Insect Walking and Biorobotics: A Relationship with Mutual Benefits

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Biorobotics represents a synergistic relationship between engineers attempting to design better robots and biologists attempting to understand principles of movement in animals. There is a long history of engineering research on legged robots, driven by the realization that devices with legs can potentially traverse complex terrains more efficiently than wheeled or track-driven vehicles (Raibert and Hodgins 1993, Beer et al. 1998). However, to achieve this potential, legged vehicles must overcome serious engineering challenges. First, they must be able to support their weight and develop coordinated leg movements to propel themselves from one place to another. They must then be able to alter these movements to change speeds and direction of movement. Speed changes can involve alteration in stepping frequency or stride length and, in extreme cases, alterations in gait (e.g., a horse going from a trot to a gallop). Traversing complex terrains also requires that the vehicle be able to climb over various barriers and to respond to unexpected changes in substrate, such as holes or bumps. During all of these movements, the vehicle must control posture to stay upright. That is, it must calculate and control its center of mass relative to its support base, even as it changes locomotion strategies and, in some cases, lifts new objects of varying weights. Finally, an efficient vehicle must overcome all of these challenges while minimizing power requirements, joint torques, and structural stresses.

Agile animals move efficiently through virtually every conceivable terrain and offer solutions to these challenges. They have solved them through millions of years of evolution, and, although natural selection does not always yield the best solution to a problem, it does yield a workable solution that provides a reasonable starting point for robotic designs. However, biological solutions are “locked away” in complex mechanical bodies and even more complex nervous systems. Biologists are only now beginning to understand how animals solve the many problems of locomotion.

Because of the unsolved problems in both robotics and biology, a successful biorobotics strategy will ultimately benefit both disciplines. What biologists know about animal locomotion can be incorporated into the initial design of a legged robot. A carefully designed robot can then provide a hardware model on which biologists can formulate and test hypotheses regarding how the animal’s nervous system controls complex mechanical legs in a physical environment. These “hardware models” can be much more effective in understanding principles of locomotion than any computer model, including dynamic models that seek to capture the physics of motion. Indeed, there is no better challenge to one’s ideas regarding movement through a complex terrain than to design and build a device based on those ideas and then test it in that terrain. By contrast, robotics problems for which current biological data are lacking must be tackled by engineering techniques. Even in the context of such problems, there can be mutual benefits between the disciplines of biology and engineering. That is, animals must deal with the same physical problems as do legged robots. Therefore, an engineering solution for the biologically based robot can provide new hypotheses about how animals solve the same problem.

In this article, we describe the strategies that we have used to generate successful interactions between biologists and engineers. We then review the types of biological data that have been useful to robotics engineers and discuss some properties of biological systems that could lead to even better robotic designs.

Strategies for biorobotic interactions

Many groups have developed biologically inspired hexapod robots. Two recent examples include Pfeiffer et al.

A BIOROBOTICS EFFORT FOLLOWING A “BIOLOGY-AS-DEFAULT” STRATEGY CAN PROVIDE IMPROVED ROBOTIC DESIGN AS WELL AS INSIGHT INTO HOW ANIMALS FUNCTION

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(1994), who worked with Holk Cruse to build a robot based on the stick insect, and Delcomyn and Nelson (in press), who describe a pneumatic robot based on the cockroach. Previous to the work described in this article, two hexapod robots were developed at Case Western Reserve University (CWRU)—Robot I (Beer et al. 1992, Quinn and Espenschied 1993) and Robot II (Espenschied et al. 1996). Robot I demonstrated that a biologically inspired neural network can control a legged device. Robot II had more insectlike legs and could walk on uneven terrain, using a distributed controller that included a set of stick insect gait coordination mechanisms and local leg reflexes. Numerous other devices have been constructed under the inspiration of various different animals. A comprehensive review of the literature in this area is beyond the scope of this article but can be found in Beer et al. (1998).

In recent years, our group has followed two strategies in biorobotics research. In one, the fundamental design of the robot is based on standard engineering techniques. Biology is then sought to solve specific problems. For example, we are designing a small, legged device for autonomous roving. Autonomy refers to designs that put all necessary control and power on the vehicle rather than having the vehicle and power source connected by tethers. This requirement means that power consumption during walking is a serious problem, and it is even more challenging in a small vehicle that must traverse long distances. Small, legged vehicles (or small animals) must cycle their legs many more times to go from point A to point B than larger vehicles (or animals) moving the same distance. Many small insects overcome the problem of leg cycling by jumping. We have, therefore, decided to incorporate a jump strategy based on cricket locomotion in this particular robot. However, we will not attempt to capture all of the design details of the cricket’s legs. The challenge to the biologists on this project is to identify what aspects of the cricket’s jump are critical to the movement and what aspects can be discarded by the engineers as they attempt to create a functional design. In this effort, biological observation coupled with dynamic computer models plays an important role.

