

10

Biomechanics of Walking and Running: Center of Mass Movements to Muscle Action

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"Locomotion is a particularly richly studied but frustrating aspect of biology," according to Loeb [91]. This is especially true when one attempts to understand how the numerous subdivisions of the neuromuscular and musculoskeletal systems interact to produce locomotion. At lower levels of organization, the structure and function of the system components become progressively more complex, making it difficult to discern general principles. One way of approaching the study of locomotion is to sequentially progress from a level of whole body dynamics toward a level of muscle-tendon dynamics. We believe this approach can be particularly useful in that information from the higher levels of organization can guide the quest to understand fundamental mechanisms of locomotion at increasingly complex lower levels of organization. Thus, we will first examine the pattern of center of mass movements during locomotion in humans and other legged animals. Next, we will consider how joint mechanics during locomotion are affected by both center of mass dynamics and leg posture. After concentrating on the joint level, we will move to the level of muscle-tendon mechanics by examining the techniques that have been used to investigate muscle-tendon function during locomotion and the conclusions that have been reached to date.

Throughout this review, the locomotion of humans will be compared to the locomotion of other animals. A wealth of information shows that human locomotion is not unique. Indeed, at the level of the center of mass, the dynamics of walking and running are similar in all legged animals that have been studied. The similarities in the dynamics of locomotion among diverse animals, including humans, suggest that there may also be similarities in the mechanisms by which locomotion is produced at other levels of organization within the neuromuscular system. Thus, by comparing diverse species, we can uncover common rules governing locomotion, and we can assess the applicability of data from animal models to biomedical issues in humans.

CENTER OF MASS MECHANICS

Our discussion of center of mass mechanics will be divided into four parts. First, we will discuss the pattern of ground reaction force that occurs during locomotion. Ground reaction force is the force exerted by the ground on the feet. It reflects the acceleration of the body's center of mass during locomotion. Second, the movements and mechanical energy fluctuations of the center of mass that occur as a result of ground reaction force will be discussed. Third, we will discuss the transition from a walking gait to a running gait, an event that is marked by a sudden and distinct change in the pattern of movement of the center of mass. By understanding the reasons for the transition from one gait to another, we can gain insight into the key factors that shape locomotion. Fourth, we will describe behavioral models for locomotion that give insight into how the musculoskeletal system produces the distinctly different ground reaction force and center of mass movements in walking as compared to running.

Ground Reaction Force

The distinct difference between walking and running gaits is apparent in the ground reaction force patterns for the two gaits (Figures 10.1 and 10.2) [26, 27, 29, 34, 35]. In human walking, there is always at least one foot in contact with the ground, and there are short phases of “double support” when both feet are in contact with the ground (Figure 10.1). In contrast, running is a series of bouncing impacts with the ground that are usually alternated with aerial phases when neither foot is in contact with the ground (Figure 10.2). This difference leads to a substantially higher magnitude vertical component of the ground reaction force for running as compared to walking. The pattern of the horizontal component of the ground reaction force is similar, however, for both walking and running (Figures 10.1 and 10.2). In the first half of the stance phase, the horizontal ground reaction force is negative, indicating that it is pushing backwards on the person. In the second half of the stance phase, the horizontal ground reaction force is positive, pushing forward on the person. The ground reaction force pattern for walking and running gaits is similar in humans and in a wide variety of other animals with a range of body shapes, body masses, and numbers of legs [14, 22, 40, 50, 64].

Mechanical Energy Fluctuations of the Center of Mass

The difference in the ground reaction force pattern between walking and running translates into dramatically different patterns of mechanical energy fluctuations for the center of mass during the two gaits [25-28]. During walking, the body vaults over a relatively stiff stance limb and the center of mass reaches its highest point at the middle of the stance phase. As a result, the gravitational potential energy of the center of mass is maximized at the

FIGURE 10.1.

Representative ground reaction force as a function of time for walking (1.25 m/s) in a human. The dashed line represents the stance phase of the right foot, and the solid line represents the stance phase of the left foot. (A) vertical component. (B) horizontal component. In both parts, the ground reaction force is expressed as a multiple of body weight.

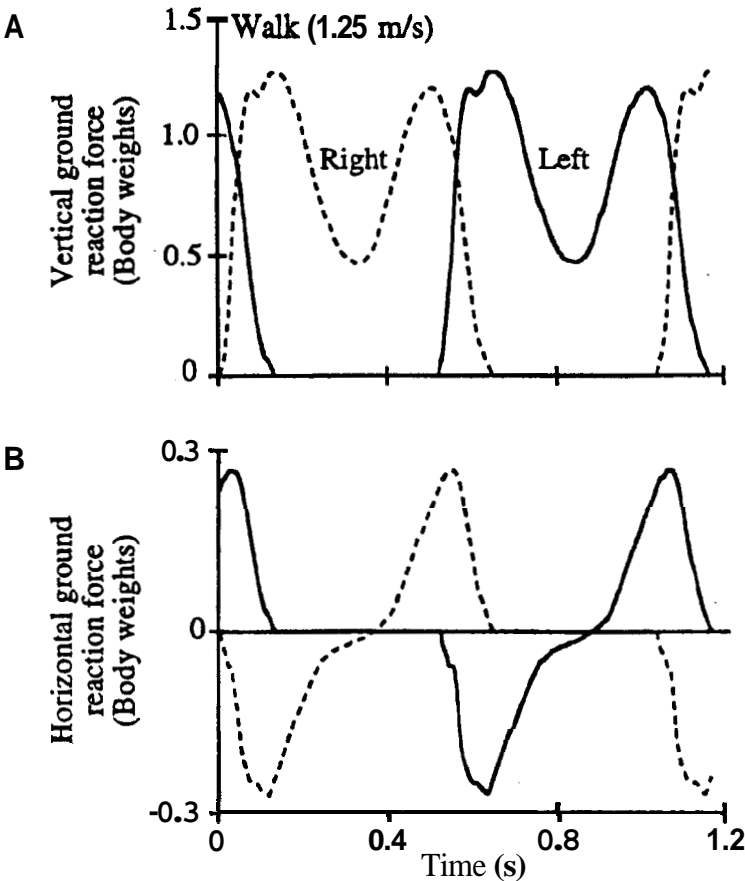


FIGURE 10.2.

Representative ground reaction force as a function of time for running (3.8 m/s) in a human. The dashed line represents the stance phase of the right foot, and the solid line represents the stance phase of the left foot. (A) vertical component. (B) horizontal component. In both parts, the ground reaction force is expressed as a multiple of body weight.

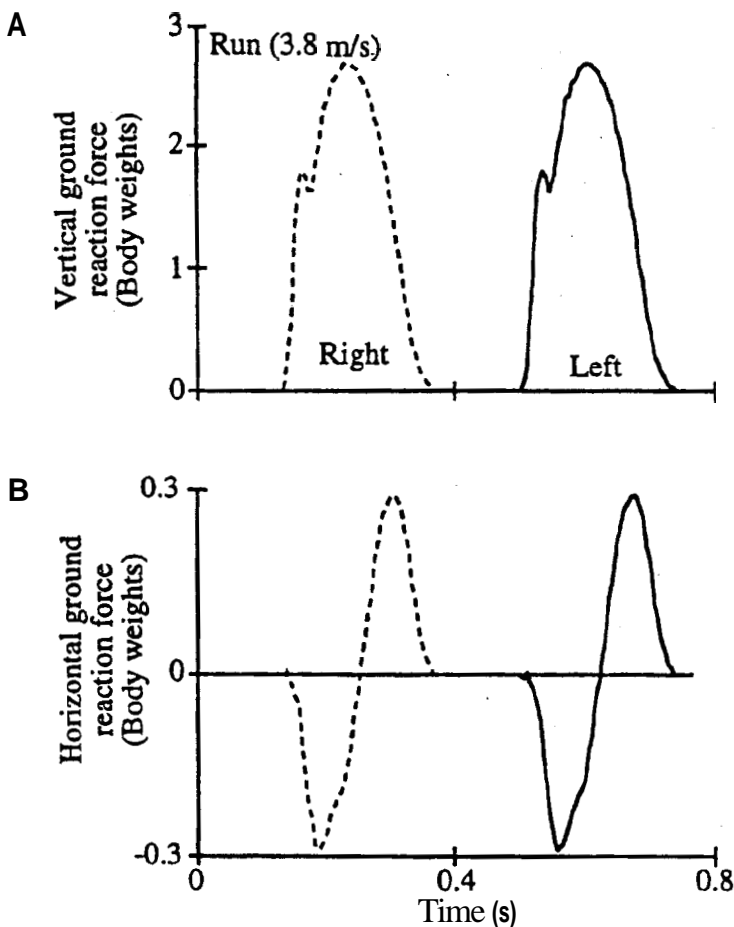
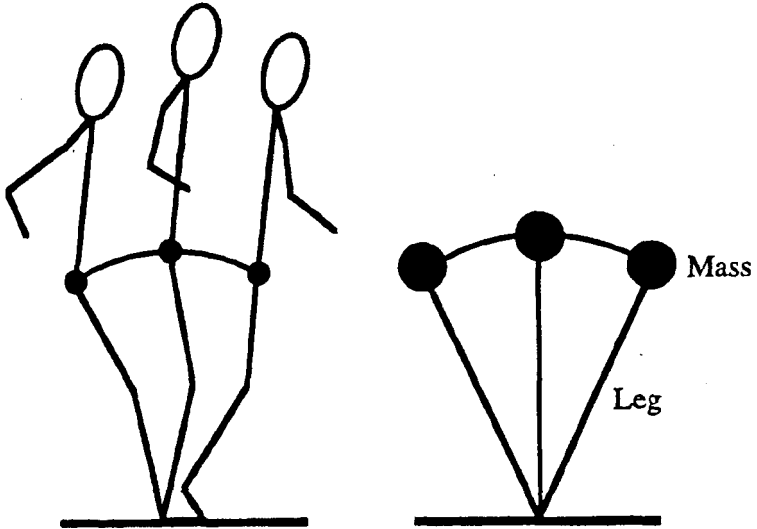


FIGURE 10.3.

An inverted pendulum model and a stick figure representation of a single stance phase of human walking. The model consists of a mass and a rigid strut that connects the point of foot-ground contact and the center of mass of the human. This figure depicts the stick figure and the model at the beginning of the stance phase (left-most position), the middle of the stance phase (center position), and the end of the stance phase (right-most position).

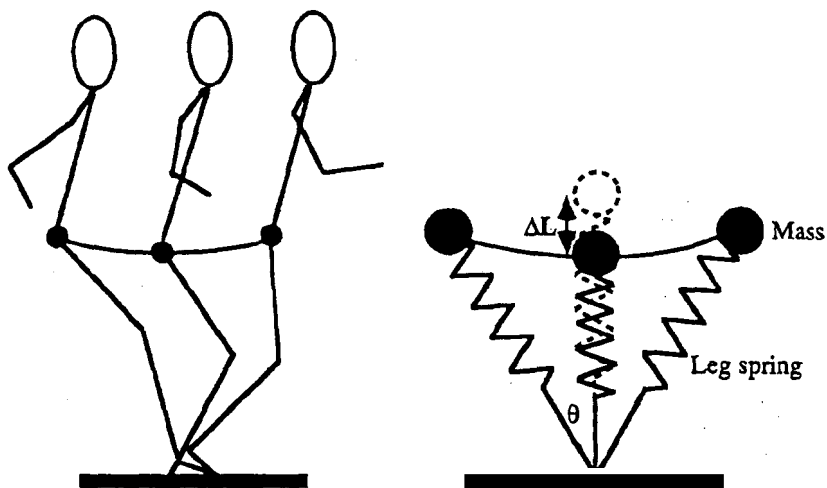


middle of the stance phase (Figure 10.3 and 10.5). In contrast, the stance limb is compliant in running so that the joints undergo substantial flexion during the first half of stance and extension during the second half of stance. This compliance causes the vertical displacement and gravitational potential energy of the center of mass to reach their minimum values at mid-stance in running (Figures 10.4 and 10.6). The pattern of movement of the center of mass has been proposed as the defining difference between a walking gait and a running gait [101].

