Chapter I

Integration of Individual Leg Dynamics with Whole Body Movement in Arthropod Locomotion

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I. Introduction

This chapter highlights recent advances in the mechanics of invertebrate legged locomotion to show why neural control studies must consider musculoskeletal dynamics. In contrast to studies of neural control, little is known about the mechanics of locomotion or, more specifically, leg dynamics. In a 1985 symposium on insect locomotion Delcomyn stated that

> [The mechanics of locomotion] is an area of research that has never attracted many adherents, yet which provides much information that is essential in order for progress to be made in our understanding of the physiological basis of locomotion.

In addition to the issue of approach, I will propose concepts that can be transferred from the mechanics of invertebrate legged locomotion to the design of more versatile legged robots.

II. Forward versus Inverse Dynamics

The last 20 years has seen substantial and significant research on the neural control of arthropod legs (see reviews by Bassler, 1987; Clarac, 1981; Cruse, 1985, 1990;
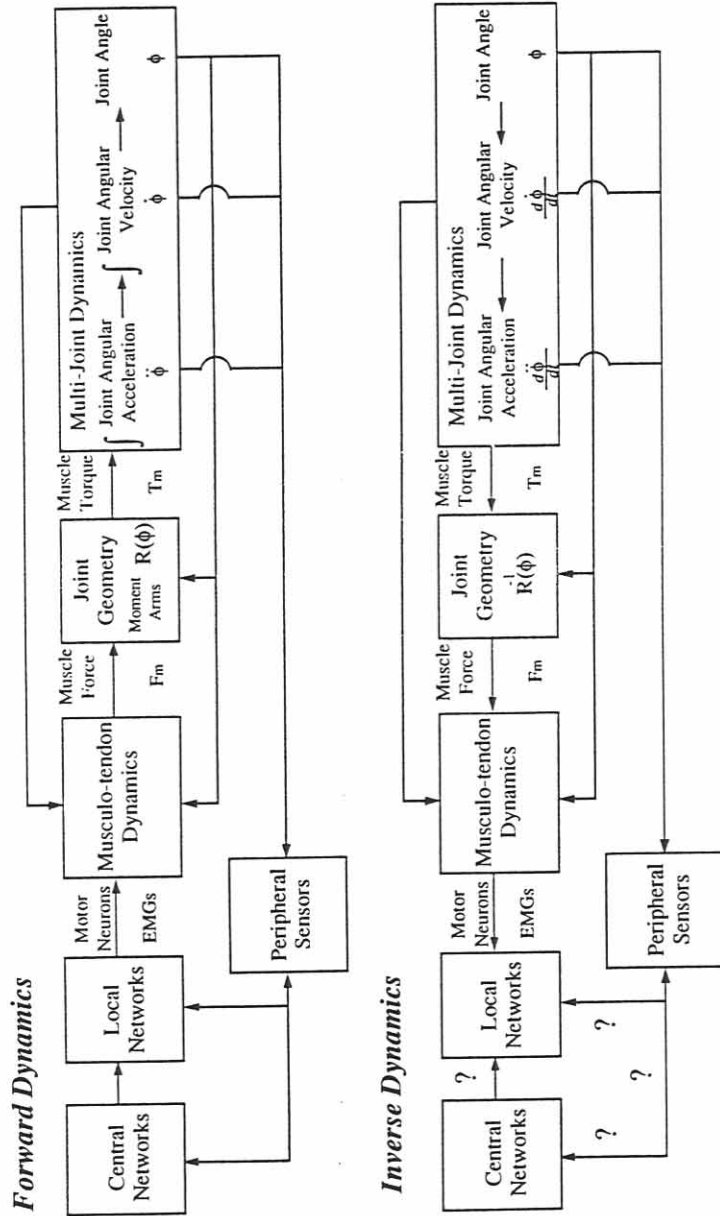
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FIGURE 1. Forward versus inverse approach to dynamics. Forward dynamics characterizes the "controller" to predict leg movements, the "plant." Inverse dynamics uses leg movement and force production to make inferences about the "controller." Most of the research on arthropod locomotion has taken the forward approach. Research using the inverse approach is necessary in the future. Adapted from Zajac, F. E., and Gordon, M. E., *Exerc. Sport Sci. Rev.* 17, p. 187. © 1989 ACSM.

Delcomyn, 1981, 1984, 1985; Graham, 1985; Pearson, 1985; Zill, 1985). Considerable progress toward understanding the control of legged locomotion has been achieved by characterizing the "controller" (i.e., the associated central and sensory neural networks; Fig. 1). Such a determination of the pathways and information flow between sensory input and motor output layers is essential to the understanding of locomotor dynamics. The characterization of central pattern generators and relaxation oscillators; the identification of servo systems based on velocity, load, and position; and the description of ipsilateral and contralateral leg coupling are evidence of the advancements.

