



Walking Robots and the Central and Peripheral Control of Locomotion in Insects

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Abstract. This paper outlines aspects of locomotor control in insects that may serve as the basis for the design of controllers for autonomous hexapod robots. Control of insect walking can be considered hierarchical and modular. The brain determines onset, direction, and speed of walking. Coordination is done locally in the ganglia that control leg movements. Typically, networks of neurons capable of generating alternating contractions of antagonistic muscles (termed central pattern generators, or CPGs) control the stepping movements of individual legs. The legs are coordinated by interactions between the CPGs and sensory feedback from the moving legs. This peripheral feedback provides information about leg load, position, velocity, and acceleration, as well as information about joint angles and foot contact. In addition, both the central pattern generators and the sensory information that feeds them may be modulated or adjusted according to circumstances. Consequently, locomotion in insects is extraordinarily robust and adaptable.

Keywords: central pattern generator, CPG, insect, walking, sensory feedback, neural modulation, reflex, robot, motor control, biomimetic robots

1. Introduction

Engineers interested in autonomous robots have for many decades looked with envy at the extraordinarily rapid and agile locomotion exhibited by many animals over rough or irregular terrain. Although controlling the movements of legs is much more difficult than controlling the rolling of wheels, legged robots can go where wheeled ones cannot, giving them a potential utility that justifies the extra effort required to control them. Some robotics engineers have built robots whose designs are based at least in part on biological principles of structure or control, especially those deriving from insects or other arthropods (Raibert, 1986; Brooks, 1989; Bares and Wettergreen, 1999). The rationale is that by looking to the physical structure and control mechanisms of successful biological systems, engineers may be able to improve the performance of walking robots (Raibert, 1986; Brooks, 1989; Beer

et al., 1992; Cruse et al., 1995, 1998a, 1998b; Pfeiffer et al., 1995; Quinn and Ritzmann, 1998; Delcomyn and Nelson, 1999).

However, there is more to designing a true biomimetic robot than building a walking machine with legs. Few legged robots have been designed with more than a superficial resemblance to the physical structure of an animal such as an insect (see Bachmann, 1997, for an exception). Furthermore, although the neural basis of walking in an insect is still not completely understood, the few principles that are known are rarely used to guide the design of the control system for a legged robot. It may be that failure to incorporate more of what is known about insect locomotor structure and function is the basis of the failure of any man-made device to attain the walking agility shown even by the simplest insect (Beer et al., 1997). This failure to use biological information may in turn be due in part to the failure of neurobiologists to communicate the information in

a form that engineers can understand, or to the failure of engineers to recognize that biological information may help them.

The purpose of this paper is to outline briefly what is known about locomotor control in insects with special regard for the neural mechanisms by which rhythmic leg movements are generated and coordinated. This knowledge may then be used as the basis for the design of controllers for legged robots. Unfortunately, much of the detailed information that might be useful to an engineer, such as circuit connections and transfer functions for them, are not available for insect locomotor control systems. Hence, this paper will of necessity be somewhat general.

2. Control of Insect Locomotion is Hierarchical and Modular

The nervous system of an insect consists of a two-part brain located in the head, and, in insects in which walking is typically studied, a chain of ganglia along the ventral (underneath) side of the body (Fig. 1(A)). Ganglia contain the bodies and branches of nerve cells (neurons). They are also where synapses, the sites of

communication between neurons, are located. Each ganglion is joined to its neighboring ganglia by connectives, thick bundles of the long branches of neurons (axons). Ganglia contain the cell bodies of neurons that control the muscles of the body (motor neurons) and that integrate information from sense organs and from elsewhere in the nervous system (interneurons). Nerves connect the ganglia with outlying regions of the body (Pipa and Delcomyn, 1982), carrying motor signals to muscles and bringing in sensory signals from sense organs. Locomotion relies on properly coordinated patterns of signals in motor neurons to muscles of the legs (and body for postural control); motor patterns, in turn, are generated by neurons of the central nervous system (CNS), influenced by input from sense organs that relay information from the animal's environment and about its motor performance, as outlined in Section 4.