Unlike the gravitational potential energy fluctuations, the pattern of kinetic energy fluctuations is similar for walking and running. In both gaits, the kinetic energy of the center of mass reaches its minimum value at mid-stance (Figures 10.5 and 10.6) since the horizontal ground reaction force tends to decelerate the body during the first half of the stance phase (Figures 10.1 and 10.2). During the second half of stance, the kinetic energy of the center of mass increases due to the accelerating effect of the horizontal

FIGURE 10.4.

A spring-mass model and a stick figure representation of a single stance phase of human running. The model consists of a linear spring representing the leg and a point mass equivalent to body mass. 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).

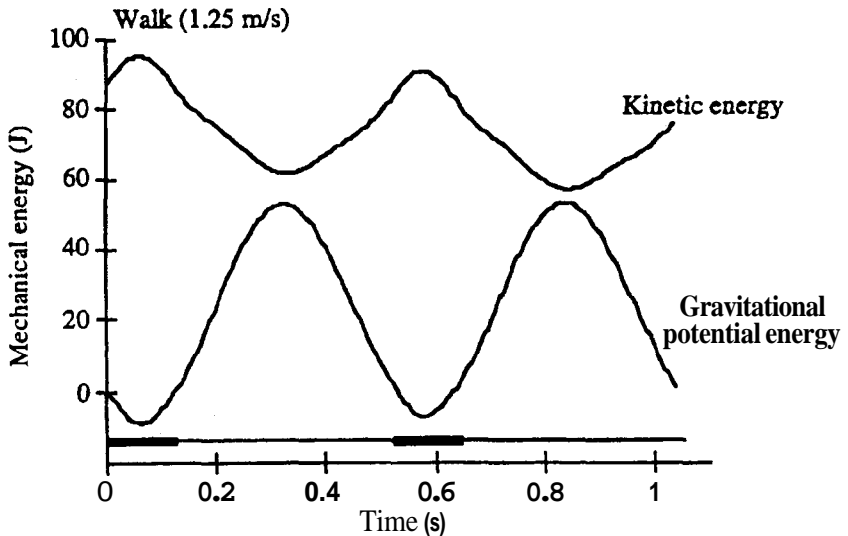


ground reaction force. Although the pattern of kinetic energy fluctuations is similar, the magnitude is much larger for running than for walking (Figures 10.5 and 10.6).

The kinetic energy and gravitational potential energy of the center of mass are approximately 180° out of phase in walking. At mid-stance in walking, the gravitational potential energy is at its maximum and the kinetic energy is at its minimum (Figure 10.5). Because these energies are approximately a half-cycle out of phase with each other and their fluctuations are similar in magnitude, substantial pendulum-like exchange occurs between them [25, 26]. During the first half of the stance phase of walking, the center of mass loses kinetic energy but gains gravitational potential energy. In this phase, kinetic energy can be converted to gravitational potential energy. During the second half of the stance phase, the center of mass loses gravitational potential energy but gains kinetic energy. Thus, during this phase, gravitational potential energy can be converted to kinetic energy. A similar energy transfer mechanism occurs as a pendulum swings or as an egg rolls across the ground. As a result, the energy transfer mechanism used in walking is often referred to as the “inverted pendulum mechanism”

FIGURE 10.5.

During moderate speed walking (1.25 m/s), the kinetic energy fluctuations of the center of mass are approximately 180° out of phase with the gravitational potential energy fluctuations, allowing substantial pendulum-like energy exchange. The thick horizontal line at the bottom of the graph represents the phases when both feet are in contact with the ground ("double support" phases), and the thin horizontal line represents the phases when only a single foot is in contact with the ground ("single support" phases).

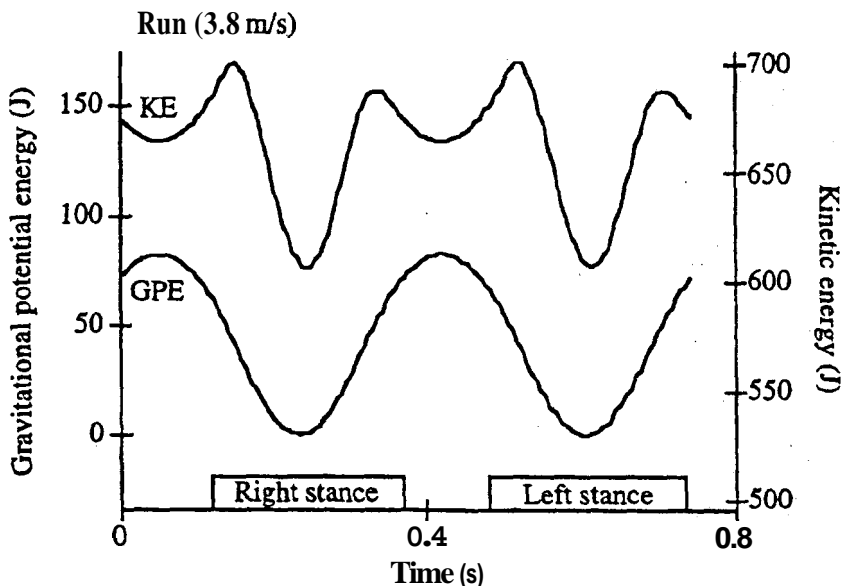


or the "rolling egg mechanism." The pattern of mechanical energy fluctuations is similar in other walking animals as it is in humans [14, 22, 40.50, 64, 1071]. As a result, many other animals, including mammals, birds, reptiles, and arthropods, also conserve substantial mechanical energy by the inverted pendulum mechanism during walking.

In human walking, as much as 60–70% of the mechanical energy required to lift and accelerate the center of mass is conserved by this energy transfer mechanism [28]. Mechanical energy savings are maximized at moderate walking speeds, and fall toward zero at very low and very high walking speeds [28]. At the walking speed where energy conservation is maximized, the magnitudes of the fluctuations in kinetic energy and gravitational potential energy are similar. Nevertheless, the maximum energy recovery by the inverted pendulum mechanism is approximately 70%, substantially less than the theoretical maximum of 100%. At the speed where energy transfer

FIGURE 10.6.

During running (3.8 m/s), the kinetic energy fluctuations of the center of mass are approximately in phase with the gravitational potential energy fluctuations. The stance phases for each limb are noted at the bottom of the graph.



is maximized, the metabolic energy **cost** per unit distance (i.e., the cost of transport) is lower **than at** any other walking speed [23]. It has been suggested that metabolic energy **cost** is minimized because **the muscles** have **to do** the **least** mechanical **work** at the speed where energy transfer is optimal [23].

The speed at which energy transfer is maximized during walking depends **on body** size. The **optimum** speed **for** energy transfer is lower for a **small** child **than for** an adult [21]. While a two-year-old child's optimum speed is about 0.6 m/s, **an** adult's optimum speed is about 1.6 m/s. A **similar** difference in optimum speed occurs **among** animal species due to their different body **sizes**. For example, a small lizard maximizes energy recovery at a much lower absolute speed **than** a sheep [22, 40]. In spite of this difference in **optimum walking** speed, energy **transfer** by the inverted pendulum mechanism reduces **the** mechanical **work** required **for** lifting and accelerating the center of mass **by** a similar fraction **in** animals **of** all body sizes. A 0.005 kg **lizard** or a 70 kg **sheep** reduce the mechanical work required to lift and accelerate the center **of** mass by about 50% **through the**

inverted pendulum mechanism of energy exchange [22, 40]. Similarly, the mechanical work required to lift and accelerate the center of mass is reduced by about 60–70% for a two-year-old child or an adult human [21]. Thus, body size has a profound effect on the optimum walking speed but has little effect on energy conservation by the inverted pendulum mechanism.

In running, there cannot be substantial pendulum-like exchange between kinetic energy and gravitational potential energy since their fluctuations are nearly in phase with each other (Figure 10.6) [27]. Both kinetic energy and gravitational potential energy reach their minimum values at approximately the middle of the ground contact phase. As a result, the exchange of kinetic energy and gravitational potential energy conserves less than 5% of the mechanical work required to lift and accelerate the center of mass during running. Substantial mechanical energy, however, is conserved through the storage and return of energy in elastic tissues (to be discussed). Because the movements of the center of mass during running are similar to a bouncing ball [27], running is often referred to as a “bouncing gait.” A similar pattern of mechanical energy fluctuations occurs during fast gaits used by other animals [14, 22, 40, 51, 52, 64]. For example, trotting dogs, hopping kangaroos, running quail, and trotting cockroaches all have a similar pattern of mechanical energy fluctuations as running humans. Although the pattern of limb movements and gaits varies among these animals, all show the characteristic pattern of kinetic energy and gravitational potential energy being nearly exactly in phase with each other. All of these gaits are referred to as bouncing gaits.

Gait Transitions

It is clear that walking and running are distinctly different in terms of their patterns of ground reaction force and patterns of mechanical energy fluctuations. Indeed, simply watching a person gradually increase her forward speed and break from a walk to a run makes it obvious that there are distinct differences between walking and running. What determines the speed range where each of these distinctly different gaits is used? It is likely that by understanding the triggers for the gait transition, we will reach a better understanding of how the neuromuscular system and the physical characteristics of the body shape locomotion.

The transition from walking to running is not a smooth and continuous event. Rather, there is a distinct transition from one gait to the other that can be observed in both the kinematic and kinetic patterns [75, 77, 139]. For example, the transition from walking to running involves sudden changes in ground contact time, duty factor, ground reaction force, and movements of the center of mass. It is not yet clear exactly what triggers the transition from walking to running or vice-versa in humans or other animals [9, 33, 75–78, 86, 102, 103].

It was long believed that humans and other animals choose their gait transition speed based on minimization of the metabolic energy cost of locomotion [73]. In humans, the most economical gait at low speeds is a walk. As walking speed is increased, a speed is eventually reached where running requires less metabolic energy than walking [95, 96]. A similar pattern exists for quadrupedal animals [73]. Walking is most economical at low speeds, trotting is most economical at moderate speeds, and galloping is most economical at the highest speeds. However, the speed where an animal prefers to switch gaits is not the speed that would minimize metabolic energy cost. Horses switch from a trot to a gallop at a speed substantially below the optimal speed for minimizing metabolic energy cost. Thus, galloping actually requires more metabolic energy than trotting at the speed where a horse chooses to switch from a trot to a gallop [41]. Similarly, humans switch from a walk to a run at a speed that is not energetically optimal [76, 103]. These findings suggest that another factor, perhaps biomechanical, actually triggers gait transitions.