Despite this progress, attempting to characterize the controller before or in isolation from the musculoskeletal system (i.e., the "plant") is extremely problematic for several reasons (Zajac and Gordon, 1989). First, the flow of information associated with neural and musculoskeletal systems is not unidirectional but is a closed loop. Muscle and joint sensors feed back information about limb and body position, velocity, and force. In this sense, the musculoskeletal system can be considered the controller, and the neural system becomes the plant. Second, a single motor neuron's activity pattern can result in several completely different musculoskeletal responses, depending on the context within which the neural activity is generated. For example, the activation of an extensor muscle while joint angle is decreasing can result in absorption of energy by that muscle, whereas identical activation of the same extensor muscle while a joint angle is increasing can result in generation of energy. If limb segments on both sides of the joint have the same angular velocity, the activation of the same extensor muscle can result in a near-isometric contraction and energy transfer. In this sense, "feedback" can occur within the musculoskeletal system, and joint position and velocity can determine musculoskeletal dynamics. Likewise, joint angle can affect joint geometry by altering moment arms that will, in turn, affect joint dynamics through torque development. The third major difficulty with conventional "forward" dynamics has been that force determination for two or more legs on the ground is an indeterminate problem.

An alternative approach, termed *inverse dynamics*, uses the output to make inferences concerning the input (Fig. 1). Muscle torque at a joint can be determined from joint dynamics. Muscle force at a joint can be estimated from joint geometry. Muscle activity patterns can be predicted from muscle force estimates. Neural function can then be inferred from muscle activity patterns. With the inverse approach, quantified behavior (i.e., leg movements and force development) can be related unambiguously to neural control. The more that is learned about the plant (i.e., the musculoskeletal system), the better the neural controller can be defined and the better the whole system can be understood from an engineering and design

standpoint. This approach is complementary to the more conventional *forward dynamics* and neuronal *circuit breaking* approaches.

Few investigations have used inverse dynamics and correlated motor neuron output, muscle activity, and kinematics (i.e., description of stepping patterns) with the actual kinetics (i.e., force development) involved in generating locomotion (Delcomyn, 1985). Studies that have been conducted underscore the diversity of leg function. Ground reaction forces of standing and slow-walking spiders differ depending on the leg measured (Blickhan and Barth, 1985). Cruse (1976) demonstrated that pairs of legs in a walking stick insect each generate a distinct ground reaction force pattern. In rock lobsters walking under water, leg four appears to control movement, whereas leg five functions as a strut (Clarac and Cruse, 1982; Cruse *et al.*, 1983). In crayfish, leg four produces most of the propulsive force, whereas leg three exerts the largest vertical force (Klarner and Barnes, 1986). Vertical force patterns are distinct in the second and third legs of crickets (Harris and Ghiradella, 1980).

Even though several of these studies have demonstrated the importance of load or force in feedback control, they have not produced an adequate model of leg function. It is not clear what types of leg dynamics neural activity patterns actually generate. For several reasons, this gap prevents the study of information flow from the nervous system to behavior.

First, in most neural studies, leg function has been oversimplified. Function is typically divided into a power stroke (or stance phase) and a return stroke (e.g., Cruse, 1990). This dichotomy assumes that all legs in a stance phase are equivalent. Yet, muscle of joints in different legs or even the same leg can be shortening to produce energy, lengthening while absorbing energy, or contracting isometrically to transfer energy. The assumption that extensors only extend and flexors only flex is unrealistic. In 1952 Hughes proposed a simple model for the function of insect legs. Legs could function as levers, inclined struts, or both, depending on the direction of the ground reaction force vector. If a significant horizontal accelerating force is observed which directs the ground reaction force in an anterior or forward direction, then the leg functions as a lever in that direction. A leg functions as a strut if the ground reaction force vector is directed back toward the joint. Hughes (1952) reported that the second and third legs function as inclined struts, while the first leg of cockroaches functions as a lever. Cruse (1976) showed that the legs of stick insects do not necessarily follow this model. First and second legs in stick insects can act as levers or inclined struts depending on the orientation of movement considered.

Second, the dynamic passive functions of the leg have been largely ignored. Legs can function as inverted pendulums and springs that may demand less, or simpler, neural control.

Third, many of the studies have focused on animals (i.e., stick insects, crayfish, and lobsters) moving at very low speeds. These animals lack the speed and maneuverability desirable in a model of legged locomotion. Moreover, leg control undoubtedly changes significantly when little or no time is available for feedback during medium to fast locomotion (Delcomyn, 1991: Zill, 1985).

III. Motion of the Body or Center of Mass

For most multilegged animals, it is difficult to predict the movement of the whole body even when the dynamics of isolated legs are known. Numerous studies have documented the enormous variation in leg position and phase (Delcomyn, 1985; Delcomyn and Cocatre-Zilgien, 1988). Does this variation represent the error resulting from a given neural output? It is unclear whether the same variation is apparent in the force and power production of legs. Results from our study of ghost crabs suggest considerable variation in force production for single legs (Blickhan and Full, 1987). Our work on insect leg force development showed somewhat less variation (Full and Tu. 1990, 1991: Full *et al.,* 1991). More important, what is most striking in all our kinetics studies is the regularity in the movement of the body or center of mass. It may be insufficient to determine the flow of information to individual legs without considering the movement produced by all the legs simultaneously. Analysis of an "effective" or "virtual" leg that represents the action of all legs would allow a link to be made between neural input and behavior. Defining leg function in the context of the motion of the whole body is essential to the understanding of locomotor control.