Locomotor behavior is hierarchically controlled (Fig. 1(B); Delcomyn, 1985; Dean and Cruse, 1995). The brain is responsible for initiating and terminating locomotion, and for determining its direction and speed. Headless insects do not initiate locomotion, and respond to stimuli that normally initiate walking either not at all or by one or two quick twitches of the legs.

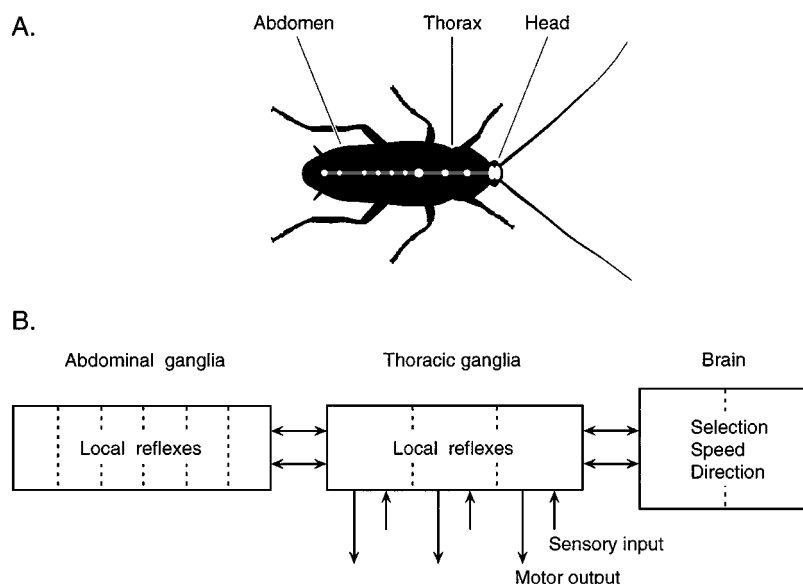


Figure 1. A. Outline of a typical insect (cockroach) showing the position of the central nervous system, which consists of a chain of ganglia (groups of nerve cells) joined by nerve connectives. The three ganglia in the thorax contain the neurons that control leg movements. B. Functional schematic showing how insect locomotion is controlled by the central nervous system. The brain is responsible for selecting the behavior and setting speed and direction. Control and coordination of the contractions of muscles in the legs are carried out locally in the ganglia that contain the leg motor neurons. For the sake of simplicity, abdominal, thoracic, and head ganglia have been lumped into single functional boxes here, individual ganglia being indicated by dashed lines.

These twitches can propel the insect forward, but do not resemble the coordinated movements characteristic of normal walking.

In contrast, control and coordination of the legs are handled locally (Burrows and Siegler, 1982). Each body segment to which a pair of legs is attached contains a ganglion in which are located the motor neurons that control the muscles of those legs and into which sense organs on the legs send their information. Moreover, the neural circuitry that underlies leg reflexes is also located within each thoracic ganglion. In our current view of locomotor control, the main role of the brain is to activate the local circuits and determine the speed of their operation, but not to influence significantly either the movements themselves or their coordination. Some motor systems in vertebrates and a few invertebrates show feedback from the local circuits and the brain (e.g., Cohen and Boothe, 1999), but such a link has not yet been demonstrated in insects.

The local control circuits themselves appear to be grouped into functional modules (Bässler and Büschges, 1998). Not only is there separate control for the movements of each individual leg, there is, at least in the stick insect, separate control of each joint in each leg (Bässler, 1993a). Coordination of several joints that are part of a single leg or of different legs relative to one another during walking is achieved through interactions of the modules that control the joints or legs. Furthermore, sensory input from the legs has a highly specific pattern of distribution within each ganglion. For example, leg mechanoreceptors send their signals to only a relatively small number of interneurons. These interneurons are members of functional modules that in turn control motor neurons innervating muscles whose actions would move the leg or leg segment away from the mechanical stimulus that excited the sense organ in the first place (Newland and Burrows, 1997). Note, however, that a module is a functional unit, not necessarily an anatomical unit; neurons may belong to more than one module.