Based on the inverted pendulum mechanics of walking, it is reasonable to think that gravity is an important factor in determining the speed where the walk-run transition occurs. In walking, the gravitational force on the center of mass must be at least equal to the centripetal force needed to keep the center of mass moving in a circular arc as it vaults over the stance limb (Figure 3). The required centripetal force is equal to mv^2/L , where m = body mass, v = forward velocity, and L = leg length. The ratio between the centripetal force and the gravitational force $(mv^2/L)/(mg)$ is the Froude number (v^2/gL) . Based on the mechanics of an inverted pendulum system, it has been predicted that humans and other animals should be able to use a walking gait only at speeds where the Froude number is less than or equal to 1 [1, 2]. This is so because the gravitational force is sufficient to keep the center of mass moving in a circular arc when the Froude number is less than or equal to 1. Experimental evidence has shown that humans and other bipeds (e.g., birds) with a large range of leg lengths prefer to switch from a walk to a run at a similar Froude number but at different absolute speeds [1, 4, 53, 78, 139]. Furthermore, when humans walk at different levels of simulated reduced gravity, they switch from a walk to a run at a similar Froude number (approximately 0.5) but at very different absolute speeds [86]. These observations suggest that the ratio of centripetal force to gravitational force is important in determining the gait transition speed. Nonetheless, it is puzzling that the gait transition occurs at a substantially lower Froude number than the theoretically predicted Froude number of 1.

Most gait transition studies to date have examined gait choice when humans or other animals move steadily at speeds near the transition speed. However, neither humans nor other animals naturally choose to move in this way in their every day lives. Generally, humans and other animals prefer to use speeds near the middle of each gait and rarely will choose other

speeds for an extended period of time [73, 118]. Thus, they tend to make rapid transitions from one gait to another, which occur in concert with abrupt changes in speed [103]. In the extreme case of accelerating from a standstill, humans and other animals seem to immediately choose the appropriate gait for the speed to which they are accelerating. For example, a human sprinter runs, not walks, out of the blocks [24]. Similarly, a dog immediately gallops at the beginning of a sprint regardless of its starting speed. These observations suggest that in the future it will be important to examine gait choices in more natural locomotor patterns, including acceleration and deceleration.

Behavioral Models for Walking and Running

One way to gain insight into the behavior of the overall musculoskeletal system during locomotion is to employ simple mechanical models of walking and running. These behavioral models simulate the movements of the center of mass during locomotion by modeling the output of the integrated musculoskeletal system using mechanical elements. These models can provide a guide for studies of lower levels of organization within the musculoskeletal and neuromuscular systems. They are particularly valuable in delimiting the potential strategies that the neuromuscular system could use to produce walking and running.

WALKING BEHAVIORAL MODELS. The simplest behavioral model for walking is an inverted pendulum. This model consists of a rigid strut that represents the leg and a point mass equal to body mass (Figure 10.3) [1]. In this model, the mass vaults over a rigid leg during the stance phase, and the center of mass reaches its highest point at mid-stance. In the inverted pendulum model, like in a standard pendulum, the gravitational potential energy of the mass is exactly 180° out of phase with the kinetic energy. As a result, at mid-stance, the gravitational potential energy is maximized and the kinetic energy is minimized. This pattern of mechanical energy fluctuations is qualitatively similar to the pattern observed during walking in humans (Figure 10.5) and other animals. In bipedal animals, including humans, it is easy to visualize that the rigid strut in the inverted pendulum model corresponds to the stance limb. For animals with four or more legs (e.g., a dog or a ghost crab), all of the legs in contact with the ground cooperate to produce movements of the center of mass similar to those of a mass vaulting over a single rigid limb.

In an idealized inverted pendulum model, 100% recovery of mechanical energy occurs due to the exchange between gravitational potential energy and kinetic energy. As previously discussed, a walking human has a maximum recovery of mechanical energy of about 60–70% [28]. Clearly, part of the reason why human walkers do not achieve 100% recovery is that their legs do not behave exactly like rigid struts. The functional leg length (i.e., distance from point of foot-ground contact to the center of mass)

changes to some extent during the stance phase [134]. This is different from the behavior of the rigid strut that represents the leg in the idealized inverted pendulum model. In fact, sensitivity analyses on mechanical models suggest that leg compression is an important parameter in determining the pattern of ground reaction force and center of mass movements during walking [109–111]. Although an inverted pendulum model with a rigid leg does a good job of predicting the mechanical energy fluctuations of the center of mass, it does not accurately predict the ground reaction force pattern [109]. Adding compliance to the leg model greatly improves the prediction of the ground reaction force pattern [5, 109–111, 134, 144].

Leg geometry at the beginning of the stance phase also plays an important role in determining the pattern of ground reaction force and the pendulum-like exchange of mechanical energies during walking. When humans are asked to walk while using exaggerated leg joint flexion during stance, the peak ground reaction force decreases [156] and the pendulum-like exchange of center of mass energy decreases [88]. Chimpanzees, animals that naturally walk with flexed limbs, have similar patterns of ground reaction force and energy exchange as humans walking with exaggerated limb flexion [88]. The role of leg geometry in determining the dynamics of walking is further emphasized by the observation that the peak ground reaction force and loading rate increase when humans walk with stiffer and straighter limbs than usual [31]. These studies suggest that one role of normal joint flexion during the stance phase is to reduce the ground reaction force and the vertical movements of the center of mass. Pelvic tilt and pelvic rotation also serve to reduce the vertical movements of the center of mass during walking [79, 132].

In spite of these deviations from the simple inverted pendulum model for walking, anthropomorphic passive walking machines with rigid stance legs demonstrate walking mechanics very similar to that of humans [98, 99]. These machines take advantage of pendulum-like energy exchange by the center of mass of the body and also by the swinging leg. The idea of having the swing limb move passively via pendulum-like energy exchange is based on mathematical models and observations of humans walking at moderate speeds [53, 97–99, 104, 105]. Electromyographic measurements show that nearly no muscle activity is present in the swing limb at some walking speeds [8]. It is thought that the limb swings forward passively after the muscles start the limb into motion during the period of double support. Because of the energy exchanged by the swing limb and the center of mass, anthropomorphic passive walking machines only need the added energy input of moving down a slight hill to counteract the small energy losses that occur with each stride. It is interesting to note that although passive walking machines do not have any control systems, they are capable of walking in a stable and predictable pattern [98, 99]. Their dynamics are determined by the physical structure of the walker, demonstrating that

inherent mechanical properties of the body can greatly simplify the **control** of locomotion.

RUNNING BEHAVIORAL MODELS. Because the movements of the center of **mass** during running are similar to those of **a** bouncing ball, it is not surprising that running models rely upon springs. Running is often modeled **as** a simple spring-mass model that consists of a single linear “leg spring” and **a** point **mass** that is equivalent to body **mass** (Figure 4) [3, 13, 100]. The leg spring stiffness represents the overall stiffness of the integrated musculoskeletal system. In bouncing gaits the leg spring compresses during **the** first half of the ground contact phase and lengthens during the second **half** of **the** ground contact phase. These changes in leg length result from flexion and extension of leg joints. In spite of its apparent simplicity, this spring-mass model describes and predicts the dynamics of running gaits in humans and numerous other species remarkably well [15, 37–39, 42, 43, 63].

Leg stiffness plays an important role in determining the dynamics of the interaction between the stance leg and the ground. Many aspects of running depend on **a** runner’s **leg** stiffness, including the time of foot-ground contact, the vertical excursion of the body’s center of mass during the ground contact phase, and the ground reaction force [39, 100]. ‘Leg stiffness is defined **as** the ratio of the ground reaction force **to** the compression of the leg spring (AL) at the instant at midstance when the leg is maximally compressed (Figure 4). In a running human, the leg stiffness represents the average stiffness of the stance limb. In animals with more than one limb simultaneously in contact with the ground, the leg stiffness in the spring-mass model represents the average combined stiffness of all of the limbs in contact with the ground [15, 38].

Leg stiffness remains the same at all forward speeds in running humans (Figure 10.7) [63]. They are able to run at higher speeds, and with shorter ground contact times, by increasing the angle swept by the leg during the stance phase (Figure 10.8). A variety of hopping, trotting, and running animals keep leg stiffness the same at **all** speeds (Figure 7) and alter the angle swept by the leg **to** adjust **for** different speeds [38]. Although the stiffness of the leg remains the same at all speeds of running, humans are capable of altering their leg stiffness during bouncing gaits. **Humans** change their leg stiffness in order to alter stride frequency during hopping in place or forward running [37, 39]. In addition, recent findings show that humans adjust the stiffness of their legs to offset changes in surface stiffness [42, 43]. If leg stiffness were not adjusted **to** accommodate surface stiffness, then many aspects of the dynamics of running would vary depending on surface stiffness. By adjusting leg stiffness, humans are able to have the same the peak ground reaction force, ground contact time, and vertical displacement of the center of mass regardless of surface stiffness [42, 43].

FIGURE 10.7.

Leg stiffness versus speed for running humans and trotting dogs. For the dogs, the leg stiffness represents the total stiffness of the two limbs on the ground during each ground contact phase.

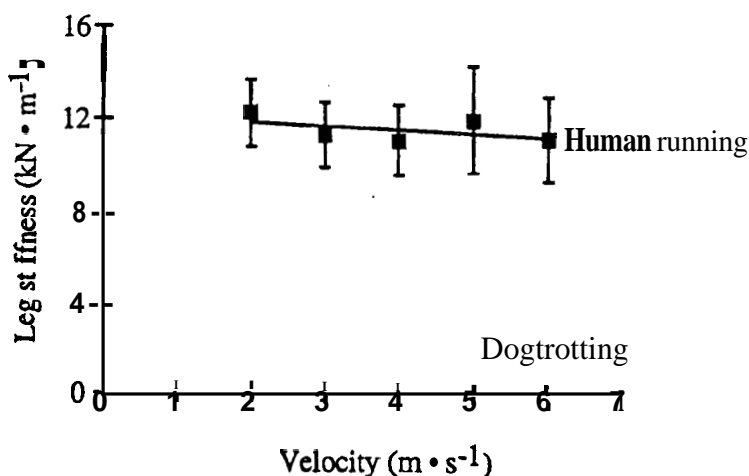
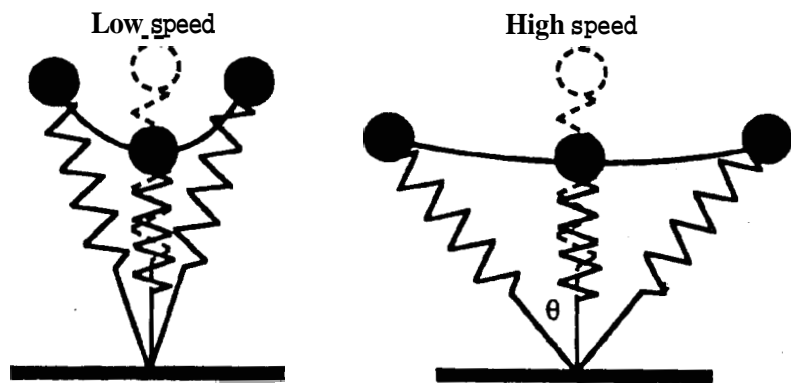


FIGURE 10.8.

The spring-mass model representing low speed running and high speed running. The leg stiffness and leg compression are the same in both model. The only difference is that the angle swept by the leg spring (θ) is greater in the model representing high speed running. Because of the greater angle swept by the leg at the higher speed, the vertical displacement of the mass during the ground contact phase is smaller at the higher speed.



Just as human legs behave like springs during running, the fastest robots also have spring-based legs [126–129]. We can gain insight into the control strategies that are possible in animal bouncing gaits by exploring the range of workable strategies in these robots. These robots use either compressed air or metal springs in their legs to store and return elastic energy with each step as they run, hop, or trot. There are many similarities between bouncing gaits in these robots and in animals. Both these robots and animals run at different speeds by altering the angle swept by their legs while keeping their leg stiffness the same [38, 63, 129]. In addition, altering the robot's leg stiffness leads to changes in stride frequency at the same speed [129], as is observed in humans [37, 39]. The control of these robots is greatly simplified by relying on the passive dynamics of spring-mass system of the robot's body. The robot's movements are largely determined by physical parameters including the stiffness of the leg spring, the angle at which the leg spring is set down, and the mass of the robot [126]. The control algorithms work in concert with the physical properties of the robot's body to produce stable locomotion. It seems logical to suggest that animals rely on the spring-mass dynamics of their bodies in a similar manner, thus simplifying the neural control of locomotion.