One might expect the whole body of many-legged animals to move like the body of some legged robots (Full *et al.,* 1989). Many multilegged vehicles or robots have been designed to be "wheel-like" (Fig. 2A). The more legs an animal has, the smoother the ride. Acceleration and deceleration of the body or center of mass are made negligible. The body of the robot is given a smooth ride to minimize energetic cost or for stabilization of sensors. Primarily vertically directed, ground reaction forces are observed. This can be achieved by using a telescoping leg, the equivalent of a bent knee. The smooth ride can also be attained by using a slider mechanism that is the equivalent of a pantograph leg design. Many models of multilegged locomotion also assume a quasi-static walking gait in which static equilibrium is maintained throughout a stride. More simply, the robot must be like a stool at all times with at least three legs supporting its body. This is especially

A

Telescoping Leg
Wheel-like Dynamics
"Bent Knee Equivalent"

Slider
Wheel-like Dynamcs
"Pantograph Leg Equivalent"

B

"Stiff Leg"
Inverted Pendulum
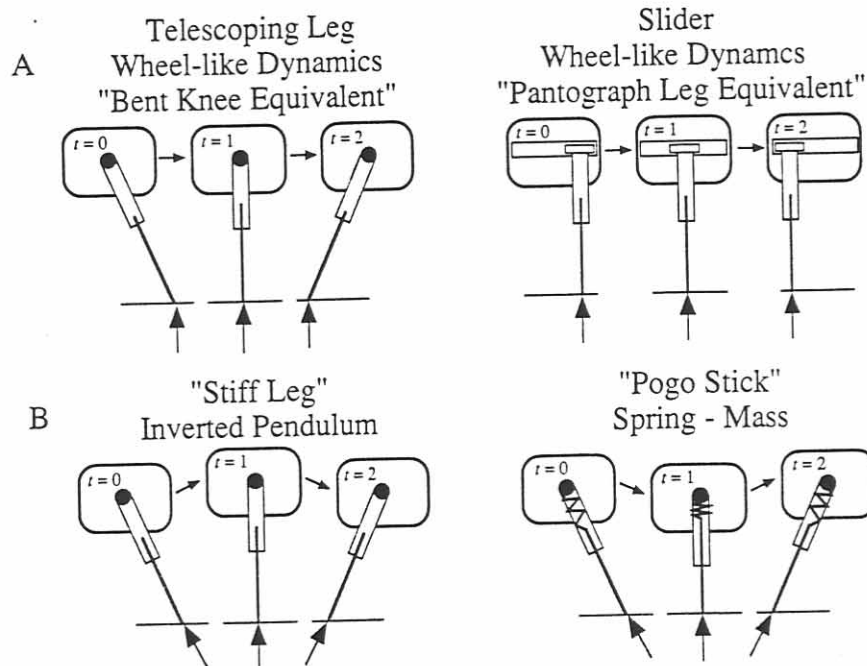
"Pogo Stick"
Spring - Mass

FIGURE 2. Leg design in terrestrial locomotion. (A) Many robots use wheel-like dynamics, where the body moves with little oscillation (horizontal arrows) and the ground reaction forces are directed vertically (vertical arrows), thereby reducing the acceleration and deceleration of the body. Wheel-like dynamics can be attained by using a telescoping joint, the equivalent of a bent knee, or by using a slide, the equivalent of a pantograph mechanism. Notice the large moments that are created around the hip of a telescoping leg. (B) In contrast to many robots, animals use legs that function as inverted pendulums and pogo sticks. Ground reaction forces show that the body is accelerated and decelerated as it oscillates up and down. In both mechanisms energy can be exchanged or stored and recovered. Reprinted from *The International Journal of Robotics Research* 9:2, "Three Uses for Springs in Legged Locomotion," by R. McN. Alexander by permission of the MIT Press, Cambridge, Massachusetts, © 1990 MIT Press.

true if the robot is close to the ground, because it doesn't take long to hit the substratum if the center of mass falls outside the base of support.

Surprisingly, multilegged arthropods are not restricted to wheel-like movement or balancing like stools. Locomotion of the whole body more closely resembles an inverted pendulum or spring–mass system than it does a wheel (Blickhan, 1989; Full, 1989, 1991; McGeer, 1990). During walking, two- and four-legged animals use an energy-conserving mechanism that is analogous to an inverted, swinging pendulum or an egg rolling end over end (Fig. 3) (Cavagna *et al.*, 1976, 1977; Heglund *et al.*, 1982). By using this pendulum-like mechanism, kinetic energy and gravitational potential energy fluctuate out of phase so as to allow recovery of
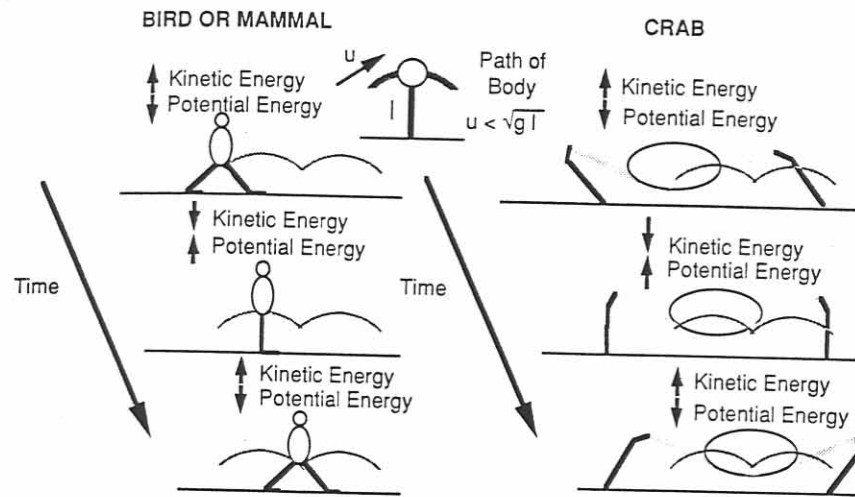
FIGURE 3. Inverted pendulum mechanism of walking for a biped and crab. One leg of a biped and four legs of a crab act to move the body through a series of arcs of radius, l. Potential energy and kinetic energy fluctuate out of phase such that kinetic energy can be recovered as potential energy and vice versa. The maximum speed (*u*) predicted must be less than the square root of the product of acceleration due to gravity (*g*) and radius. After Blickhan and Full (1987).