In the second biorobotics strategy, information gained from biological studies on a single species is used throughout the design of the robot. Under this strategy, the engineers and biologists must work together closely from the outset. A basic tenet of this approach is that the biological system provides a default design that should be altered significantly only if there is a good engineering reason for doing so. For example, the biologist might urge the engineer to incorporate all of the animal’s leg movements into the design of the robot. However, the weight and complexity of that many actuators (devices that perform a role analogous to that of muscles) in the robotic legs would be impossible to implement. Thus, there would be a good engineering reason to eliminate some of those joints. Nevertheless, the design for the remaining joints and segments would still capture the dimensions, orientation, and excursion of the animal’s leg, and these joints and segments would be capable of moving like the animal does in the locomotion goals of interest (e.g., walking, climbing, or turning).

This “biology-as-default” notion is subtle, but it is actually the opposite of many biorobotics ventures, in which traditional engineering practices are used unless there is a good engineering reason for seeking biological parameters. The advantage of the biology-as-default strategy is that benefits of biological design will be gained that were not anticipated at the outset. Moreover, a biologically accurate initial design will facilitate interactions between biologists and engineers in dealing with later problems. The amount of biological information necessary to follow this strategy led us to adopt cockroaches as the model system for these robots. As we will discuss subsequently, there
was already a wealth of information on cockroach walking when we entered into this venture, and cockroaches are well suited for further studies.

The biology-as-default strategy also gives the most payback to biology. If mechanical designs are carefully taken from the biological parameters of an actual insect, the struggles faced by the engineers in controlling the resulting robot can provide tremendous insight into control of the biological system. Because this article emphasizes the benefits derived by biology from biorobotics as well as the benefits to robotics from biology, we focus primarily on our projects that follow the biology-as-default strategy in creating insect-inspired vehicles. In so doing, we hope to give readers a flavor for the dynamic interaction between engineers and biologists using this strategy.

**Overview of insect locomotion**

At the time that we started working on insectlike robots, considerable information was already available on how insects walk and run. A complete review of the insect locomotion literature is beyond the scope of this review but can be found in several recent reviews (e.g., Pearson 1993, Burrows 1996, Bässler and Büschges 1998). It has been known since the observations of Hughes (1952) and Wilson (1966) that insects typically employ a tripod gait. That is, the animal is supported by a statically stable tripod formed by the front and rear legs on one side along with the middle leg on the other side (Delcomyn 1971). The remaining three legs swing ahead while the tripod of supporting legs develops ground reaction forces to drive the animal forward (Full and Tu 1990). As the animal walks, this tripod alternates with the tripod formed by the remaining three legs.

Studies of motor activity during horizontal walking over smooth surfaces have shown reproducible patterns in the muscles of each pair of legs (Pearson and Iles 1970, Pearson 1972, Delcomyn 1973, 1987). Each leg goes through a cycle that consists of a stance and a swing phase. During stance, the foot is in contact with the substrate, and the muscles that are active extend the leg and push the animal forward. During swing, an opposing set of muscles lifts and returns the leg to its starting position. In insects, the muscles that generate the stance phase are innervated by a small set of motor neurons. Two excitatory motor neurons control extension of the coxa–trochanter (CTr) joint (Figure 1a), and another two motor neurons—a slow motor neuron and a fast motor neuron—control extension of the femur–tibia (FTi) joint (Pearson and Iles 1971). The slow motor neuron is responsible solely for slower leg cycles, and it requires several action potentials to generate meaningful movement. In unloaded legs (i.e., legs that are not supporting body weight), the fast motor neuron can generate large joint movements with only a single action potential.