3. Central Pattern Generators Control Rhythmic Leg Movements

One of the fundamental issues in the field of motor control is how the proper alternating activity of extensor and flexor muscles in a limb is generated. Alternating activity of muscles is due to alternating activity of motor neurons that control the muscles. Hence the basic issue is how the nervous system is able to generate the

appropriate sequence of activity in motor neurons. Experiments in a variety of animals representing every major phylum suggests that the central nervous system is capable of generating such a rhythmic pattern of activity without the necessity for any sensory feedback to set or maintain the timing (Delcomyn, 1980; Getting, 1989). The notion is that a small network of neurons can generate the appropriate pattern entirely as a result of a combination of intrinsic neuronal properties and specific synaptic interactions among the participating neurons. The network is referred to as a *central pattern generator*, or *CPG*, and can be thought of as the controller for the particular movement that it generates.

The arrangement and connections among neurons that constitute a pattern generator are known for some vertebrate and invertebrate animals. The two best known vertebrate CPGs are those that underlie swimming in lampreys (Grillner et al., 1998; see also Cohen and Boothe, 1999) and certain tadpoles (Roberts et al., 1997). Among invertebrates, the neural basis of swimming in several shell-less molluscs has been described (e.g., Arshavsky et al., 1993), as has the basis of swimming in the medicinal leech (Brodfuehrer et al., 1995). The CPG understood in the greatest detail, however, is that which controls the regular churning of the stomach of crustacea such as lobsters (Selverston and Moulins, 1987; Selverston et al., 1998). The neurons constituting this CPG are contained in the stomatogastric ganglion, which lies just over the stomach. Detailed study at the cellular level of these and other CPGs have revealed that a common feature of most is reciprocal inhibition between one or more pairs of neurons (Friesen, 1994). That is, each cell of the pair sends an inhibitory connection to its partner, an arrangement that leads to an alternating rhythm of firing in the two cells when they are activated by some common input. It is also clear that there is a great deal of redundancy in the circuits, a feature that seems to make the circuits more stable, but which has made it difficult to determine the precise role of each cell in the circuit.

CPGs that control insect locomotion are not as well known as are those that control rhythmic behavior in other animals. However, it appears that at least some of the neurons that constitute the network in these animals are nonspiking (Pearson and Fournier, 1975; Büschges et al., 1994). This means that they are incapable of generating action potentials, communicating with other neurons only through the modulated release of neurotransmitter. Nonspiking neurons in principle operate more like analog elements than digital elements as

represented by spiking neurons. Evidence suggests that during a cycle of leg movement, the nonspiking neurons alternately excite and inhibit the motor neurons that control leg muscles. An arrangement in which all active flexor or all extensor muscles are excited more or less together may work well for some legs in insects because the joints in these legs are flexed or extended at the same time and roughly at the same rate. Some legs show more complex movements, however. Some joints may change angle at different rates, or a single joint may show flexion followed by extension during the stance phase of a single step. Such movements require more complex control. Recent experiments in stick insects suggest that this more complex control may be manifest in separate CPGs for each joint, a reflection of the modular organization of leg control (Büschges et al., 1994).

How the legs are coordinated with one another is less well understood. Experiments with crayfish, insects, and various vertebrates suggest that interneurons that run between adjacent ganglia may provide

coordinating information. The idea is that information about the cyclic output of each CPG is conveyed to adjacent CPGs by spiking neurons that cross over to the other side of a ganglion or that extend to adjacent ganglia, where they can influence the cycle being generated by slowing it down or speeding it up (Skinner and Mulloney, 1998).