JOINT MOMENTS, WORK AND POWER

So far, we have discussed the mechanics of locomotion at the whole body level, including the ground reaction force, mechanical energy of the center of mass, and the behavior of the overall leg. During locomotion, muscles generate moments and perform mechanical work at the joints, producing the ground reaction force and the movements of the body. The next section will concentrate on the current understanding of joint dynamics during walking and running. The focus of this section will be the moments and mechanical work produced by muscles at each joint. Understanding locomotion at the level of muscle action at each joint provides a bridge for understanding the link between the movements of the center of mass and the actions of individual muscle-tendon units. Little published information is available about muscle moments and mechanical work at each joint during locomotion in diverse animal species [44, 94, 136]. Thus, it is difficult to assess the similarities and differences between humans and other animals at this level of organization.

Net Muscle Moments

The muscles of the body operate by exerting moments about joints. To begin to understand how the neuromuscular system produces walking and running, researchers often examine the “net muscle moment” or “generalized muscle moment” about a joint [149, 163]. A net muscle moment includes the moments produced by all of the muscles, tendons, ligaments, and contact forces at the joint. The moment produced by muscle-tendon

forces is thought to be much higher than the moment produced by the ligaments or other joint forces over the range of joint angles that occur during locomotion [149, 154]. As a result, the net muscle moment gives a reasonable approximation of the net moment produced by all the muscles at a joint [12, 46]. An inverse dynamics approach can be used to determine the net muscle moments during locomotion. This involves using force platform, kinematic, and anthropomorphic measurements in concert with a rigid linked segment model. The Newtonian equations of angular and translational motion are applied to each segment starting distally and moving proximally [34, 149, 163].

This type of approach has revealed that the net muscle moment during the ground contact phase of walking is the largest at the ankle and is substantially lower at the knee and hip [18, 19, 32, 34, 115, 135, 143, 146, 148, 162]. At the ankle, the net muscle moment tends to extend (equivalent to "plantarflex") the joint throughout the ground contact phase. Electromyographic (EMG) measurements have revealed that both extensor muscles (e.g., gastrocnemius) and flexor muscles (e.g., tibialis anterior) are active during the ground contact phase, occasionally simultaneously [32]. The observation that the net muscle moment tends to extend the ankle shows that the ankle extensor muscles are creating a larger moment than the ankle flexor muscles. The net muscle moment about the ankle is very small during the swing phase.

The net muscle moments at the knee and hip during the ground contact phase of walking are much smaller and more variable than at the ankle [18, 19, 34, 115, 116, 135, 143, 146, 148, 162]. The ground reaction force vector is closely aligned with the knee and hip. As a result, small net muscle moments at the knee and hip are required in order to exert a given force on the ground [135, 143]. The exact pattern of net muscle moment at the knee and hip varies between subjects and is matched by variation in the EMG patterns of the major limb muscles [115]. This observation has led to the proposal that different individuals use different motor strategies for walking [116, 117]. It has been suggested that these individual patterns are consistent with a strategy that minimizes the total muscle effort for each individual [117].

Walking kinematics are far less variable than the net muscle moments or the muscle activation patterns at the knee and hip [148, 151]. A comparison of strides that have dramatically different net muscle moment patterns at the knee and hip shows that the limb kinematics are remarkably similar. This observation led Winter [146] to propose the idea of a "support moment" equal to the sum of the net muscle moments at the ankle, knee, and hip. Data on walking humans show that the support moment is substantially less variable than the net muscle moment at each individual joint. Thus, it seems that changes in muscle activation and net muscle moment at one joint are offset by changes at another joint. This conclusion is further

supported by the observation that humans with various injuries can still walk in a kinematically normal manner by changing the pattern of muscle activation [150].

As one would expect, the peak magnitude of the net muscle moment at each joint is higher during running than during walking [32, 92, 93, 147]. The leg is compliant during running, and the major leg joints undergo substantial flexion and extension during the ground contact phase. In contrast, during walking, the limb behaves more like a stiff strut, and the joints undergo smaller angular displacements, remaining relatively extended throughout the ground contact phase. As a result of the postural difference, the muscles must generate larger joint moments in order to exert a given force on the ground during running than during walking. The net muscle moment tends to extend the joint at the ankle, knee, and hip during running (Figure 10.9) [32, 92, 93, 147]. The peak net muscle moment is larger at the knee than at the other joints. Indeed, this is a major difference between running and walking. The magnitude of the peak net muscle moment at the knee is much larger during running than walking. The knee is substantially more flexed at the middle of the ground contact phase of running, and as a result, a higher net muscle moment is required in order to exert a given ground force during running compared to walking.

In contrast to walking, running involves little variability in the pattern and magnitude of the ground reaction force or the net muscle moments [147]. It has been speculated that the net muscle moments are less variable in running than in walking because the muscles are operating closer to their force limits [147].

Joint Power and Work

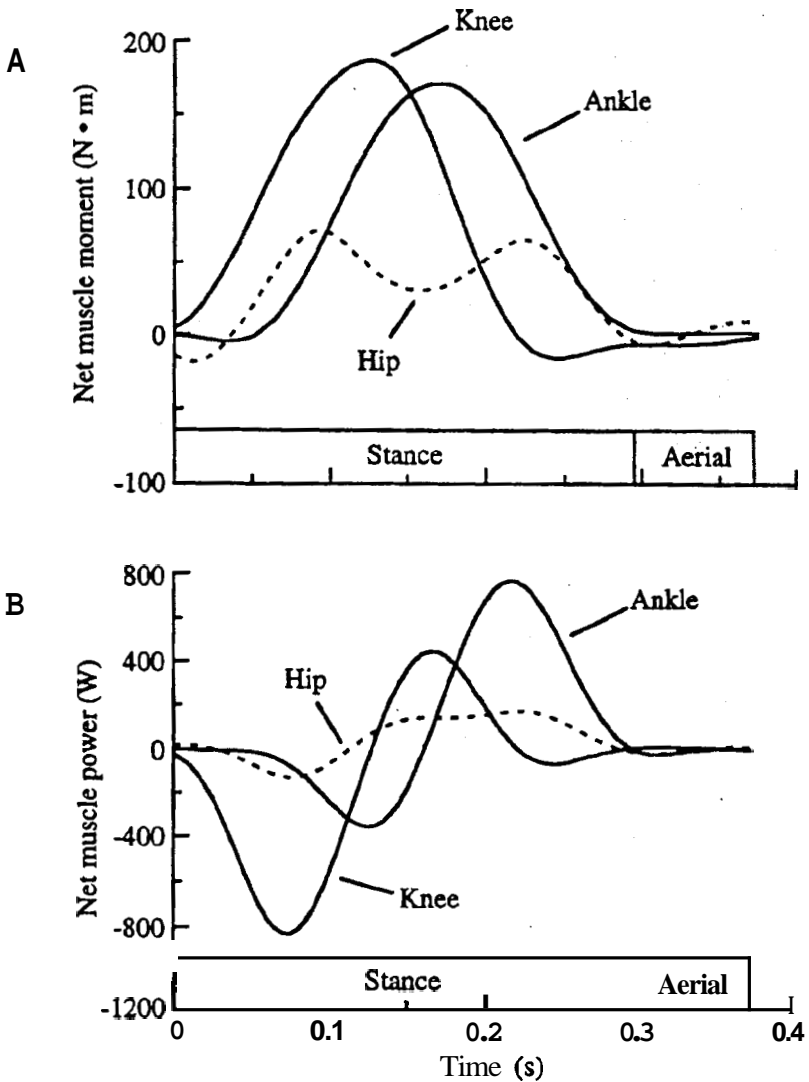
The net power output at a joint can be calculated from the product of the net muscle moment and the joint angular velocity. When the net muscle moment and the angular velocity are both in the same direction, there is net power production at the joint. Conversely, when the net muscle moment and the joint angular velocity are in opposite directions, there is net power absorption at the joint. The net muscle mechanical work can be calculated from the integral of the power with respect to time.

It is important to realize that the net power output measured at a joint is not necessarily produced by muscles that cross that particular joint. This is because there are many muscles in the body that cross more than one joint. These muscles can transport power produced by muscles acting across one joint and allow them to contribute to the power output at another joint [140]. The extent to which this transfer occurs during human walking or running is not clear [80, 122], but there is evidence that energy transfer by biarticular muscles is substantial during cat locomotion [123].

The net power and net work output are substantially lower at all the joints during walking than during running [131, 162]. During walking, both

FIGURE 10.9.

(A) Net muscle moment at the ankle, knee, and hip during running at 2.5 m/s. A positive net muscle moment indicates that it tends to extend the joint. (B) Net muscle power output at the ankle, knee, and hip during running. Positive values indicate that power is produced, and negative values indicate that power is absorbed.



the net muscle moments and the joint angular velocities are lower **than** in running. **The** low net power and work outputs at the **major** limb joints observed during walking would be expected for a limb that is behaving like **a stiff strut**.

The net power output and **work** output are much higher during running than **walking**. The net power **outputs** for slow jogging have been described extensively [147]. **At the ankle and knee**, **an** extensor net muscle moment throughout the ground contact phase exists (Figure 10.9). Meanwhile, the ankle **and** knee **both** **flex and** absorb mechanical energy during **the** first part **of** the ground contact phase. **Later** in the **ground** contact phase, the ankle **and** knee **both** extend and produce mechanical power. The net power output **is small** and unpredictable at the hip. **During** low speed jogging, the ankle produces more mechanical energy **than** it **absorbs**. In contrast, the knee absorbs more mechanical energy **than** it produces.

MUSCLE-TENDON MECHANICS

Examining the net muscle action at joints provides **a** link between whole body dynamics **and** muscle-tendon dynamics during locomotion. This section will discuss muscle-tendon action during locomotion. Unfortunately, it has been difficult to quantify muscle-tendon forces and length changes during locomotion, although recent technological advances have yielded new and exciting findings. In addition, the incredible complexity and apparent redundancy **of the** musculoskeletal system has made discerning general principles about muscle-tendon action during locomotion extremely challenging. In **this** section, we will examine information about muscle-tendon forces and muscle-tendon length changes during locomotion. We will then discuss how **this** information **can** be incorporated into forward dynamics **and** inverse dynamics approaches in order to uncover fundamental rules about how the neuromuscular system produces locomotion.

Muscle-Tendon Force During Locomotion

While center of mass movements **and** net muscle moments at joints can be calculated relatively easily from force platform and video data using an inverse dynamics approach, muscle-tendon forces during locomotion are much more difficult to determine. Each leg joint has multiple muscle-tendon units that **span** it, and each muscle-tendon **has** its own unique force-generating capabilities. Thus, **the** contribution of each muscle-tendon unit acting about a joint **to** the net muscle moment **is** not easily determined. It may seem reasonable **to** use simplifying assumptions to partition the net muscle moment among different muscles that have a given action (e.g., all synergists experience equal stresses), but direct measurements **in vivo** have **shown** that the distribution of muscle force is not so simple. In fact, the

contribution of each synergist changes for different locomotion speeds, different gaits, and even during the course of a single stance phase [10, 44, 68, 70, 145].