As the insect runs faster, the slow motor neurons are activated at higher frequencies and in shorter bursts. Kine
dy analysis of leg extension combined with electromyograms (EMGs) of leg muscles showed that the mean frequencies of muscle potentials associated with slow motor neurons are linearly related to the mean veloc-

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**Figure 2. Robot III and its leg designs.** (a) The kinematics of the front, middle, and rear legs (from left to right) of Robot III reflect the kinematics of the cockroach’s legs needed for walking, running, turning, and climbing. The three independent joint degrees of freedom of the body–coxa joint in Robot III’s front legs are labeled as $\alpha$, $\beta$, and $\gamma$. The middle leg’s $\gamma$ degree of freedom is fixed, and the rear leg’s $\alpha$ and $\gamma$ degrees of freedom are fixed. The front, middle, and rear legs each have one degree of freedom at their CF joint and also at their FTi joint. (b) Robot III is actuated with air cylinders that are clearly seen in this image. Hoses supply compressed air from the six blocks of control valves on the “abdomen” of the robot to the actuators. The robot’s “tarsi” are constructed of flexible plastic tubing and are attached to the tibias. The forward stance of the front legs and the rearward stance of the rear legs reflect that of the cockroach. The robot is 30 inches long.

Working in Roger D. Quinn’s lab, Richard Bachmann built the robot and Gabriel Nelson developed its postural controller.
ities of the joint movements that they produce (Watson and Ritzmann 1998a). However, both motor activity (Delcomyn 1973) and joint movement (Watson and Ritzmann 1998a) are more constant in the swing phase than in the stance phase. These observations are consistent with control models in which oscillator circuits generate swing activity and gate stance activity by inhibiting stance motor neurons during swing. In these so-called flexor burst generator models, an oscillator in each hemi-ganglion of the segmental nervous system controls swing of the associated leg and inhibits the legs on the opposite side of the animal and in adjacent segments (Pearson 1972). At very fast running speeds, fast motor neurons are recruited. The resulting fast muscle activity appears to stiffen the leg joints, much like an active spring might do, thereby making the transition from stance to swing significantly shorter (Watson and Ritzmann 1998b). Even at these speeds, frequency of slow motor neuron activity is still correlated with joint velocity.

Turning movements are associated with asymmetrical interleg motor activities in homologous muscles. For example, in a turn to the right the slow extensor motor neurons to the left middle (or hind) leg are excited at a higher frequency than those to the right hind (or middle) leg (Watson and Ritzmann 1998a). Such asymmetrical motor activation during the turn results in a larger force being developed by the outside leg than by the inside leg (Jindrich and Full 1998). Thus, the insect central nervous system controls speed and orientation through relatively straightforward changes in slow motor neuron frequency.

Cruse and his colleagues formalized many similar observations on walking in stick insects into mechanisms for coordination of legs (Cruse 1990), pointing out that much of the basic walking pattern in stick insects and other arthropods can be accounted for by postulating local control rules for each leg that are coupled by a series of “influences.” For example, the controller for a middle leg would “influence” all adjacent legs to not enter into swing while the middle leg is in its swing phase. Gait controllers based on these coordination mechanisms have been successfully implemented in at least three hexapod robots, one by Pfeiffer et al. (1994) and two by members of our group at CWRU (Espenschied et al. 1993, 1996).

**Detailed biological observations for Robot III**

Although we constructed two successful robots before our current effort, Robot III (Figure 2), this newest robot represents our first attempt to incorporate detailed biological parameters into a mechanical design (Nelson et al. 1997). This project required a greater understanding of joint movements in freely moving insects than was available at the time. To gather the necessary data, we constructed a treadmill with a transparent belt that allowed us to view leg movements from two orthogonal directions. We could then use high-speed video systems to monitor the three-dimensional leg movements of freely moving cockroaches as they walked on the treadmill and climbed over barriers. To get a sense of how the motor system controls these behaviors, we recorded EMGs from specific muscles. We could then compare motor activity to the simultaneous joint movements that the related muscles control (Figure 1b).

**Design and control of joints in each pair of insect legs.** Insect legs follow a general plan that is found in virtually all legged animals. Each leg has multiple segments joined by rotary joints that are controlled by opposing muscles. Segments that are located near the body tend to be larger, while those that are farther out on the limb, near the foot, are smaller and lighter. This arrangement minimizes the mass at the distal end of the limb, thereby reducing inertia and making rapid leg cycling easier. The most forceful muscles are in the proximal segments near the body. The muscles in those positions add to the increased proximal mass of the leg and provide a mechanically advantageous lever system between the source of actuation and the foot. The most proximal joints, such as the shoulder joint of a mammal, tend to have multiple degrees of freedom and related complex musculature. Small movements of these joints produce large movements at the end of the limb. The most distal joints, at the other end of the leg (near the foot), are small and flexible. They produce fine movements and adjustments for grasping the substrate. For even more efficient gripping, movable fingers or claws are often found on distal joints. However, muscles that actuate those structures are typically found in more proximal segments that are linked to the distal structures by long tendons, again reducing the mass of distal segments.

