of the leg spring ( $\Delta l$ ) is lower on less stiff surfaces.

could open new doors toward the transfer of novel concepts and hypotheses among comparative biologists, researchers on humans and biomedical engineers. Species very different from ourselves and often more amenable to experimental manipulation can provide new insights, so long as we understand if or how the differences among species alter our conclusions (Full 1997). We suggest greater use of phylogenetic analysis in cases where evolutionary history is the prime reason why structures function the way they do. If no clear selection or constraint on function is apparent, then instead of pursuing unfounded dynamic optimization studies, perhaps we should look at function in closely related species, our sister taxa.

### 3.2 The Explicit Goal Should Be Integration in an Effort to Understand Mechanism

Raibert and Hodgins (1993) state, "It is ironic that while workers in neural motor control tend to minimize the importance of the mechanical characteristics of an animal's body, few workers in biome-

chanics seem very interested in the role of the nervous system. We think that the nervous system and the mechanical system should be designed to work together, sharing responsibility for the behavior that emerges." Certainly, part of the reason for the division is that each group asks different questions. Neurobiologists want to know how control systems can function. Muscle physiologists wish to characterize the capability of muscles. Biomechanists desire to define the performance of the mechanical system. Specialists must continue to specialize, but each group could benefit from the common goal of integration and the complete understanding of the system as a whole. Whether by direct experimentation or optimization and sensitivity analyses using large scale models, we all benefit from restricting the set of possible input or output functions. A trainable artificial neural network model may be extraordinarily valuable to a biomechanist as a controller for one behavior, but wholly inadequate for another behavior. Characterization of the capabilities and limitations of actual neural networks could be invaluable toward explaining observed behaviors. We must re-

member that complex biological systems with all their redundancies have evolved to be “just good enough” at a whole variety of tasks (subsystem criteria of Chapter 35). In addition, however, we must not be fooled into thinking that evolution results in optimal design of the whole system or the sub-systems. Animals are constrained by their evolutionary history, by how their ancestors looked and functioned in the past. If we are to understand the unique design solution of one species, then we must move to an integrative approach using a variety of species where each sub-system can limit the set of possible solutions for another (see Chapter 14 and Chapter 16).

### 3.3 Limit the Number of Possible Solutions: The Leg-Spring Example

We could imagine a seemingly infinite number of possible solutions to explain the locomotion of many-legged animals, especially given the tremendous diversity present. The field simply had no starting point to begin to understand how legs function, let alone how multiple muscles produced leg movement. Fortunately, a single solution gives us a place to begin an effort at integration with lower levels of organization. The concept of the “leg spring” allowed biomechanists to characterize the spring-like properties of the overall musculoskeletal system during locomotion. This characterization led to the surprising discovery of leg spring constancy, despite differences in leg number and speed of locomotion. These findings, in turn, sparked investigation into how the system could be adjusted during changes in frequency and surface stiffness. Before these studies, it was not possible to predict leg stiffness from joint stiffness, since it wasn’t known whether leg spring stiffness even changed or instead if the geometry of leg operation (i.e., landing angle,  $\theta$ ) was altered while leg spring stiffness remained constant.

Knowledge of how the whole system behaves like a spring limits the range of potential solutions for the behavior of the individual joints and their interactions. Joint stiffness is complex and depends on the number of muscles (agonists and antagonists) that are active and the stiffness of the individual muscles acting about the joint (Feldman 1966, 1980; Smith 1981; Abend et al. 1982; Akazawa et al. 1983; Bizzi et al. 1984, Carter et al. 1993; Nielsen et al. 1994). The control of muscle stiffness is equally elaborate and depends on a variety of factors in-

cluding activation, reflexes, muscle force, muscle length, and architecture (Rack and Westbury 1969, 1974; Nichols and Houk 1976; Agarwal and Gottlieb 1977; Gottlieb and Agarwal 1978, 1980, 1988; Akazawa et al. 1983; Hoffer and Andreassen 1981; Rack et al. 1983; Nichols 1987; Sinkjaer et al. 1988; Weiss et al. 1988; Gollhofer et al. 1992). Given the complexity of stiffness control in a single muscle or joint, it was nearly impossible to use a forward dynamics approach that begins at the level of individual muscle stiffness control and attempts to explain the mechanics of locomotion. In such a complex system, it was useful to begin by using an inverse dynamics approach that characterizes the overall behavior of the musculoskeletal system. In this case, we learned that the whole musculoskeletal system behaves like a spring-mass system during locomotion, and have uncovered some of the rules underlying the link between the stiffness of the complete musculoskeletal system and the mechanics of locomotion. Thus, the broad understanding of the overall behavior of the leg during locomotion provided by the spring-mass model can guide future work examining the integration of the actions of multiple joints and muscles whose function must result in spring-like behavior.