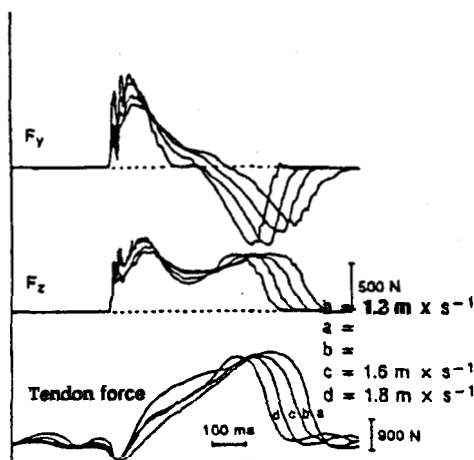
One way researchers have attempted to solve this problem is by employing inverse optimization techniques. Inverse optimization (sometimes called static optimization [161]) uses a model of the musculoskeletal system and requires it to produce specified movement dynamics while optimizing a given cost function (e.g., minimization of the sum of muscle forces) [152]. Although numerous optimization criteria have been suggested for use in the cost function (e.g., minimal muscle force, minimal muscle stress, minimal energy expenditure, minimal ligament force, minimal intra-articular contact force, minimal instantaneous muscle power, and minimal muscle fatigue), no single “best” parameter has been found. In fact, when several of the most commonly used criteria were compared, they predicted remarkably similar patterns of muscle activation, but none demonstrated a close match to the actual EMG patterns over a complete stride cycle [30]. At present, we do not yet sufficiently understand the distribution of forces among synergists to identify any general rules [65].

Muscle-tendon force calculations from an inverse dynamics approach are also complicated by the possibility of coactivation of antagonistic muscle groups. When antagonistic muscle groups are simultaneously active, a higher agonist force is required to exert a given net muscle moment. For example, during the ground contact phase of running, there is an extensor net muscle moment at the knee. EMG studies have shown that knee extensor (e.g., vasti muscles) and knee flexor muscles (e.g., gastrocnemius) are active simultaneously. As a result of this coactivation, a higher force is required from the knee extensors than if there were no coactivation. The coactivation makes it impossible to determine the force in either muscle group from an inverse dynamics approach, since there are an infinite number of combinations of extensor and flexor forces that could produce the same net muscle moment. It is interesting to note, however, that there is little coactivation of extensor and flexor muscles at the ankle during bouncing gaits. Thus, an inverse dynamics approach to calculating ankle extensor force yields reasonably similar values as a direct measurement of the muscle-tendon force [11, 12, 46]. There is substantial antagonist coactivation at the knee and the hip during locomotion, and as a result, an inverse dynamics approach is less likely to yield accurate muscle force values at those joints.

Forces in muscle-tendon units are measured *in vivo* through the use of force transducers on tendons (recently reviewed by Gregor and Abelew [57]). In a few cases, a buckle transducer was placed on the Achilles' tendon of humans [46, 47, 58, 59, 82, 84]. The results from these studies show that the peak Achilles' tendon force slightly decreases or remains about the same (-2.6 kN or 3.6 bodyweights) as humans increase walking speed from

FIGURE 10.10.

Horizontal ground reaction force, vertical ground reaction force, and Achilles tendon force (measured with a tendon buckle) for a human walking at different speed. Reprinted with permission from Komi et al. [84].



1.2 to 1.8 m/s (Figure 10.10) [84]. As they increase speed further and begin running, the peak tendon force increases to a maximum (9 kN or 12.5 bodyweights) at a speed of approximately 6 m/s and then changes very little at higher running speeds [84]. Interestingly, both walking and running involve greater peak Achilles' tendon forces than maximal height squat jumps or countermovement jumps [84]. While these studies have provided rare *in vivo* muscle-tendon data for human locomotion, the invasiveness of the technique limits the possibilities for human studies.

Alternatively, the use of force transducers on the tendons of animals has enabled researchers to investigate numerous different research questions [10, 57, 69, 121, 122, 125, 130]. With animals, tendons can be surgically separated so that force data can be collected from individual muscle-tendon units. Unfortunately, current buckle-type transducers may affect the muscle's force generation since they sometimes damage the tendon, causing it to fray and break [57]. However, new types of force transducers that are actually inserted within a tendon or ligament are being developed that should correct this problem [55, 66, 67, 71, 72, 83, 85].

Muscle-Tendon Length Changes During Locomotion

Perhaps surprisingly, the calculation of muscle and tendon length changes during locomotion is even more complicated than the determination of

muscle-tendon forces. The most common method for calculating muscle-tendon length change has been to use a combination of kinematic and anatomical data. In this approach, the instantaneous muscle-tendon length is estimated from the approximate origin and insertion sites for a given muscle-tendon unit, and from joint kinematic data [6, 45, 56, 60, 106, 120]. However, this technique does not partition the total displacement of the muscle-tendon unit into the length changes due to muscle fiber displacement, muscle fiber pennation angle change, or tendon strain. Each of these factors can substantially affect the total muscle-tendon length, and each has different implications for muscle-tendon function [48, 49, 62, 108, 130].

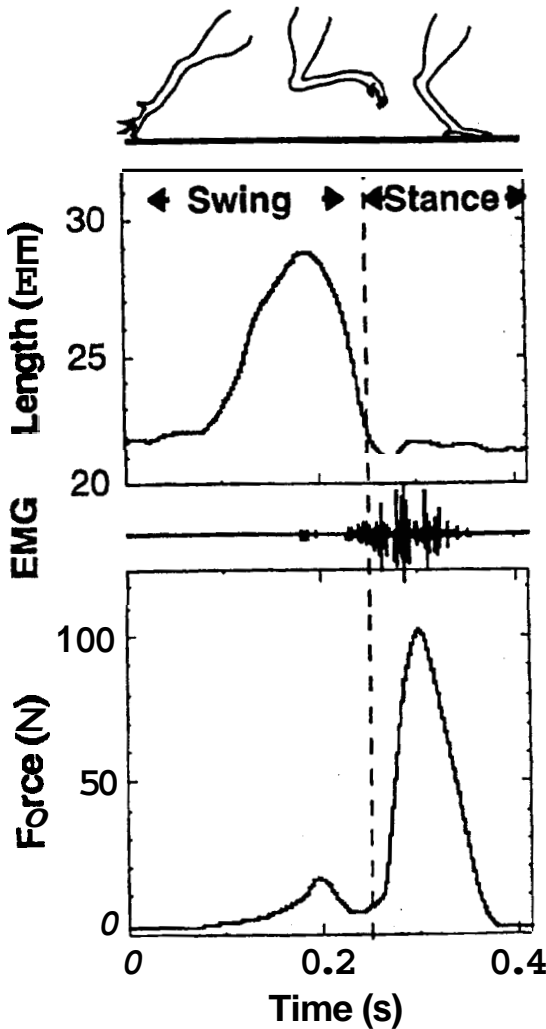
The relevance of partitioning muscle-tendon displacements into respective components becomes evident during "isometric" contractions in which isolated muscle-tendon units are held at a constant total length. When electrically stimulated, the fibers of muscles with long compliant tendons can shorten considerably as the tendon is stretched [36, 62]. Even though the whole muscle-tendon length remains unchanged, each component of the unit changes length substantially. Thus, although it is possible to estimate the length changes of the overall muscle-tendon unit during locomotion, this information tells us little about the relative length changes of the different components of the muscle-tendon unit.

A recent technological innovation is the use of sonomicrometry to measure muscle fiber displacements and velocities *in vivo* [20, 61]. By suturing piezoelectric crystals into a muscle fiber bundle, the time required for ultrasound pulses to travel from one crystal to another can be measured. The transit time can then be used to calculate the instantaneous muscle fiber length. Studies on walking cats and running turkeys have shown that the muscle fiber does not always follow the same displacement pattern as the whole muscle-tendon unit [62, 130]. In walking cats, the medial gastrocnemius muscle fibers shorten at the beginning of the ground contact phase, even though the overall muscle-tendon unit lengthens during this phase [62]. As a result, the tendon is stretched more and stores more elastic energy than would be predicted based on the overall muscle-tendon unit length change. Similarly, when turkeys run on level ground, the gastrocnemius muscle fibers remain nearly isometric during the stance phase while the tendon undergoes substantial length change (Figure 10.11) [130]. The tendon performs the majority of the combined muscle-tendon work while the muscle does very little work. Thus, during level locomotion in both cats and turkeys, the work done by some muscles is greatly reduced by the storage and return of elastic energy in tendons.

Elastic energy storage in tendons is particularly important for bouncing gaits [3]. The ankle extensor tendons have been studied most often, and the results have shown that they play a key role in the storage of elastic energy. In a running human, these tendons can store and return up to 35% of the mechanical energy needed to lift and accelerate the center of

FIGURE 10.11.

*Lateral gastrocnemius muscle fiber length, EMG, and force in a turkey during running at 3 m/s on level ground. Muscle fiber length was measured using sonomicrometry, and muscle force was measured using a strain gauge attached to a calcified portion of the tendon. Reprinted with permission from Roberts, T.J., R.L. Marsh, P.G. Weyand, and C.R. Taylor. Muscular force in running turkeys: the economy of minimizing work. *Science* 275:1113–1115, 1997. Copyright 1997, American Association for the Advancement of Science.*



mass during a stride [81]. Tendon buckle studies on hopping wallabies have revealed that the ankle extensor tendons store and return **enough** elastic energy to reduce the metabolic cost of locomotion by about 50% [10]. It is important to realize that tendon can **be** divided into **two** components—the external free tendon and the aponeurosis [159]. A number of recent **studies** have examined the relative compliance of these **two portions** of the tendon and have come to different conclusions [36, 89, 124, 125, 133, 137, 164]. As a result, it is not clear which part of the tendon is most important in elastic energy **storage** during locomotion.

Role of Forward Dynamics Simulations in Understanding Muscle-Tendon Function During Locomotion

A promising alternative to invasive *in vivo* muscle-tendon measurements in human locomotion is forward dynamics computer simulations of human locomotion [160]. Instead of calculating net muscle moments from the ground reaction force and kinematic **data** (i.e., inverse dynamics), **forward** dynamics simulations rely on musculoskeletal models and computer software **to** predict the muscle activation patterns and muscle-tendon dynamics during **normal** locomotion. The difficulties with this approach, however, are that the results from detailed musculoskeletal models can be extremely sensitive to the specifics **of the** model [87, 155], and experimental validation of the muscle-tendon mechanics **is** difficult to **obtain**. Nonetheless, this approach has been used to simulate human walking with **some** success [119, 157, 158].

Forward dynamics simulations have **also** been used **in** conjunction with sensitivity **analyses** to determine which aspects of musculoskeletal design are most important in dictating the mechanics of locomotion [54]. In the future, this combination of forward dynamics simulations **and** sensitivity analyses should prove valuable in providing insight into how muscle-tendon properties and activation patterns can affect joint dynamics and center of **mass** movements during locomotion.

When **forward** dynamics simulations are employed in conjunction with optimization techniques, they **allow** the researcher **to** probe the link between muscle-tendon properties **and** muscle activation patterns based on **possible** goals **of** the central nervous system (called “dynamic optimization” by Zajac [160] and “**forward** dynamic optimization” by Winters [152]). In this approach, a parameter **or** function **is** assumed to be optimized **by** the neuromuscular system, and the pattern of muscle activation that optimizes **that** parameter or function is identified. **This** approach **is** used most often **to** study movements in **which** an optimality criterion is **obvious**, such as a **single maximum** height vertical jump [7, 16, 17, 112-114, 140-142]. For locomotion, it **is** difficult to determine which parameter or function should be optimized. One possibility is **that the** minimization of metabolic energy cost **is** the most important factor in determining which neuromuscular strat-

egy is used in sustained locomotion [4, 138]. However, controlling the level of musculoskeletal forces and stresses can **also play an** important role [41, 118]. Indeed, it seems most likely that multiple factors work in concert to shape locomotion, suggesting that multiple optimization criteria should be used [153].