4. Sensory Feedback is Important for Leg Coordination

CPGs may underlie walking in every insect (although they seem to play a reduced role in stick insects—Bässler, 1993a), but it is nevertheless clear that feedback from sense organs in the moving legs is critical to a properly coordinated sequence of steps, at least during slow walking. Insect legs are heavily invested with sense organs that can provide relevant information (Fig. 2; Delcomyn et al., 1996). These sense organs range from tactile spines that sense contact with an

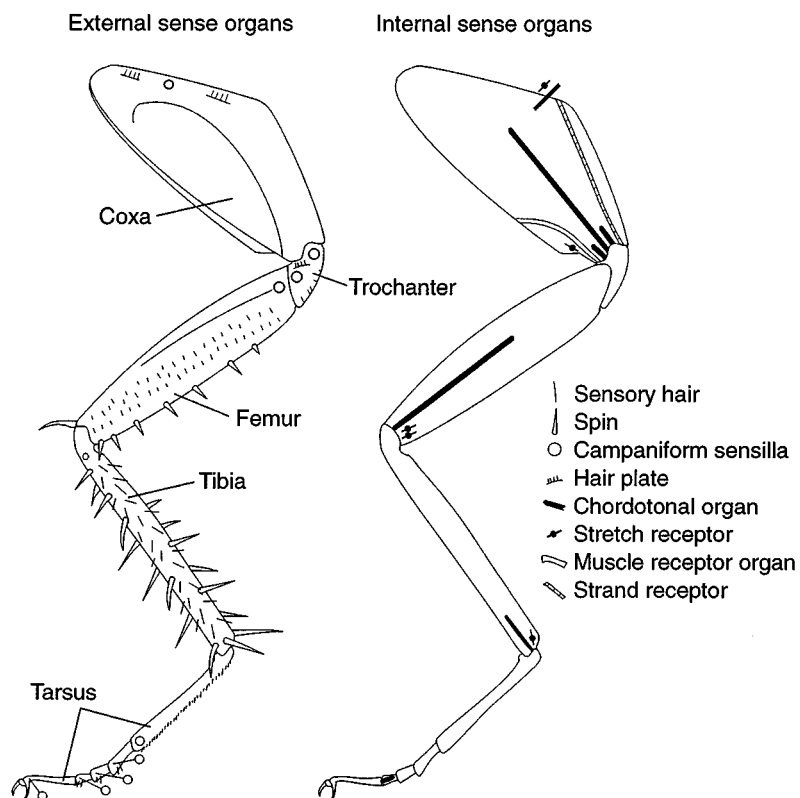


Figure 2. Structure of the rear leg of a cockroach showing the locations of the main internal and external sense organs of the leg. Adapted from Delcomyn et al. (1996).

obstacle to cuticular strain-sensing organs (called campaniform sensilla) capable of detecting load on a leg. Other organs that may provide information important for coordination include stretch receptors, hair plates, and chordotonal organs, all of which sense changes in joint angles. Chordotonal organs, which are quite complex, also sense leg velocity and even acceleration (Büschges, 1989).

Specific sense organs have been identified that influence such parameters of stepping as the degree of flexion at a joint (e.g., Wong and Pearson, 1976; Kuenzi and Burrows, 1995), foot placement (e.g., Pearson and Franklin, 1984), and the transition from stance to swing (e.g., Cruse, 1985). In the stick insect, a considerable body of work has shown that sensory input from sense organs around the joints that provide information about leg movements and joint angles, and the cuticular sense organs called campaniform sensilla that provide information about strain in the insect's external skeleton, provide important information for the proper control of leg movements (e.g., Cruse, 1979, 1985; Cruse and Knauth, 1989; see review by Cruse, 1990). However, elimination of any single sense organ from one leg usually has little or no effect on the *pattern* of leg movements, i.e., the timing of one leg relative to another. This is presumably because each leg carries an enormous number of sense organs, many of which provide the same functional kinds of information (Cruse et al., 1984).

The most compelling evidence that feedback from sense organs is critical to the *timing* of leg movements comes from amputation experiments. Removing a leg from an insect, especially a middle leg, has a dramatic effect on the timing and pattern of stepping of the remaining legs. As long as the speed of locomotion is low, such a procedure causes the legs in front of and behind the absent leg to step out of phase with one another, whereas before the amputation these legs move together. The change in gait is usually attributed to the loss of sensory input from the missing leg. However, if the amputated leg is replaced with a sliver of wood that acts as an artificial limb, the gait of the insect will immediately revert back to normal. Hence, this experiment shows that most sense organs in the leg can be lost without any substantive effect on the timing of the movement of the legs relative to one another and with minimal effects even on the movement of the leg itself.