Within this basic design, each pair of insect legs has unique properties that distinguish it from the other two pairs and better suit it for specific functions. These design specializations are reflected in the kinematics, motor control patterns (Watson and Ritzmann 1998a), and ground reaction forces (Full et al. 1991) that are developed during normal walking.

The hind legs are the largest of the three pairs of appendages. Their greatest movement is generated by the proximal CTr joint moving in conjunction with the distal FTi joint. Because these are rotary joints, the leg can make a linear movement only by moving two joints at the same time. For all of the hind leg movements we have studied, the activation of extensor muscles and the resulting movements at both the CTr and FTi joints are nearly identical, both in amplitude and in timing (Nye and Ritzmann 1992, Watson and Ritzmann 1998a). The simultaneous extension of these two joints extends the tibia rearward, in a movement nearly parallel to the long axis of the animal’s body, generating positive ground reaction forces that propel the animal forward (Full and Tu 1990).

The middle legs also move the CTr and FTi joints at the same time, but the range of movement of the FTi joint is
smaller than that of the CTr joint (Watson and Ritzmann 1998a). The more limited extension of the middle FTi joint is accompanied by lower frequencies in the slow motor neuron innervating the extensor tibia muscle. The relative joint movements, along with the mechanical arrangement of the leg joints, generates a more sweeping movement than is seen in the hind legs. In a freely moving animal, the middle legs generate a complex force pattern that is composed of an initial braking force that opposes the animal’s movement followed by an accelerating force that assists its forward motion (Full et al. 1991). As we describe in the next section, the middle legs also play a crucial role in rearing the animal up during climbing movements.

The front legs are the most biomechanically complex of the three pairs of appendages. During the tripod gait, they reach forward and produce braking ground reaction forces as the animal is propelled forward (Full et al. 1991). To accomplish these movements, the front legs make much more use of the body–coxa (BC) joint than do the other legs. During swing, the BC joint moves the coxa forward while the CTr joint extends, pushing the leg forward (Watson et al. 1996). Upon touchdown of the leg, the BC joint rotates backward while the CTr and FTi joints flex, drawing the leg back and moving the tarsus (foot) under the BC joint while absorbing forward energy. In some cases, a second phase of stance movement is also observed. After flexion, the CTr joint may extend along with the FTi joint, thereby pushing the tarsus even farther backward relative to the body. The patterns of muscle activation for the front legs are as complex as the kinematics, mirroring the relative phases in CTr and FTi extension and flexion.

**Leg design needed for climbing.** To design legged robots that can traverse complex natural terrains, we had to extend our studies beyond horizontal walking to climbing behaviors. During climbing, the specialized function of each leg is especially evident as the front legs perform armlike movements to reach the top of the barrier and the middle legs redirect their movements to pitch the animal upward (Watson et al. 1997). The armlike movements of the front legs are made possible by the many degrees of freedom that are evident in these legs even during walking. However, the change in middle leg movement requires a rotation of one or both middle legs so that their tibia(s) are more perpendicular to the ground than they are during horizontal walking.

Rotation of the tibia can be accomplished at either of two leg joints (Watson et al. 1998). The most obvious one is the BC joint. Contraction of the muscles that control the middle leg’s BC joint rotates the coxa around its long axis. Because the BC joint is located proximally on the leg, its movement generates a large rotation of the tibia. In addition to the BC joint, the joint between the trochanter and the femur (TrF) can also contribute to tibial rotation. Although the TrF joint is often described as fused, it can make a small flexion movement. Again, with the joint’s proximal position, this flexion results in a substantial rotation of the tibia. Not only can the TrF joint be moved passively, but also the femoral remotor muscle, which is located in the trochanter, can actively generate the same movement (Watson et al. 1998).

With the middle legs rotated, their extension causes the animal to rear up. Extension of the hind legs will then push the animal up and over the barrier. Our preliminary EMG recordings suggest that during the actual climb, the depressor motor neurons of the hind legs are activated at very high frequencies. This increased muscle activity could contribute to the greater vertical force that would be needed for the climbing movement.