Data from experiments on equine locomotion **support** the idea that **multiple** factors **work** in concert to shape locomotion, **and thus, that** multiple optimization criteria should be used. Experiments have revealed that there are at least **two** factors involved in **the** choice of locomotor speed and gait in horses—metabolic energy cost minimization **and** musculoskeletal force minimization. During unrestrained overground locomotion, horses only use a small **range** of speeds within each gait, and within this range of speeds, the metabolic energy cost is lower **than** at **any** other speed within the **gait** [74]. **This** observation suggests that metabolic energy cost is an important factor that influences the choice of speed during locomotion [73]. Nevertheless, when the mechanics and energetics of the transition from trotting to galloping are examined more closely, it is clear that horses do **not** choose to switch **from** one gait to another at the speed that would minimize **the** metabolic energetic cost of locomotion [41]. **Rather**, the choice of gait transition speed seems to be most influenced **by** the level of musculoskeletal force [41]. **Thus**, at least **two** factors are important in shaping locomotion in horses, emphasizing the need to consider multiple optimization criteria in forward dynamics simulations of locomotion.

Role of an Inverse Dynamics Approach in Understanding Muscle-Tendon Function During Locomotion

The complexity of the neuromuscular system has hindered progress in gaining a fundamental understanding of **how** locomotion is produced. This complexity has made it difficult to reach a synthesized understanding of locomotion. **As a** result, it may be helpful to pursue an alternative to a reductionist approach that begins with detailed descriptions of individual muscles and their neural control. This possibility may have been best expressed by **Loeb** who asked whether “it is useful to collect yet more inexplicable data,” and suggested that “it **may** be useful to consider the performance goals of the whole behavior” [90]. Given the tremendous complexity of the nervous **sys-**tem **and** the musculoskeletal system, we can imagine a seemingly infinite number of possible neuromuscular strategies that could produce the locomotion of humans and other animals. Indeed, numerous different patterns of joint moments and muscle activation can produce normal walking [115, 116, 148]. By reaching an understanding of overriding performance **goals** (e.g., the need **for** a given “support moment” **during** walking, [146], **we** can focus in on a more limited range of potential strategies that will produce normal locomotion. **An** inverse dynamics approach that begins with defined performance **goals** at the whole organism level allows us to do this.

Simple behavioral models play an important role in an inverse dynamics approach to understanding locomotion. They provide a mechanical description of the overall behavior (or "performance goals") of the musculoskeletal system during locomotion. Behavioral models represent the behavior but not the structure of the musculoskeletal system during locomotion. For example, as described previously, a simple spring-mass system provides a reasonably accurate model of running. This model works because the human leg behaves much like a spring during running. However, we are all well aware that the human leg is not actually a spring. Rather, it is made up of multiple muscles, tendons, and ligaments that span several joints. Thus, after identifying an appropriate behavioral model, we must begin to consider how the real musculoskeletal system produces the observed behavior.

In the example case of running, the observation that the overall leg behaves like a spring suggests that the production of spring-like behavior may be an important organizing principle for the actions of multiple muscle-tendon units. The goal of producing spring-like behavior limits the number of potential solutions for the behavior of individual joints, interactions between multiple joints, and actions of individual muscle-tendon units that span each joint. It also makes it clear that an important next step is to examine the spring-like properties of individual joints and muscle-tendon units during running. At this point in the progression, a combination of information from behavioral models and realistic musculoskeletal models is likely to be most powerful in dissecting the roles of individual joints and muscle-tendon units in determining leg stiffness, and thus, the mechanics of running.

CONCLUSIONS

Humans use the same basic mechanisms to walk and run as other legged animals. Walking gaits rely on a transfer of kinetic and gravitational potential energies with each step similar to an inverted pendulum. Running gaits, on the other hand, can be characterized as bouncing gaits and modeled with a simple spring-mass system. These two behavioral models, the inverted pendulum and the spring-mass system, provide researchers with simple descriptions of overall limb behavior and center of mass movements during walking and running. This information can provide guidance in attempts to discern general rules by which the neuromuscular system produces locomotion at the increasingly complex lower levels of organization.

ACKNOWLEDGMENTS

This work was supported in part by the National Institutes of Health (R29 AR44008) and the National Aeronautics and Space Administration (NGT-51416).

REFERENCES

1. Alexander, R.M. Mechanics and scaling of terrestrial locomotion. T.J. Pedley (ed.). *Scale Effects in Animal Locomotion*. New York: Academic Press, 1977, pp. 93–110.
2. Alexander, R.M. Terrestrial Locomotion. P.M. Alexander and G. Goldspink (eds.), *Mechanics and Energetics of Animal Locomotion*. London: Chapman & Hall, 1977, pp. 168–203.
3. Alexander, R.M. *Elastic Mechanisms in Animal Movement*. Cambridge: Cambridge University Press, 1988.
4. Alexander, R.M. Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* 69:1199–1227, 1989.
5. Alexander, R.M. A model of bipedal locomotion on compliant legs. *Philos. Trans. R. Soc. Lond. B* 338:189–198, 1992.
6. Alexander, R.M., and A. Vernon. Mechanics of hopping by kangaroos (Macropodidae). *J. Zool. (London)* 177:265–303, 1975.
7. Anderson, F.C., and M.C. Pandy. Storage and utilization of elastic strain energy during jumping. *J. Biomech.* 26:1413–1427, 1993.
8. Basmajian, J.V., and C. De Luca. *Muscles Alive: Their Function Revealed by Electromyography*. Baltimore: Williams & Wilkins, 1985.
9. Beuter, A., and F. Lalonde. Analysis of a phase transition in human locomotion using singularity theory. *Neurosci. Res. Comm.* 3:127–132, 1988.
10. Biewener, A.A., and R.V. Baudinette. In vivo muscle force and elastic energy storage during steady-speed hopping of tammar wallabies, (*Macropus eugenii*). *J. Exp. Biol.* 198: 1829–1841, 1995.
11. Biewener, A.A., and R. Blickhan. Kangaroo rat locomotion: design for elastic energy storage or acceleration? *J. Exp. Biol.* 140:243–255, 1988.
12. Biewener, A.A., R. Blickhan, A.K. Perry, N.C. Heglund, and C.R. Taylor. Muscle force during locomotion in kangaroo rats: force platform and tendon buckle measurements compared. *J. Exp. Biol.* 137:191–205, 1988.
13. Blickhan, R. The spring-mass model for running and hopping. *J. Biomech.* 22:1217–1227, 1989.
14. Blickhan, R., and R.J. Full. Locomotion energetics of ghost crab. II. Mechanics of the center of mass during walking and running. *J. Exp. Biol.* 130:155–174, 1987.
15. Blickhan, R., and R.J. Full. Similarity in multilegged locomotion: bouncing like a monopode. *J. Comp. Physiol. A* 173:509–517, 1993.
16. Bobbert, M.F., and A.J. Van Soest. Effects of muscle strengthening on vertical jump height: a simulation study. *Med. Sci. Sports Exerc.* 26:1012–1020, 1994.
17. Bobbert, M.F., and J.P. Van Zandwijk. Dependence of human maximum jump height on moment arms of the bi-articular m. gastrocnemius: a simulation study. *Hum. Mov. Sci.* 13:697–716, 1994.
18. Bresler, B., and J.P. Frankel. The forces and moments in the leg during level walking. *J. Appl. Mech.* 7:227–36, 1950.
19. Cappozzo, A., F. Figura, and M. Marchetti. The interplay of muscular and external forces in human ambulation. *J. Biomech.* 9:35–43, 1976.
20. Caputi, A.A., J.A. Hoffer, and I.E. Pose. Velocity of ultrasound in active and passive cat medial gastrocnemius muscle. *J. Biomech.* 25:1067–1074, 1992.
21. Cavagna, G.A., P. Franzetti, and T. Fuchimoto. The mechanics of walking in children. *J. Physiol. (London)* 343:323–339, 1983.
22. Cavagna, G.A., N.C. Heglund, and C.R. Taylor. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* 233: R243–R261, 1977.
23. Cavagna, G.A., and M. Kaneko. Mechanical work and efficiency in level walking and running. *J. Physiol. (London)* 268:647–681, 1977.
24. Cavagna, G.A., L. Komarek, and S. Mazzoleni. The mechanics of sprint running. *J. Physiol. (London)* 217:709–721, 1971.

25. Cavagna, G.A., and R Margaria. Mechanics of walking. *J. Appl. Physiol.* **21**:271-278, 1966.
26. Cavagna, G.A., F. P. Saibene, and R. Margaria. External work in walking. *J. Appl. Physiol.* **18**:1-9, 1963.
27. Cavagna, G.A., F.P. Saibene, and R Margaria. Mechanical work in running. *J. Appl. Physiol.* **19**:249-256, 1964.
28. Cavagna, G.A., H. Thys, and A. Zamboni. The sources of external work in level walking and running. *J. Physiol. (London)* **262**:639-657, 1976.
29. Cavanagh, P.R., and M.A. LaFortune. Ground reaction forces in distance running. *J. Biomech.* **13**:397-406, 1980.
30. Collins, J.J. The redundant nature of locomotor optimization laws. *J. Biomech.* **28**:251-267, 1995.
31. Cook, T.M., K.P. Farrell, I.A. Carey, J.M. Gibbs, and G.E. Wiger. Effects of restricted knee flexion and walking speed on the vertical ground reaction force during gait. *J. Orthop. Sports Phys. Ther.* **25**:236-244, 1997.
32. DeVita, P. The selection of a standard convention for analyzing gait data based on the analysis of relevant biomechanical factors. *J. Biomech.* **27**:501-508, 1994.
33. Diedrich, F.J., and W.H. Warren, Jr. Why change gaits? Dynamics of the walk-run transition. *J. Exp. Psychol. Hum. Percept. Perform.* **21**:183-202, 1995.
34. Elftman, H. Forces and energy changes in the leg during walking. *Am. J. Physiol.* **124**:339-356, 1939.
35. Elftman, H. The work done by muscles in running. *Am. J. Physiol.* **129**:672-684, 1940.
36. Ettema, C.J., and P. A Huijing. Properties of the tendinous structures and series elastic component of EDL muscle-tendon complex of the rat. *J. Biomech.* **22**:1209-1215, 1989.
37. Farley, C.T., R. Blickhan, J. Saito, and C.R. Taylor. Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits. *J. Appl. Physiol.* **71**:2127-2132, 1991.
38. Farley, C.T., J. Glasheen, and T.A. McMahon. Running springs: speed and animal size. *J. Exp. Biol.* **185**:71-86, 1993.
39. Farley, C.T., and O. Gonzalez. Leg stiffness and stride frequency in human running. *J. Biomech.* **29**:181-186, 1996.
40. Farley, C.T., and T.C. Ko. Two basic mechanisms in lizard locomotion. *J. Exp. Biol.* **200**:2177-2188, 1997.
41. Farley, C.T., and C.R. Taylor. A mechanical trigger for the trot-gallop transition in horses. *Science* **253**:306-308, 1991.
42. Ferris, D.P., and C.T. Farley. Interaction of leg stiffness and surface stiffness during human hopping. *J. Appl. Physiol.* **82**:15-22, 1997.
43. Ferris, D.P., M. Louie, and C.T. Farley. Adjustments in running mechanics to accommodate different surface stiffnesses. *Physiologist* **39**:A59, 1996.
44. Fowler, E.G., R.J. Gregor, J.A. Hodgson, and R.R. Roy. Relationship between ankle muscle and joint kinetics during the stance phase of locomotion in the cat. *J. Biomech.* **26**:465-483, 1993.
45. Frigo, C. Determination of the muscle length during locomotion. E. Asmussen and K. Jorgensen (eds.). *Biomechanics VII-A*. Baltimore, MD: University Park Press, 1978. pp. 355-360.
46. Fukashiro, S., P.V. Komi, M. Jarvinen, and M. Miyashita. Comparison between the directly measured Achilles tendon force and the tendon force calculated from the ankle joint moment during vertical jumps. *Clin. Biomech.* **8**:25-30, 1993.
47. Fukashiro, S., P.V. Komi, M. Jarvinen, and M. Miyashita. In vivo Achilles tendon loading during jumping in humans. *Eur. J. Appl. Physiol.* **71**:453-458, 1995.
48. Fukunaga, T., Y. Ichinose, M. Ito, Y. Kawakami, and S. Fukashiro. Determination of fascicle length and pennation in a contracting human muscle in vivo. *J. Appl. Physiol.* **82**:354-358, 1997.
49. Fukunaga, T., Y. Kawakami, S. Kuno, K. Funato, and S. Fukashiro. Muscle architecture and function in humans. *J. Biomech.* **30**:457-463, 1997.
50. Full, R.J. Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. W. Wieser and E. Cnaiger (eds.). *Energy Transformations in Cells and Animals*. Stuttgart: Thieme, 1989. pp. 175-182.