### 3.4 Practical Applications

Finally, the ability to represent the complex musculoskeletal system as a single spring will have practical applications. The properties of the leg spring give information about the mechanical interactions between the human musculoskeletal system and the ground during running. This information is valuable to engineers who are designing equipment for use during human locomotion. For example, knowledge of the stiffness of the overall musculoskeletal system during locomotion has aided in the design of running tracks for maximizing sprint speed (McMahon and Greene 1979) and the design of running shoes. In the future, it will undoubtedly aid in the design of surfaces that minimize overuse injuries during aerobic exercise, the design of spring-based prostheses for running that allow normal running mechanics, and the design of legs for running robots.

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## Commentary: Cyclic Movements and Adaptive Tissues

Jack M. Winters

The chapters in Section IV of this book focus on rhythmic movements in animals. Such cyclic movements are important in life, especially with regard to moving around within one’s environment. By choosing to look at such movements via smaller animals, we are able to study more closely the neuromechanical behavior underlying movements. While some chapters within this section have focused more on the neural components and others more on mechanical aspects (e.g., this chapter), a recurring theme is that neural and mechanical subsystems have

*co-evolved* (in both structure and properties) to meet the demands of various environments, and *furthermore co-developed* over the course of an animal's life. Chapter 12, Section 4 states that, if anything, the neural control system develops primarily to meet the requirements of the mechanical system as it develops, rather than *visa-versa*. I agree. For instance, neural pattern generators (PGs) often must adapt to the natural resonant frequencies of the musculoskeletal system, and modulatory tonic drives can often be effective in initiating cyclic movement because of such subservient PGs that are complemented by sensory input that detect discrete mechanical events that may trigger transitions between states. This clearly makes the phylogenetic approach advocated by Full and Farley intriguing, and the authors successfully articulate the advantages of utilizing the comparative method and focusing on natural experiments. However, it is suggested that there are also limitations to such approaches, and this will be our focus here. Two are addressed.

1. *Approaches based on observation of macrobehavior, interpreted using simple macromodels, have limitations.* In Figures 13.2 to 13.10, the authors' use the concept of leg springs, and spring-mass systems in general, to provide a fascinating classification scheme for legged locomotion behavior. But rather than being awestruck by the data in these figures, a worthwhile question is: Could the results have been otherwise? Why should the general similarity of ground reaction forces between diverse animals (relative to their weight) be expected, given that all of these legged creatures locomote while subject to the laws of physics (e.g., inertial dynamics, the same gravitational field)? Indeed, after examining Figure 13.2, I was more surprised by the magnitude of the *differences* in shape of the ground reaction forces than by the similarities. And what about the remarkable plots of relative leg stiffness vs body mass (Figure 13.4)? I would suggest an alternative, *rule-based* interpretation: animals don't like to be overly squashed during propulsion. Using a fuzzy rule analogy, if the variable  $\Delta/l$  is too large, say over about 50%, the degree of membership in the fuzzy set "squashed" is pretty high. Being squashed is bad, and creatures might not like to be squashed for several reasons: mechanical disadvantage at joints, a less stable visual field, societal humiliation. Given that  $F/mg$  per leg in ground contact should be over 1.0 but not by too much, it seems to me rather unsurprising that the relative individual

leg stiffness is reasonably independent of mass (Figure 13.5)—especially on a logarithmic scale. What about speed variation within a given animal? The story is clean: stiffness does not change, while the angle swept by the legs grows with speed. The trouble I have with the global spring-mass macromodel is that while it effectively tells us *what* happens, it does not really tell us *why or how* this happens. I prefer relating function (and behavior) to specific tissue structure and properties. There has a track record here, for instance in the evolving writings of Alexander. Based on biomechanical inspection of the different musculoskeletal *structures*, Alexander (1968) sheds light on why the horse is better at running fast, yet the armadillo better at borrowing holes. Based on a consideration of the function of human leg vs arm muscles (i.e., propulsion vs manipulation), Alexander and Ker (1990; see also Alexander 1988) were able to show why the factor of safety of key tendons (related to the tendon cross sectional area relative to the muscle physiological cross-sectional area) differs.