**Mechanical design and postural control of Robot III**

The mechanical designs of each pair of legs in Robot III had to capture the joint movements described above to generate efficient walking and climbing behaviors (Figure 2). However, to create a workable robot, we had to simplify these mechanical designs. Consistent with the biology-as-default strategy, we minimized the number of joints in each leg while maintaining those that were crucial to the behaviors we sought to reproduce.

To accomplish this task, we used a computer-based dynamic simulation tool that was designed in the CWRU Birobotics Laboratory (Nelson and Quinn 1995). The kinematic data from our behavioral observations on real cockroaches were used as equilibrium positions for the simulated animal. We could then manipulate various joints while monitoring the effect on the behavior of the simulated animal. We found that we could neglect the TrF joint in all of the legs and still produce the leg movements necessary to satisfy the goals of the robot. Its rear legs are the largest pair of legs and the most powerful, yet they are also the simplest, having only two independent rotations. Based on our biological observations, we mechanically coupled the rear legs of the robot’s coxa–femur (CF) and FTi joints so that those joints would move together at the same amplitude. The BC joint was also simplified to have only one direction of rotation. Because the middle legs pitch the body upward during climbing, they are more complex and have four independent rotations: two at the BC joint, one at the CF joint, and one at the FTi joint. The rotation of the BC joint makes up for the lack of a TrF joint in climbing and is still biologically accurate. The movements of the front legs require them to be the most complex. They have five independent rotations: three at the BC joint, one at the CF joint, and one at the FTi joint.

The resulting legs that were built and implemented on Robot III provide significant advantages for a legged vehicle. The specialized functions of each pair of legs mean that Robot III not only has the potential to perform all of the behaviors that we have observed in the cockroach but can do so in kinematically similar ways. For example, the
cockroach can rapidly accelerate forward because of its powerful rear legs. The robot’s rear legs are also powerful, and the mechanical linkage between the CF and FTi joints ensures that its legs move in a manner similar to those of the cockroach. The middle legs of the robot can rotate their tibiae relative to the substrate by altering their BC joints. Then, by extending its middle legs, the robot can pitch itself upward in a manner that is similar to the movements made by a cockroach as it climbs over barriers. Finally, the front legs of the robot are able to perform the searching movements that the animal uses to investigate its immediate environment.

Because the robot’s legs were designed not only to capture cockroach behavior but to do so by moving the same joints in the same manner, we gain two significant benefits. First, it is relatively easy to acquire new information from the cockroach to solve future problems. If we had designed the robot to move its body by using different joints than the cockroach actually uses, then we could not directly seek answers from the biology to questions posed in the robot. Second, we can expect to gain unforeseen advantages that are found in the cockroach but were not anticipated in the original design process. For example, the forces exerted on the ground by the cockroach (Full et al. 1991) indicate that its joint torques are nearly minimized as it supports itself. This is an efficient configuration, and the robot does support itself in this way.

Postural control. As we noted at the outset of this article, legged vehicles must solve the problem of postural control while performing vigorous behaviors. That is, a robot has to be able to stand and maintain its balance while it walks. Posture includes the position of the body in all three dimensions (forward, sideways, and vertical), as well as the three-dimensional orientation of the body. The importance and complexity of postural control has also been recognized in animal studies. For example, cats that no longer have connections between their brain and spinal cord can walk on a treadmill (Pearson and Collins 1993). However, they need help in staying upright. Although our previous robots also had postural controllers, the characteristics of Robot III’s pneumatic actuators required that we design a postural controller that was more capable and prominent.

The task of a postural controller is to calculate the position and orientation (i.e., the posture) of the robot (or the animal) from a variety of sensory cues and then adjust the legs to maintain a stable configuration. An animal maintains its balance by using circuits in its brain to compute its center of mass from numerous proprioceptive sensors (e.g., those that sense joint position), visual inputs, and gravity sensors (e.g., the vestibular system of vertebrates; Horak and Macpherson 1996). Robot III’s postural controller performs a similar computation and then adjusts the forces applied by each of the stance legs to place the center of pressure appropriately to cause the desired motion of the body (Nelson and Quinn 1998, 1999).

The postural controller allows Robot III to maintain its balance as it moves into a variety of positions in an animal-like fashion. It is particularly good at rejecting disturbances and exhibits an uncanny, animal-like swaying behavior while maintaining its balance when it is pushed sharply from its front, back, or sides. In response to commands, the robot can alter its posture and generate movement. For example, it can be made to repeatedly adjust its height, thereby performing pushups, while lifting a payload equal to its own weight of 30 pounds.