energy as the animal's center of mass rises and falls during a stride. Vaulting over a relatively stiffened leg in humans can conserve up to 70% of the energy that must otherwise be provided by muscles and tendons. Blickhan and Full (1987) have shown that eight-legged ghost crabs do not move with a constant velocity of the center of mass and are not wheel-like. Crabs can use a pendulum-like mechanism during walking (Fig. 3). Energy recovery in these arthropods can reach 55%.

Cockroaches don't appear to use this walking mechanism, even at lower speeds (Full and Tu, 1990, 1991). The percent recovery averages about 6–15% and is not a function of speed. At all intermediate speeds, cockroaches use a regular, symmetric alternating tripod gait. The right front, left middle, and right hind legs all move simultaneously in a step, while each moves out of phase with its contralateral pair (Fig. 4). In this gait, cockroaches do not move with a constant velocity of the center of mass and are also not wheel-like. Distinct maxima and minima in the whole ground reaction forces are apparent. Each vertical force peak is correlated with a step of an alternating set of legs. As the animal's body comes down on a tripod, it decelerates in the horizontal direction. Its vertical force increases above body weight. As the body lifts up, it is accelerated and the vertical force decreases below body weight. This pattern is repeated for the next step of the tripod. In contrast to a pendulum-like walk-
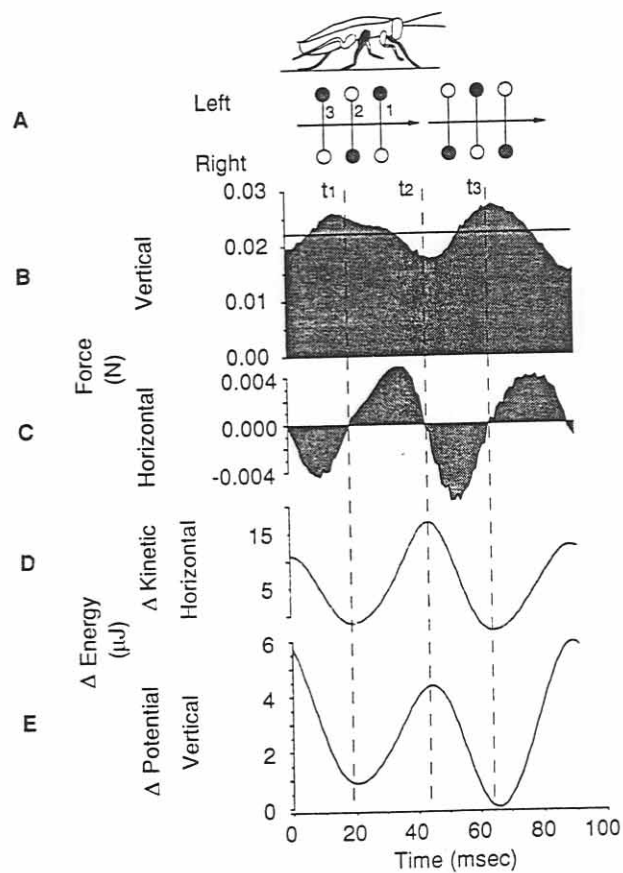
FIGURE 4. Gait, ground reaction force, and energy of the center of mass during one stride (i.e., one complete leg cycle) of a 2.3 g cockroach traveling at 0.25 m s^{-1}. Tracings represent the following: (A) The gait used is an alternating tripod in which the right front, left middle, and right hind legs all moved simultaneously, while each moved out of phase with its contralateral pair. In the gait diagram filled circles represent legs on the ground (retracting or in stance phase), whereas open circles show legs in protraction (swing phase). (B) Vertical and (C) horizontal forces obtained from a force platform. (D) Horizontal kinetic energy and (E) gravitational potential energy fluctuations of the center of mass. Horizontal line in B represents the animal's weight.

ing gait, potential energy and kinetic energy fluctuate in phase during cockroach locomotion.