51. Full, R.J., and M.S. Tu. Mechanics of six-legged runners. *J. Exp. Biol.* 148:129-146, 1990.
52. Full, R.J., and M.S. Tu. Mechanics of a rapid running insect two-, four- and six-legged locomotion. *J. Exp. Biol.* 156:215-231, 1991.
53. Garcia, M. A. Chatterjee, A. Ruina, and M. Coleman. The simplest walking model: stability, complexity, and scaling. *Biomech. Eng.* In Press.
54. Gerritsen, K.G., A.J. van den Bogert, and B.M. Nigg. Direct dynamics simulation of the impact phase in heel-toe running. *J. Biomech.* 28:661-668, 1995.
55. Glos, D.L. D. L. Butler, E.S. Grood, and M.S. Levy. In vivo evaluation of an implantable force transducer (IFT) in a patellar tendon model. *J. Biomech. Eng.* 115:335-343, 1993.
56. Goslow, C.E., Jr., R.M. Reinking, and D.G. Stuart. The cat step cycle: hind limb joint angles and muscle lengths during unrestrained locomotion. *Morph.* 141:1-41, 1973.
57. Gregor, R.J., and T.A. Abelew. Tendon force measurements and movement control: a review. *Med. Sci. Sports Exerc.* 26:1359-1372, 1994.
58. Gregor, R.J., P.V. Komi, R.C. Browning, and M. Jarvinen. A comparison of the triceps surae and residual muscle moments at the ankle during cycling. *J. Biomech.* 24:287-297, 1991.
59. Gregor, R.J., P.V. Komi, and M. Jarvinen. Achilles tendon forces during cycling. *Int. J. Sports Med.* 8(Suppl. 1):9-14, 1987.
60. Grieve, D.W., S. Pheasant, and P.R. Cavanagh. Prediction of gastrocnemius length from knee and ankle posture. E. Asmussen and K. Jorgensen (eds.), *Biomechanics VI-A*, Baltimore, MD: University Park Press, 1978, pp. 405-412.
61. Griffiths, R.I. Ultrasound transit time gives direct measurement of muscle fiber length in vivo. *J. Neurosci. Methods* 21:159-165, 1987.
62. Griffiths, R.I. Shortening of muscle fibers during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *J. Physiol. (London)* 436:219-236, 1991.
63. He, J.P., R. Kram, and T.A. McMahon. Mechanics of running under simulated low gravity. *J. Appl. Physiol.* 71:863-870, 1991.
64. Heglund, N.C., J.A. Cavagna, and C.R. Taylor. Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97:41-56, 1982.
65. Herzog, W. Force sharing among synergistic muscles: theoretical considerations and experimental approaches. *Exerc. Sport Sci. Rev.* 24:173-202, 1996.
66. Herzog, W., J.M. Archambault, T.R. Leonard, and H.K. Nguyen. Evaluation of the implantable force transducer for chronic tendon-force recordings. *J. Biomech.* 29:103-109, 1996.
67. Herzog, W., E.M. Hasler, and T.R. Leonard. In-situ calibration of the implantable force transducer. *J. Biomech.* 29:1649-1652, 1996.
68. Herzog, W., and T.R. Leonard. Validation of optimization models that estimate the forces exerted by synergistic muscles. *J. Biomech.* 24(Suppl 1):31-39, 1991.
69. Henog, W., and T.R. Leonard. Soleus forces and soleus force potential during unrestrained cat locomotion. *J. Biomech.* 29:271-279, 1996.
70. Hodgson, J.A. The relationship between soleus and gastrocnemius muscle activity in conscious cats: a model for motor unit recruitment? *J. Physiol. (London)* 337:553-562, 1983.
71. Holden, J.P., E.S. Grood, and J.F. Cummings. Factors affecting sensitivity of a transducer for measuring anterior cruciate ligament force. *J. Biomech.* 28:99-102, 1995.
72. Holden, J.P., E.S. Grood, D.L. Korvick, J.F. Cummings, D.L. Butler, and D.I. Bylski-Austrow. In vivo forces in the anterior cruciate ligament direct measurements during walking and trotting in a quadruped. *J. Biomech.* 27:517-526, 1994.
73. Hoyt, D.F., and C.R. Taylor. Gait and energetics of locomotion in horses. *Nature* 292:239-240, 1981.
74. Hoyt, R.W., J.J. Knapik, J.F. Lanza, B.H. Jones, and J.S. Staab. Ambulatory foot contact monitor to estimate metabolic cost of human locomotion. *J. Appl. Physiol.* 76:1818-1822, 1994.

75. Hreljac, A. Determinants of the gait transition speed during human locomotion: kinetic factors. *Gait Post.* 1:217-223, 1993.
76. Hreljac, A. Preferred and energetically optimal gait transition speeds in human locomotion. *Med. Sci. Sports Exerc.* 25:1158-1162, 1993.
77. Hreljac, A. Determinants of the gait transition speed during human locomotion: kinematic factors. *J. Biomech.* 28:669-677, 1995.
78. Hreljac, A. Effects of physical characteristics on the gait transition speed during human locomotion. *Hum. Mov. Sci.* 14:205-216, 1995.
79. Inman, V.T., H.J. Ralston, and F. Todd. Human locomotion. J. Rose and J. G. Gamble (eds.). *Human Walking (2nd ed.)*. Baltimore, MD: Williams & Wilkins, 1994, pp. 2-22.
80. Jacobs, R., M.F. Bobbert, and G.J. van Ingen Schenau. Function of mono- and biarticular muscles in running. *Med. Sci. Sports Exerc.* 25:1163-1173, 1993.
81. Ker, R.F., M.B. Bennett, S.R. Bibby, R.C. Kester, and R.M. Alexander. The spring in the arch of the human foot. *Nature* 325:147-149, 1987.
82. Komi, P.V. Relevance of in vivo force measurements to human biomechanics. *J. Biomech.* 23(Suppl 1):23-34, 1990.
83. Komi, P.V., A. Belli, V. Huttunen, R. Bonnefoy, A. Geysant, and J.R. Lacour. Optic fibre as a transducer of tendomuscular forces. *Eur. J. Appl. Physiol* 72:278-280, 1996.
84. Komi, P.V., S. Fukashiro, and M. Jarvinen. Biomechanical loading of Achilles tendon during normal locomotion. *Clin. Sports Med.* 11:521-531, 1992.
85. Korvick, D.L., J.F. Cummings, E.S. Grood, J.P. Holden, S.M. Feder, and D.L. Butler. The use of an implantable force transducer to measure patellar tendon forces in goats. *J. Biomech.* 29:557-561, 1996.
86. Kram, R., A. Domingo, and D.P. Ferris. Effect of reduced gravity on the preferred walk-run transition speed. *J. Exp. Biol* 200:821-826, 1997.
87. Lehman, S.L. Input identification depends on model complexity. J.M. Winters and S.L.Y. Woo (eds.). *Multiple Muscle Systems: Biomechanics and Movement Organization*. New York: Springer-Verlag, 1990, pp. 94-100.
88. Li, Y., R.H. Crompton, R.M. Alexander, M.M. Gunther, and W.J. Wang. Characteristics of ground reaction forces in normal and chimpanzee-like bipedal walking by humans. *Folia Primatologica* 66:137-159, 1996.
89. Lieber, R.L., M.E. Leonard, C.G. Brown, and C.L. Trestik. Frog semitendinosus tendon load-strain and stress-strain properties during passive loading. *Am. J. Physiol.* 261: C86-C92, 1991.
90. Loeb, G.E. Hard lessons in motor control from the mammalian spinal cord. *Trends Neurosci.* 10:108-113, 1987.
91. Loeb, G.E. Neural control of locomotion: how do all the data fit together? *Bioscience* 39: 800-804, 1989.
92. Mann, R., and P. Sprague. A kinetic analysis of the ground leg during sprint running. *Res. Quart. Exerc. Sport* 51:334-348, 1980.
93. Mann, R.V. A kinetic analysis of sprinting. *Med. Sci. Sports Exerc.* 13:325-328, 1981.
94. Manter, J. The dynamics of quadrupedal walking. *J. Exp. Biol* 15:522-540, 1938.
95. Margaria, R. Sulla fisiologia e specialmente sul consumo energetico della marcia e della corsa a varie velocità ed inclinazioni del terreno. *Atti Accad. Naz. Lincei Memorie* 7:299-368, 1938.
96. Margaria, R. *Biomechanics and Energetics of Muscular Exercise*. Oxford: Clarendon Press, 1976.
97. McGeer, T. Passive dynamic walking. *Int. J. Robotics Res.* 9:62-82, 1990.
98. McGeer, T. Principles of walking and running. R.M. Alexander (ed.). *Mechanics of Animal Locomotion*. Berlin: Springer-Verlag, 1992, pp. 113-139.
99. McGeer, T. Dynamics and control of bipedal locomotion. *J. Theor. Biol* 163:277-314, 1993.
100. McMahon, T.A., and C.C. Cheng. The mechanics of running: how does stiffness couple with speed? *J. Biomech.* 23(suppl. 1):65-78, 1990.