Robotic design limitations and potential biological solutions

Robot III captures much of the cockroach’s leg design and postural control. However, creating cockroach-like movements, such as running and climbing, are an ongoing challenge. It is in this context that we hope the biology-as-default strategy will ultimately pay off. By studying the properties of the cockroach that are still lacking in Robot III, we hope to improve the robot while simultaneously gaining insight into the roles of those biological features in insect locomotion.

The limitations to agile locomotion that exist in Robot III can be grouped into three classes: actuator technology, richness of sensory information, and design of sensory processing and motor control circuits. Suggestions for improvements in all three of these areas are available from the biological literature and from our own experimental observations.

Actuator technology. Many of the problems in artificial legged locomotion could be alleviated if the actuators that move the joints had properties more similar to muscle. The pneumatic actuators that are used in Robot III have a sufficiently high power-to-weight ratio for the robot to walk, run, and climb, but they are difficult to control. They are referred to as double-acting pneumatic cylinders, meaning that each side of the piston can be independently pressurized or vented. Currently, there are 22 sets of cylinders, which are controlled by 44 valves. Without doubling the number of valves (which would pose control, volume, and weight problems), the cylinders cannot be held at an arbitrary pressure other than the maximum pressure of 100 psi. That is, they cannot generate an arbitrary passive stiffness. In muscle, by contrast, passive forces have been measured even in legs that are removed from the animal (Chesler and Fournier 1981). These passive forces may be an important factor in supporting the weight of the animal as well as contributing to active movements (Cavagna 1970, Goslow et al. 1973, Biewener and Baudinette 1995, Prilutsky et al. 1996, Roberts et al. 1997, Full et al. 1998).

The electric motors that were used in a previous robot (Robot II) are easier to control than pneumatic actuators and can provide a controllable active stiffness (Espen-
schied et al. 1996). However, they cannot, by themselves, deliver passive stiffness. Moreover, their power-to-weight ratio is not sufficient for energetic legged robots. Pratt et al. (1997) have shown that electric motors powering a joint through a spring can provide the joint with passive stiffness, and that this elastic energy can provide the energy sufficient for walking and jumping. One problem with this approach, however, is that it is difficult to vary the passive stiffness of the spring.

Considerable work is currently being done to design actuators that are more like muscle. However, one of the more promising musculolike actuator technologies has existed for several decades. This approach makes use of braided pneumatic cylinders (Chou and Hannaford 1996), which are made of a hose (bladder) that is encased in a restraining mesh. The mesh is very stiff longitudinally but is flexible circumferentially. As air is pumped into the bladder, it increases in diameter and expands the mesh circumferentially, causing it to shorten in length, thus pulling on the segments that span a joint and producing a flexion movement. As the actuator shortens, the force it develops decreases—that is, it has nonlinear force–length properties similar to those of muscle. To extend the joint, an opposing actuator is set on the opposite side of the joint. Active or passive stiffness similar to that seen in animals can be accomplished by activating opposing actuators simultaneously. However, the number of valves that must be controlled is still a problem with braided pneumatiques. Nevertheless, we have successfully used these actuators in another robotic leg, as we discuss below.

Other actuator technologies are currently in development to achieve even more musculolike properties (Kornbluh et al. 1998). As these technologies become available in forms that can generate rapid, forceful movement with large enough displacement, they will clearly have an enormous impact on the development of legged robots. More efficient actuation will also be accomplished as scientists better understand and emulate the passive properties of the materials that make up animal limbs and the inertial properties of animal bodies.

Richness of sensory information. Any legged device must have sensors on its legs to monitor the position and condition of that leg during walking movements. Many behaviors that have been studied in animals appear to be controlled by pattern generation circuits with elements largely in the central nervous system. However, even the most centrally controlled behaviors typically incorporate sensors in peripheral structures to adapt the patterned movements to unexpected events (Pearson and Ramirez 1997). Again, space prevents us from providing a complete review of insect leg sensors, and we direct the reader to recent reviews on this important topic (e.g., Zill 1990, Burrows 1996, Delcomyn et al. 1996, Zill and Seyfarth 1996, Field and Matheson 1998).

Agile legged locomotion probably requires a particular-ly large amount of sensory information. The movement of multiple joints in several legs to propel the animal’s body forward is in itself so mechanically complex that even walking on a level, flat surface may require sensory information to generate a smooth, efficient movement. Each joint makes a rotary movement as muscles shorten. As the joint rotates, the mechanical advantage of the muscle on the joint changes. Further complicating matters, force production by muscle is inherently nonlinear, changing as the muscle shortens. In addition, loading effects change as the animal moves its center of mass relative to the leg’s point of contact with the substrate. Given these factors and the additional requirements necessary for climbing and carrying loads, it is difficult to see how a central pattern generator that lacks sensory information could control a leg efficiently while it propels the animal’s, or the robot’s, body forward.