In 1978 Alexander and Jayes made a link between the vertical force pattern and the gait an animal was using. They found that vertical force patterns could be described by a modified Fourier series and a single measure called the shape
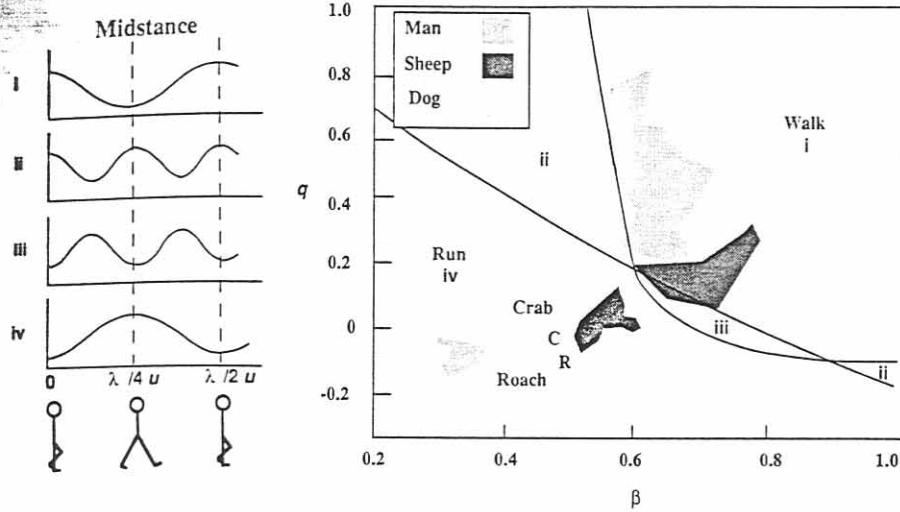
FIGURE 5. Gait characterization by shape and duty factor. The shape of the vertical force pattern (Fv) can be described at any time T by a modified Fourier series where $Fv = a\,[\cos(\pi t/T) - q\,\cos(3\pi t/T)]$ from the time a foot is set down ($-T/2$) to when it is lifted ($+T/2$). For crabs and cockroaches, the shape factor describing the force pattern ($q = -0.1$ to 0) and duty factor (the fraction of a stride duration a foot is on the ground, $\beta = 0.5$) corresponds to a run or trot when compared with two- and four-legged vertebrates. From Alexander and Jayes (1978).

factor, q. If the shape factor is plotted as a function of duty factor (β), the fraction of a stride the leg is on the ground, different gaits or styles of locomotion can be separated (Fig. 5). For example, if an animal was walking, at midstance the position of the center of mass would be at its lowest point, whereas if the animal was running, the position of the center of mass would be at the highest point. On the basis of q and β, walks and runs fall into distinct zones. If the shape factor for cockroaches and crabs (i.e., at higher speeds) is plotted as a function of duty factor, both arthropods fall clearly in the area of a run (Fig. 5). Cockroaches and crabs can use a running gait even though at these trotting speeds they don't show aerial phases. In both species, potential energy and kinetic energy fluctuate in phase as they would if the body were bouncing with springs. McMahon *et al.* (1987) have shown that an aerial phase is not a requirement for the definition of a bouncing or running gait. Humans running with bent legs, like Groucho Marx, show this pattern and don't have aerial phases.

Despite the differences in morphology, at intermediate and high speeds, two-, four-, six-, and eight-legged animals produce ground force patterns that are fundamentally similar. All can run or bounce. Running humans, trotting dogs, cockroaches, and sideways-running crabs can move their bodies by producing

alternating propulsive forces. Two legs in a trotting quadrupedal mammal, three legs in an insect, and four legs in a crab can act as one leg does in a biped during ground contact. The center of mass of the animal undergoes repeated acceleration and deceleration with each step, even when traveling at a constant average velocity (Blickhan and Full, 1987; Cavagna et al., 1977; Full and Tu, 1990, 1991; Heglund et al., 1982). Horizontal kinetic energy and gravitational potential energy of the center of mass fluctuate in phase.

The dynamics of crabs and cockroaches suggest that arthropods can use springs and bounce during running like mammals. Equivalent gaits may exist among pedestrians that differ greatly in morphology. Further evidence of this equivalence or similarity comes from examining the relationship between stride frequency and running speed. In quadrupedal mammals, stride frequency increases linearly with speed during trotting (Heglund et al., 1974; Heglund and Taylor, 1988). Stride frequency becomes independent of speed as they switch to a gallop. Galloping quadrupeds move faster by increasing stride length. Blickhan and Full (1987) found a similar pattern in ghost crabs. At the fastest galloping speeds, ghost crabs use fewer legs. leap. and have aerial phase (Burrows and Hoyle. 1973). Full and Tu (1990) discovered a similar relationship in cockroaches. As speed increases, stride frequency eventually attains a maximum. After finding this pattern in the cockroach. we wondered whether equivalent gait transitions in two-, four-, six-, and eight-legged animals could be identified. We scaled the maximum sustainable stride frequency and the speed at which it was attained in crabs and cockroaches with the data already available for mammals (Heglund et al., 1974; Heglund and Taylor, 1988). Surprisingly, when the effect of size is removed, legged animals attain a similar maximum sustainable stride frequency at a similar speed (Full, 1989, 1991). For example, a crab and a mouse of the same mass change gait at the same stride frequency (9 Hz) and speed (0.9 m/s; Blickhan and Full, 1987). These data suggest that legged animals may consist of multijointed springs.