101. McMahon, T.A., G. Valiant, and E.C. Frederick. Groucho running. *J. Appl. Physiol.* 62: 2326-2337, 1987.
102. Mercier, J., D. Le Gallais, M. Durand, C. Goudal, J.P. Micallef, and C. Prefaut. Energy expenditure and cardiorespiratory responses at the transition between walking and running. *Eur. J. Appl. Physiol.* 69:525-529, 1994.
103. Minetti, A.E., L.P. Ardigo, and F. Saibene. The transition between walking and running in humans: metabolic and mechanical aspects at different gradients. *Acta Physiol. Scand.* 150:315-323, 1994.
104. Mochon, S., and T.A. McMahon. Ballistic walking. *J. Biomech.* 13:49-57, 1980.
105. Mochon, S., and T.A. McMahon. Ballistic walking: an improved model. *Math. Biosci.* 52: 241-260, 1980.
106. Morrison, J.B. The mechanics of muscle function in locomotion. *J. Biomech.* 3:431-451, 1970.
107. Muir, G.D., J.M. Gosline, and J.D. Steeves. Ontogeny of bipedal locomotion: walking and running in the chick. *J. Physiol. (London)* 493:589-601, 1996.
108. Narici, M.V., T. Binzoni, E. Hiltbrand, J. Fasel, F. Terrier, and P. Cerretelli. In vivo human gastrocnemius architecture with changing joint angle at rest and during graded isometric contraction. *J. Physiol. (London)* 496:287-297, 1996.
109. Pandy, M.G., and N. Berme. Synthesis of human walking: a planar model for single support. *J. Biomech.* 21:1053-1060, 1988.
110. Pandy, M.C., and N. Berme. Quantitative assessment of gait determinants during single stance via a three-dimensional model-Part 1: normal gait. *J. Biomech.* 22:717-724, 1989.
111. Pandy, M.G., and N. Berme. Quantitative assessment of gait determinants during single stance via a three-dimensional model-Part 2: pathological gait. *J. Biomech.* 22:725-733, 1989.
112. Pandy, M.C., and F.E. Zajac. Dependence of jumping performance on muscle strength, muscle-fiber speed, and tendon compliance. J.L. Stein, J.A. Ashton-Miller, and M.C. Pandy (eds.), *Issues in the Modeling and Control of Biomechanical Systems: 1989 ASME Winter Annual Meeting in San Francisco*. New York: The American Society of Mechanical Engineers, 1989, pp. 59-63.
113. Pandy, M.G., and F.E. Zajac. Optimal muscular coordination strategies for jumping. *J. Biomech.* 24:1-10, 1991.
114. Pandy, M.C., F.E. Zajac, E. Sim, and W.S. Levine. An optimal control model for maximum-height human jumping. *J. Biomech.* 23:1185-1198, 1990.
115. Pedotti, A. A study of motor coordination and neuromuscular activities in human locomotion. *Biol. Cyber.* 26:53-62, 1977.
116. Pedotti, A., and P. Crenna. Individual strategies of muscle recruitment in complex natural movements. J.M. Winters and S.L.Y. Woo (eds.), *Multiple Muscle Systems: Biomechanics and Movement Organization*. New York: Springer-Verlag, 1990, pp. 542-549.
117. Pedotti, A., V. Krishnan, and L. Stark. Optimization of muscle-force sequencing in human locomotion. *Math. Biosci.* 38:57-76, 1978.
118. Pern, A.K., R. Blickhan, A.A. Biewener, N.C. Heglund, and C.R. Taylor. Preferred speeds in terrestrial vertebrates: are they equivalent? *J. Exp. Biol.* 137:207-219, 1988.
119. Piazza, S.J., and S.L. Delp. The influence of muscles on knee flexion during the swing phase of gait. *J. Biomech.* 29:723-733, 1996.
120. Pierrynowski, M.R. Analytic representation of muscle line of action and geometry. P. Allard, L.A.F. Stokes, and J.P. Blanchi (eds.), *Three-Dimensional Analysis of Human Movement*. Champaign, IL: Human Kinetics, 1995, pp. 215-256.
121. Prilutsky, B.I., W. Herzog, and T.L. Allinger. Force-sharing between cat soleus and gastrocnemius muscles during walking: explanations based on electrical activity, properties, and kinematics. *J. Biomech.* 27:1223-1235, 1994.
122. Prilutsky, B.I., W. Herzog, and T.L. Allinger. Mechanical power and work of cat soleus, gastrocnemius and plantaris muscles during locomotion: possible functional significance of muscle design and force patterns. *J. Exp. Biol.* 199:801-814, 1996.

123. Prilutsky, B.I., W. Herzog, and T. Leonard. Transfer of mechanical energy between ankle and knee joints by gastrocnemius and plantaris muscles during cat locomotion. *J. Biomech.* 29:391-403, 1996.
124. Prilutsky, B.I., W. Henog, T. Leonard, and T.L. Allinger. Role of the muscle belly and tendon of soleus, gastrocnemius, and plantaris in mechanical energy absorption and generation during cat locomotion. *J. Biomech.* 29:417-434, 1996.
125. Prilutsky, B.I., W. Herzog, T. Leonard, and T.L. Allinger. Authors' response. *J. Biomech.* 30:309, 1997.
126. Raibert, M.H. *Legged Robots That Balance*. Cambridge, MA: MIT Press, 1986.
127. Raibert, M.H. Trotting, pacing and bounding by a quadruped robot. *J. Biomech.* 23(suppl. 1):79-98, 1990.
128. Raibert, M.H., and J.K. Hodgins. Legged robots. RD. Beer, RE. Ritzmann, and T. McKenna (eds.). *Biological Neural Networks in Neuroethology and Robotics*. Boston: Academic Press, 1993, pp. 319-354.
129. Raibert, M.H., R.R. Playter, J.K. Hodgins, et al. *Dynamically Stable Legged Locomotion*. Cambridge, MA: Massachusetts Institute of Technology, 1993.
130. Roberts, T.J., R.L. Marsh, P.G. Weyand, and C.R. Taylor. Muscular force in running turkeys: the economy of minimizing work. *Science* 275:1113-1115, 1997.
131. Robertson, D.G. and D.A. Winter. Mechanical energy generation, absorption and transfer amongst segments during walking. *J. Biomech.* 13:845-854, 1980.
132. Saunders, J.B., V.T. Inman, and H.D. Eberhart. The major determinants in normal and pathological gait. *J. Bone Jt. Surg.* 35:543-558, 1953.
133. Scott, S.H., and G.E. Loeb. Mechanical properties of aponeurosis and tendon of the cat soleus muscle during whole-muscle isometric contractions. *J. Morph.* 224:73-86, 1995.
134. Siegler, S., R. Seliktar, and W. Hyman. Simulation of human gait with the aid of a simple mechanical model. *J. Biomech.* 15:415-425, 1982.
135. Simonsen, E.B., P. Dyhre-Poulsen, M. Voigt, P. Aagaard, and N. Fallentin. Mechanism contributing to different joint moments observed during human walking. *Scand. J. Med. Sci. Sports* 7:1-13, 1997.
136. Smith, J.L., S.H. Chung, and R.F. Zernicke. Gait-related motor patterns and hindlimb kinetics for the cat trot and gallop. *Exp. Brain Res.* 94:308-322, 1993.
137. Solomonow, M. Comment on "Role of muscle belly and tendon of soleus gastrocnemius and plantaris in mechanical energy absorption and generation during cat locomotion." *J. Biomech.* 30:307-308, 1997.
138. Taylor, C.R. Relating mechanics and energetics during exercise. *Adv. Vet. Sci. Comp. Med.* 38A:181-215, 1994.
139. Thorstensson, A., and H. Rotherthson. Adaptations to changing speed in human locomotion: speed of transition between walking and running. *Acta. Physiol. Scand.* 131:211-214, 1987.
140. van Ingen Schenau, G.J., M.F. Bobbert, and A.J. van Soest. The unique action of bi-articular muscles in leg extensions. J.M. Winters and S.L.Y. Woo (eds.). *Multiple Muscle Systems: Biomechanics and Movement Organization*. New York: Springer-Verlag, 1990, pp. 639-652.
141. van Soest, A.J., M.F. Bobbert, and G.J. van Ingen Schenau. A control strategy for the execution of explosive movements from varying starting positions. *J. Neurophysiol.* 71: 1390-1402, 1994.
142. van Soest, A.J., A.L. Schwab, M.F. Bobbert, and G.J. van Ingen Schenau. The influence of the biarticularity of the gastrocnemius muscle on vertical-jumping achievement. *J. Biomech.* 26:1-8, 1993.
143. Vaughan, C.L. Are joint torques the Holy Grail of human gait analysis? *Hum. Mov. Sci.* 15:423-443, 1996.
144. Vukobratovic, M., A.A. Frank, and D. Juricic. On the stability of biped locomotion. *IEEE Trans. Biomed. Eng.* 17:25-36, 1970.

145. Walmsley, B., J.A. Hodgson, and R.E. Burke. Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *J. Neurophysiol.* 41: 1203–1216, 1978.
146. Winter, D.A. Overall principle of lower limb support during stance phase of gait. *J. Biomech.* 13:923–927, 1980.
147. Winter, D.A. Moments of force and mechanical power in jogging. *J. Biomech.* 16:91–97, 1983.
148. Winter, D.A. Kinematic and kinetic patterns in human gait: variability and compensating effects. *Hum. Mov. Sci.* 3:51–76, 1984.
149. Winter, D.A. *Biomechanics and Motor Control of Human Movement*. New York: Wiley, 1990.
150. Winter, D.A. Human movement: a system-level approach. M.A. Arbib (ed.). *The Handbook of Brain Theory and Neural Networks*. Cambridge, MA: MIT Press, 1995, pp. 472–477.
151. Winter, D.A., G.K. Rudner, and C.D. MacKinnon. Control of balance of upper body during gait. J.M. Winters and S.L.Y. Woo (eds.). *Multiple Muscle Systems: Biomechanics and Movement Organization*. New York: Springer-Verlag, 1990, pp. 534–541.
152. Winters, J.M. Concepts in neuromuscular modeling. P. Allard, I.A.F. Stokes and J.P. Blanchi (eds.). *Three-Dimensional Analysis of Human Movement*. Champaign, IL: Human Kinetics, 1995, pp. 257–292.
153. Winters, J.M. Studying posture/movement selection and synergia via a synthesized neuro-optimization framework. J.M. Winters and P.E. Crago (eds.). *Biomechanics and Neural Control of Movement*. New York: Springer-Verlag, In Press.
154. Winters, J.M., and L. Stark. Analysis of fundamental human movement patterns through the use of in-depth antagonistic muscle models. *IEEE Trans. Biomed. Eng.* 32:826–839, 1985.
155. Winters, J.M., and L. Stark. Muscle models what is gained and what is lost by varying model complexity. *Biol. Cyber.* 55:403–420, 1987.
156. Yaguramaki, N., S. Nishizawa, K. Adachi, and B. Endo. The relationship between posture and external force in walking. *Anthropological Science* 103:117–139, 1995.
157. Yamaguchi, C.T. Performing whole-body simulations of gait with 3-D, dynamic musculoskeletal models. J.M. Winters and S.L.Y. Woo (eds.). *Multiple Muscle Systems: Biomechanics and Movement Organization*. New York: Springer-Verlag, 1990, pp. 663–679.
158. Yamaguchi, G.T., M.G. Pandy, and F.E. Zajac. Dynamic musculoskeletal modeling of human locomotion: perspectives on model formulation and control. A.E. Paüa (ed.). *Adaptability of Human Gait*. Amsterdam: North-Holland, 1991, pp. 205–240.
159. Zajac, F.E. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *Crit. Rev. Biomed. Eng.* 17:359–411, 1989.
160. Zajac, F.E. Muscle coordination of movement: a perspective. *J. Biomech.* 26:109–124, 1993.
161. Zajac, F.E., and M.E. Gordon. Determining muscle's force and action in multi-articular movement. *Exerc. Sport Sci. Rev.* 17:187–230, 1989.
162. Zarrugh, M.Y. Kinematic prediction of intersegment loads and power at the joints of the leg in walking. *J. Biomech.* 14:713–725, 1981.
163. Zernicke, R.F., and J.L. Smith. Biomechanical insights into neural control of movement. L.B. Rowell and J.T. Shepherd (eds.). *Handbook of Physiology, Section 12. Exercise: Regulation and Integration of Multiple Systems*. New York: Oxford University Press, 1996, pp. 293–330.
164. Zuurbier, C.J., A.J. Everard, P. van der Wees, and P.A. Huijting. Length-force characteristics of the aponeurosis in the passive and active muscle condition and in the isolated condition. *J. Biomech.* 27:445–453, 1994.