Sensory devices on insect legs. What types of sensors are important to walking? Insects have a variety of sensory devices on their legs (Zill 1990, 1993). Joint angle detectors, such as the chordotonal organs, monitor joint position and velocity of movement. Their extreme sensitivities to changes in position ensure that the animal’s nervous system is provided with ongoing information about the progress of limb movements as well as signals of events that disrupt anticipated arcs of movement. Hair plates—patches of small hairs that are deflected as a joint closes—also detect joint angles, but these sensory devices typically become active only as a limb is moved toward the extremes of flexion.

Forces that occur in an insect leg are monitored by receptors known as campaniform sensilla, which measure mechanical strains in the exoskeleton (Schmitz 1993, Zill 1993). The exoskeleton is both the animal’s interface with the environment and the structure that is directly moved by muscle contractions. The information from campaniform sensilla, therefore, provides an extremely rapid way of detecting the effectiveness of limb muscles in generating forces to counter the changing loads that occur in walking.

The locations of insect leg sensors (Zill 1990) follow the principles of efficient leg design. The position of the foot is influenced by the angle of each leg joint. Chordotonal organs, found at nearly every leg joint, provide the information that is necessary to identify the exact position of the foot as the leg moves. Campaniform sensilla are concentrated in the trochanteral segment of the cockroach leg, an arrangement that is common to all insects that have been studied.

Why are so many sensory structures concentrated on the trochanter, which is the smallest segment on the leg, apart from the tarsus? Although the trochanter is short, it is the focal point for the action of the largest intrinsic limb muscles, which attach to its proximal surface. The trochanter is also the anchoring point for the femur, which transmits ground reaction forces to the trochanter as a
long lever that is opposed by the much shorter moment arms of the coxal musculature. Furthermore, insects often use their claws when clinging to a surface, and the claw muscle originates in the femur, so that forces from the claw muscle’s contraction are also transmitted to the trochanter. Therefore, from a sensory standpoint, the trochanter is a location that is particularly well suited to monitor both the effects of loading applied to the legs and the forces that the animal generates to counter those loads.

Functions of proprioceptive sensory organs in walking. The discharges of these leg proprioceptors, as a whole, provide ongoing feedback about the effective use of each leg in posture and in walking. The effects of the inputs from these sensory organs are diverse. The activities of some sensory organs elicit simple reflexes in leg muscles, whereas the influences of other receptors are more complex and can alter the motor pattern by changing the timing of leg movements. A major problem confronting both neurobiologists and robotic engineers is to understand how the diverse information about joint angles and the forces exerted by a leg are integrated to generate the smooth and continuous movements that occur during locomotion. To find solutions to this problem, we have formulated the effects of individual types of receptors in a way that allows them to be individually tested and evaluated in models or robotic systems.

Figure 3 graphically summarizes the discharges and reflex effects of some proprioceptors in the step cycle. A complete description of these events is beyond the scope of this article. Nevertheless, it should be noted that the discharges of some receptors, such as the trochanteral hair plate, are limited to particular events or transitions of the step cycle, in which they exert discrete reflex effects. Other receptors show more prolonged discharges that permit outputs to be tuned and adjusted throughout a phase of the cycle. For example, the campaniform sensilla are all activated during the stance phase, when forces exerted by the leg are maximal.

Leg sensors on robotic devices provide inspiration for further biological observations. Initially, the principal leg sensors on Robot III were limited to potentiometers monitoring the 22 joint angles on the legs. Although position sensors provided sufficient information for posture control during small disturbances, they were inadequate for smooth walking, in which loads on the legs change rapidly between swing and stance modes and in which legs that support the body shift back and forth between the two tripods. As we worked with Robot III, it became increasingly clear that some information on loading was necessary to generate better walking. At the very least, the circuitry that controls movement needs to “know” when a particular leg has touched down and is participating in the stance phase. Even better results should be achieved with more precise information on loading, such as the campaniform sensilla might provide.