IV.   Quasi-Static Versus Dynamic Stability

Our results from the study of six- and eight-legged runners (Blickhan and Full, 1987; Full and Tu. 1990, 1991; Full et al., 1991) provide strong evidence that dynamic effects cannot be ignored in multilegged runners that are maneuverable, as has been done in the design of multilegged robots (e.g., Bressonov and Umnov, 1973; Song, 1984; Song and Waldron, 1989).

Most six-legged insects use an alternating tripod gait at most speeds such that at least three legs are on the ground at any time during locomotion. The legs of arthro-

TABLE I. Comparison of Legged Locomotion in Animals and Vehicles

	No. of legs	Hip height, h (m)	Speed u (m/s)	Frequency, f (Hz)	Froude no., $u^2/(gh)$
Crab walking	8	0.035	0.4	3.2	0.4
Man walking	2	0.9	1.6	1	0.3
Dog walking	4	0.5	1.3	1.6	0.4
Crab trotting	8	0.035	0.9	6.2	2.4
Cockroach trotting	6	0.004	0.3	13	1.7
Man jogging	2	0.9	3.3	1.6	1.2
Dog trotting	4	0.5	2.7	2.2	1.5
Turtle	4	0.07	0.1	0.6	0.02
3-D hopper	1	0.6	2.2	1.5	0.9
Kenkaku 1	2	0.6	0.8	1.1	0.1
PV II	4	0.4	0.02	—	0.0001
NCTU quadruped	4	0.6	0.01	0.02	0.00002
Quadruped trotting	4	0.6	2.2	1.2	0.9
Quadruped bounding	4	0.6	2.9	2.4	1.5
Sutherland hexapod	6	0.2	0.1	—	0.005
ASV	6	1.8	3.6	—	0.7
ReCUS	8	3.5	0.07	0.03	0.0001

After Alexander (1989).

pods generally radiate outward, providing a wide base of support. It has been suggested that the morphology of the limbs provides stability against such disturbances as wind and uneven terrain. Alexander (1982) has suggested that an insect such as a cockroach is so close to the ground that the animal must always have three legs in contact with the surface or it would fall to the ground before taking the next step. Hughes (1952) stated that the six-legged condition is the "end-product of evolution" because the animal can always be statically stable. Several robots have been designed with a quasi-static gait criterion that seems very similar to insect locomotion. The center of mass moves smoothly and is contained within a triangle or quadrilateral of support. However, these walking machines move very slowly, so a quasi-static condition is required (Alexander, 1989; Song and Waldron, 1989). Speeds and frequencies used by these robots are low compared to those of animals. Froude numbers (i.e., the ratio of inertial to gravitational forces) indicate that most robots do not move in a dynamically similar fashion to animals (Table I). Most legged robots are dynamically more similar to turtles. Raibert's amazing robots at MIT are an obvious exception because they rely on dynamic stability (Raibert and Sutherland, 1983).

Contrary to the hypothesis that static stability is one of the most important design criteria in arthropods and in the design of robots, we have found that

dynamic stability is crucial even in small, multilegged animals (Ting *et al.,* 1990). First, we have shown that crabs and cockroaches employ a running or bouncing gait that is dynamically similar to trotting in quadrupeds and to running in bipeds (Blickhan and Full, 1987; Full, 1989; Full and Tu, 1990). Second, at high speeds ghost crabs propel themselves with two legs on the trailing side of the body as they leap into the air (Blickhan and Full, 1987; Burrows and Hoyle, 1973). The American cockroach can run quadrupedally and bipedally at high speeds (Full and Tu, 1991). These gaits demand dynamic stability. Third, cockroaches with ablated middle legs run with a duty factor of less than 0.75 without falling (Pham and Full, 1989). Fourth, the stability margin (i.e., the minimum distance from the center of mass to the base of support) decreases linearly with speed and becomes negative at the lowest speeds (i.e., statically unstable, Fig. 6) (Ting *et al.,* 1990). Moreover, the position of the center of mass moves posteriorly with speed. Stability margin is actually related to speed and momentum because if the animal attempts to stop instantaneously, it will keep moving forward, essentially tossing itself into the support triangle. Fifth, ground reaction forces create moments about the center of mass that cause pitching and rolling of the body. The resultant force or center of pressure is not directed through the center of mass. If the animal was stopped (i.e.,
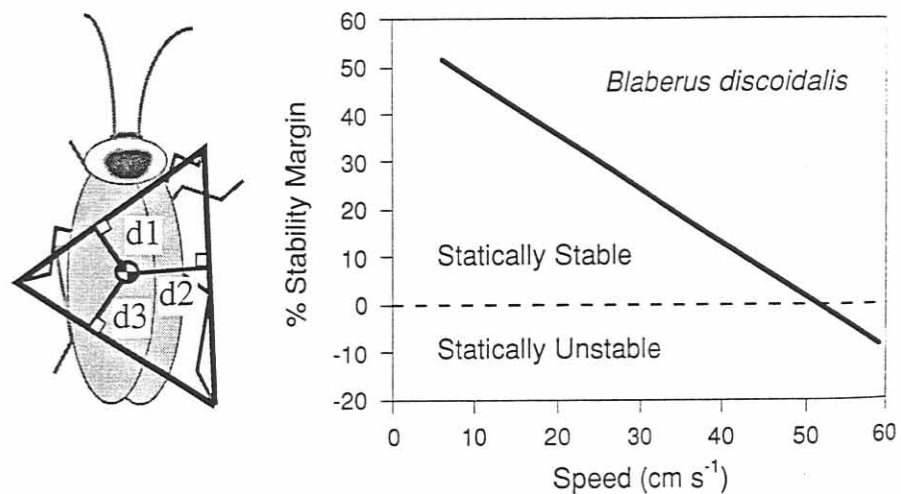