2. *Adaptive tissues and optimum design.* Full and Farley state that "we must not be fooled into thinking that evolution results in optimal design of the whole system or the sub-systems" after noting that "complex biological systems with all their redundancies have evolved to be 'just good enough' at a whole variety of tasks (subsystem criteria, Chapter 35, Winters). . . ." While I agree in spirit with the latter statement, the authors' come painfully close to denying a role for optimization as an adaptive process that can lead to change in structure and tissue. With this I would have to disagree. As noted in Chapter 7, adaptive processes can happen on roughly three time scales: (1) very long (evolutionary, multi-generational effects); (2) moderate length (adaptive tissue/behavioral effects, occurring during animal lifespan); and (3) on-the-fly learning (the "iterations" or "epochs" of an optimal neurocontrol problem). The first two of these especially apply here.

In engineering terms, the first of these relates primarily to changes in structure, and to optimal design. A rapidly emerging tool for dealing with such problems are genetic algorithms (Holland 1975; Davis 1991), which are literally categorized as a type of stochastic search optimization algorithm (e.g., Michalewicz 1992; Lin and Lee 1996, Chapter 35)! They are especially adept at using the optimization *process* to address *structural* optimization, with the emerging "solution" being near-

optimum (and never static). As the criteria for success changes (e.g., a natural predator starts to disappear; the climate slowly changes), so will this solution—it evolves, using at minimum mathematical descriptions of the three classic operations of reproduction, crossover and mutation. In engineering practice one often uses hybrid approaches, with the core genetic algorithm performing global search to get close to a solution (“substantial convergence”), with a local optimization procedure (usually gradient-based) refining the solution. Of note is that these algorithms can still get caught in local minima, and perhaps this helps explain the wonderful collection of solutions (creatures) that exist.

In engineering terms, the second relates to tissue adaptation, a generalization of the well developed “use it or lose it” principle. Let’s develop this further. Consider the animal as a wonderful structural assembly of tissues: connective, skeletal, muscular, neural, and so on. With remarkably few exceptions (e.g., certain types of cartilage), tissues (with adequate blood supply) are known to adapt in response to how they are used—hence the reason for weight rooms and therapists. This implies that within limits, tissues can change their properties (e.g., size, responsiveness to “stimulation”). In Chapter 35, I make a case is that this represents a local optimization process, where change is governed by tissue adaptation laws. As in a recent commentary by Huijing and Winters (1998), here we do not distinguish between the adaptive properties of “mechanical” tissues such as ligaments from “electrical” tissues such as neurons, and view muscle as an electrochemomechanical transducer between these subsystems. Some tissues happen to be most sensitive to mechanical inputs, others electrical, still others chemical—heart muscle (a tissue responsible for a cyclic movement) provides an exquisite example of a tissue that is very sensitive to all three. Thus calluses form on well-used skin, bones and muscles decay when underused for a while, and skills develop with practice.

Some would argue the following: So why are we all not able to just adapt to have near-optimum athletic skills like Michael Jordan?). In other words, is not the inherent variety within a species a case against optimization? My answer is still no. Genetic (optimum search) algorithms require “mutations” to work, and variety adds robustness to a species (an important performance subcriteria). Optimization is a cybernetic process toward a biosolution defined by criteria, subject to constraints. One constraint is that

structural and tissue changes must occur relatively slowly (but then, we are free to choose our relevant time scales). And criteria change; for instance, a short five generations ago shooting balls through a 10 ft high hoop was not high on the priority list. And even now sometimes a leisurely life is fun. When such proactive local processes prove beneficial to the creature, this adaptive process may gradually affect the ongoing evolution of the species.

In conclusion, we return to our start, on synthesized neuromechanical systems. Perhaps effective leg springs exist because the structural assembly of tissues is tuned for this task. But the more intriguing question might be: Why do the tissues have the shapes and properties that they do? If these biosystems are so clearly suboptimal, why could we not just interchange parts between some of the species shown in the figures—say a femur here, a knee flexor there, and so on. My guess is that we would then really experience suboptimal design, and Figures 13.2 to 13.10 would change dramatically. What governs why structures and tissues are what they are, if not an evolving optimization process?

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