The realization that Robot III needed more sensory information challenged us to study the campaniform sensilla in greater detail, and we found that they provide even more information than had previously been recognized. For example, in addition to force amplitude, the largest sensilla also detect the rate of change of force (dF/dt).
Moreover, some sensilla discharge in response to decreasing levels of force and can thereby signal the rate of declining load (Ridgel et al. 1999). These findings may be important for walking in both insects and robots. Ground reaction forces in walking insects vary continuously during the stance phase (Full and Tu 1990), and the discharges of the campaniform sensilla could provide ongoing monitors of those changing levels. They should also provide intense, active signals when forces suddenly decrease, as when a leg loses friction with the surface and slips. Such signals often precede the resultant changes in joint angles and, therefore, provide a rapid way to compensate for environmental perturbations. Thus, the use of sensors that can detect rate of force changes or decreases in load to reflexively alter the responses of actuators could decrease response time significantly, thereby increasing the agility of a machine traversing irregular terrain.

Even more information on the role of specific sensory structures on the leg will be derived from a more accurate robotic model of the cockroach leg that we have recently developed (Figure 4). In this leg, each joint is a scale model of that found in the animal’s leg, with particular attention paid to the tarsus (foot) and the trochanter. Each joint is powered by braided pneumatic actuators with insertion points located on the leg in positions similar to where muscles actually insert. For example, the actuator that moves the tarsus is located in the tibia and is connected to the tarsus by a cable whose position and function mimic those of the tendon in the cockroach leg. With this very accurate situation, the sensors on the tarsus and trochanter become important. One of the goals in developing this leg was to test hypotheses on leg sensors in a hardware model. For example, because this leg’s joints and segments so accurately reproduce those of the animal’s leg, it is possible to position sensory structures at both normal and abnormal locations and examine how variation in position alters the proprioceptive picture that is returned to the control circuits.

**Design of sensory processing and motor control circuits.** From a neurobiological perspective, the design of sensory processing and motor control circuitry is both the most complex and potentially the most interesting problem. In animals, complex movement requires an interaction between posture control from higher centers acting in concert with local reflexes and pattern generators (Horak and Macpherson 1996). The nature of this interaction is not well understood. Moreover, even in the absence of higher centers, local circuits exhibit context dependence—such as reflex reversals or phase changes—when the animal changes its behavior from standing to walking (Pearson and Collins 1993, Bässler and Büschges 1998) or from walking to searching (Pearson and Franklin 1984, Delcomyn 1987, Tryba and Ritzmann 1998).

A greater understanding of the interactions between higher centers and local control circuits and the changes that occur in either region as the animal alters its behaviors would allow us to design more effective locomotion controllers. To that end, we have developed biological techniques that allow us to monitor activity in individually identified neurons as the animal initiates walking, standing, and searching behaviors (Tryba and Ritzmann 1998) and as higher centers are disconnected from thoracic ganglia containing local circuits (Schaef er et al. 1997). We are just now beginning this work. However, as we incorporate this new biological information into more advanced robotic control circuits, their performance will in turn provide new insights into the roles played by the neural circuits in controlling complex movements in insects.

**Conclusion**

Engineers are, of course, far from producing robots that walk as efficiently as an insect. Neurobiologists are also a long way from completely understanding how legged locomotion is controlled in any animal. Moreover, we certainly do not wish to imply that a biorobotics strategy is the only way to reach that understanding. However, such efforts nicely complement more traditional biological forms of analysis. For example, comparative studies of legged animals from groups as diverse as mammals (cats) and insects (cockroaches) reveal fascinating similarities (Pearson 1993). The finding that robots that are designed to capture the kinematic properties of insect legs require similar properties in the circuits that control their movements suggest that convergent evolution is often driven by physical properties that are common to all forms of legged locomotion.

Clearly, many strategies will be needed to unlock the secrets of control in both natural and manmade locomotion systems. We believe that careful collaboration between roboticists and biologists will make an important contribution to that task. The biology-as-default strategy feeds on close communication between engineer and biologist. Careful measurements of an animal’s legs as it runs and climbs lead to basic robot designs. Limitations in the robot’s walking performance then lead to hypotheses about how animals solve specific problems. These hypotheses direct biological experiments that provide new ideas for refined robot designs. If implementation of new ideas from biology enhances specific aspects of the robot’s performance, then it is possible to conclude something about the role those features play in the animal. For example, if Robot III makes better leg adjustments when force detectors are added, then that finding would confirm a role for campaniform sensilla in cockroach walking. Such collaborations should result in more efficient walking machines as well as a better understanding of how legged animals walk.

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References cited


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