FIGURE 6. Percent stability margin as a function of speed in cockroaches. Stability margin is the minimum distance (e.g., d1) from the center of mass to the edge of the triangle of support. Percent stability margin is the stability margin normalized to the maximum possible stability margin. Static instability (less than zero percent stability margin) occurs when the center of mass falls outside the base of support.

was examined statically), the resultant force vector would create a moment that could cause the animal to flip over.

Dynamic stability appears to be an important consideration in the analysis of gaits, even in polypedal animals. In fact, at high speeds, the gait in the large tropical cockroach can be best explained using a dynamic, spring–mass model of running and hopping (Blickhan, 1989; McMahon and Cheng, 1990; Raibert *et al.*, 1986; Ting *et al.*, 1990) (Fig. 7). At low speeds, the cockroach uses a running gait, but due to limitation in vertical displacement the stride frequency is not matched to the natural frequency of the spring–mass model, causing increased angular rotation of the body. The best model at low speeds is one in which there are periods when two springs (i.e., two tripods or all six legs) are on the ground at the same time.
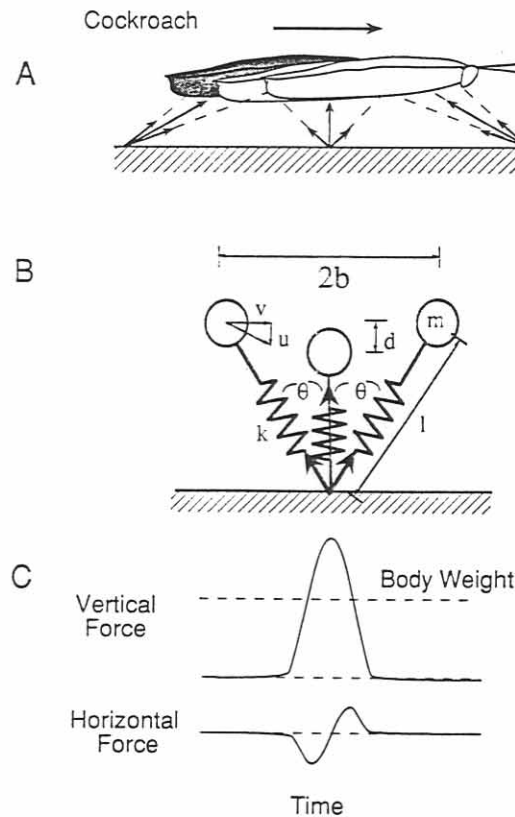

FIGURE 7. Spring–mass model for cockroaches. Three legs of a cockroach, one leg of a biped, two of a trotting quadruped, and four of a trotting crab can be represented by one spring. The dynamics of each of these runners can be described by a spring attached to a mass, the body.

V.   Variation in Individual Leg Dynamics—Similarity in "Effective" Leg Function

Whole-body mechanics in two-, four-, six-, and eight-legged runners is dynamic, not wheel-like, and can be remarkably similar, despite variation in body form or morphology (Full, 1989, 1991; Full *et al.*, 1989). Pedestrians that vary in leg number and design can generate similar ground reaction force patterns. Similarities between mammalian and arthropod whole-body mechanics suggest that rigid constraints may exist on the possible mechanisms by which a leg or legs can function during walking and running.

Trotting quadrupedal mammals, such as dogs, bounce by producing nearly the same force pattern with each leg, just as do humans (Alexander, 1977). In fact, successful trotting quadrupedal robots have been designed so that the kinetics of each leg are the same, differing only in relative phase (Raibert *et al.*, 1986). Individual leg force patterns have the same shape as whole-body force patterns. We hypothesized that similarities in leg function were less likely to be characteristic of six-, and eight-legged runners, even though two-, four-, six-, and eight-legged animals all show a common whole-body, ground-reaction force pattern. It was not obvious how a common pattern could result in runners that have impressive differences in leg morphology.

To explain how diverse leg designs could result in common whole-body dynamics, we used a miniature force platform to measure the ground reaction forces produced by individual legs of a cockroach (Full *et al.*, 1991). Hexapedal runners are not like quadrupeds with an additional set of legs. At a constant average velocity, each leg pair of the cockroach is characterized by a unique ground reaction force pattern. The first leg decelerates the center of mass in the horizontal direction, whereas the third leg is used to accelerate the body. The second leg does both, much like legs in bipedal runners and quadrupedal trotters. Vertical force peaks for each leg are equal in magnitude and significant lateral forces are present.

The orientation of leg ground-reaction forces in the cockroach has several consequences (Fig. 8). Foremost, it rejects the hypothesis that legs result in wheel-like motion of the body. Arthropod legs do not necessarily function according to the design of many existing robot legs, (Fig. 8) where ground reaction forces are primarily vertical and little or no fluctuation of body position is observed (Fig. 2A) (Alexander, 1990). Arthropods legs do not function like sliders or operate like pantograph mechanisms. Instead, legs appear to function as inverted pendulums and springs that result in oscillations of the body (Fig. 2B). The center of mass undergoes accelerations and decelerations that are not necessarily unwanted. Legs in crabs that function as inverted pendulums allow as much as 50% of the energy to be exchanged and recovered (Blickhan and Full, 1987). The energy recovered need not be supplied

Zero Horizontal
"Foot-Force" Interaction

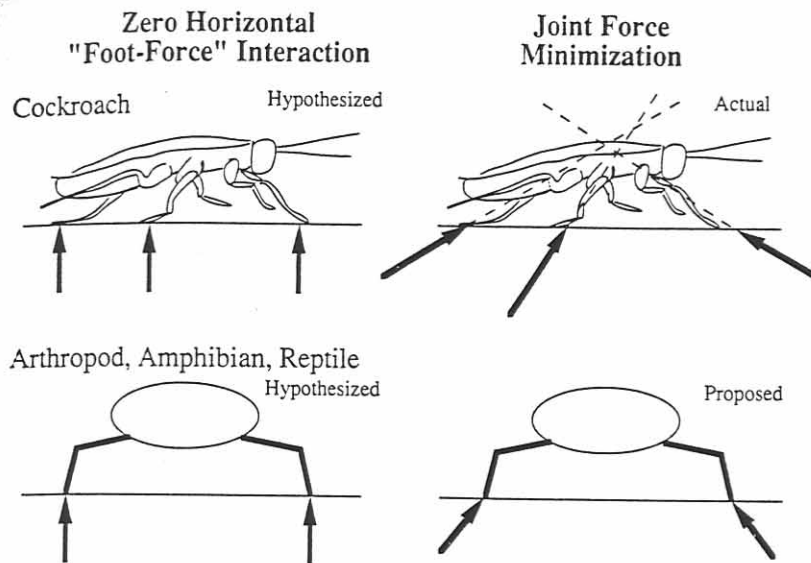**Joint Force**
Minimization

FIGURE 8. Zero horizontal foot-force interaction versus joint force or torque minimization. Zero foot-force interaction, a criterion in the design of many multilegged robots, minimizes accelerations and decelerations of the body but can result in large moments around the "hip" joints. Lateral, anterior, and posterior placement of the limbs results in large moments if zero foot interaction applies. Ground reaction forces in cockroaches are directed more in line with the hip (coxal joint) and tend to minimize torque as they may in other arthropods, amphibians, and reptiles.

by muscles or actuators. Legs in cockroaches may function more like springs (Full *et al.*, 1991). Energy can be absorbed, stored on landing as elastic strain energy, and returned upon takeoff. Both pendulum and spring-like leg functions result in forces that accelerate and decelerate the body, but both can recover or exchange energy.

An equally important consequence stemming from our study on cockroach leg function is related to muscle force production. In the cockroach, peak ground reaction forces are oriented toward the coxal joints (or "hip" equivalent), which articulate with the body (Fig. 8). This arrangement tends to minimize joint moments and muscle forces (Full *et al.*, 1991). Legs of animals do not generate vertically directed ground reaction forces that result in large torques about the "hip" as do some legged robots. They also do not operate under the horizontal, zero-foot force criterion used in the design of legged robots (Waldron, 1986). Legs or "feet" push against one another. Yet, production of horizontal and lateral ground forces that account for most of the mechanical energy generated during locomotion can actually reduce total muscle force by directing the ground reaction forces through the leg joints.

Locomotion with a sprawled posture as seen in small mammals, amphibians, reptiles, and arthropods does not necessarily result in large moments around joints or large muscle forces. This is consistent with the finding that the minimum metabolic cost of locomotion in species that differ in posture can be similar (Full, 1991).

Our investigation of cockroach leg function (Full *et al.*, 1991) has shown a strut/ lever model to be insufficient. Whole-body dynamics common to two-, four-, six-, and eight-legged runners can be produced by different numbers of legs that vary in orientation with respect to the body, generate unique ground reaction force patterns, but combine to function as one leg of a biped.

VI.   Conclusions

We assert that a dynamic analysis of arthropod locomotion is required to develop general principles of motor control. The "plant" must be studied in close association with the "controller." Static hypotheses of the "plant" are insufficient to explain the link between morphology and performance of terrestrial locomotion. Many-legged animals are not like wheels, cars, or most robots. They accelerate and decelerate their bodies. Dynamic stability is an important consideration in the analysis of polypedal locomotion. Locomotion in many pedestrians can be modeled by an inverted pendulum or spring–mass system, and this may explain why equivalent gaits may exist in species that differ so in morphology.

In general, animals do not function like many of the multilegged robots that have been built thus far. To design the most versatile legged robot possible:

1. Dynamic capacities must be integrated with the more thoroughly studied quasi-static capacities that are notable in many legged animals that have the advantage of high stability, a wide base of support, and a low center of mass (i.e., design a six- or eight-legged robot that has spring-like dynamics).
2. Isolated leg dynamics must be integrated with whole-body dynamics.
3. Compensation for environmental perturbations must be studied by integrating neural control with the dynamics of the musculoskeletal system.

Acknowledgments

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