The sense organs thought to be critical for coordination are the campaniform sensilla. These sense organs

are typically located near joints (Krämer and Markl, 1978), presumably because strain appears to be greatest there during walking (Cocatre-Zilgien and Delcomyn, 1999). The campaniform sensilla are directionally selective, meaning that they sense strain in a particular direction only. They are typically arranged on the legs in groups, each group having a particular orientation and therefore being sensitive to strain from a specific direction. Hence, different groups will respond to strain caused by bending or twisting of the leg in different directions.

Amputation of a leg is usually done at the junction between the trochanter and the femur (see Fig. 2), where there is already a natural line of weakness in the leg for autotomy (spontaneous loss of the limb). When a leg is severed at this level, the resulting stump is too short to touch the ground and the numerous campaniform sensilla on the trochanter do not receive any stimulation during walking. When an artificial limb is attached to the trochanter, the load of the body will be felt at the trochanter when the artificial limb touches the ground. It is thought that the resulting strain in the trochanter activates appropriate campaniform sensilla, which in turn will produce the pattern of sensory input that is necessary to generate the normal pattern of leg movements.

More recent analysis of amputation experiments suggests that another factor contributing to the altered timing of leg movements during walking after an amputation is the altered input to the campaniform sensilla in the intact legs. When a leg is amputated, the load that this leg normally bears during its stance phase must be taken up by the nearby legs. At times when the absent leg would normally be placed on the walking surface, these neighboring legs are carrying a load they normally would not bear. In consequence, the campaniform sensilla in these legs will provide a strong signal at a time when in intact insects there is none. This signal presumably contributes to the altered timing of the remaining legs.

A number of ingenious experiments have been conducted in which individual sense organs have been induced to provide incorrect or incorrectly timed signals. In contrast to the result of eliminating sensory input, these experiments reveal a strong effect on the movements and coordination of a leg (e.g., Graham and Bässler, 1981), supporting the view that altered input from campaniform sensilla in the intact legs may be as important as loss of input from the missing leg in inducing a change in gait.

5. Modulation of Neural Circuits

Undoubtedly the biggest change in the past two decades in our view of the neural basis of locomotion, not only in insects but in other animals as well, is the realization that the neural circuits that underlie the behavior are far from static. It was once thought that except for specific neural networks involved in memory formation or storage, or modifiable by learning, neural circuits, once formed during development, were thereafter essentially unchanged. Instead, it has now become abundantly clear that there are a variety of ways in which neural circuits can temporarily be modified preceding, during, or after some behavior. In the context of this overview of locomotor control in insects I will discuss three kinds of modulatory effects, modulation of control circuits themselves, modulation of sensory input or its effects, and modulation of motor output.

Perhaps the most important recognition has been that neural circuits are not immutable. That is, the functional connections between neurons in a neural circuit can be altered to produce a circuit that has different functional properties. The best known example of such a change is the stomatogastric system that controls the churning movements of the stomach of crustaceans (Selverston and Moulins, 1987). Typically, there are separate rhythms for the esophagus and the gastric and pyloric parts of the stomach. However, occasionally the animal stops churning food and swallows what it has. To do this, it reorganizes the pattern generator circuits that have been producing the three independent rhythms into a single CPG that produces a new rhythm with completely different timing characteristics (Harris-Warrick et al., 1997). The switch is triggered by the release of neuromodulatory neurotransmitters by the terminals of special neurons in the stomatogastric ganglion. These neuromodulators, by activating or inactivating certain ion channels in the membranes of selected neurons in the ganglion, cause synapses to become active, become inactive, or change strength. These changes in synaptic strength, in turn, bring about functional changes in the ways in which the neurons interact, and thereby cause the network of neurons to produce a different pattern than they did before.

No neural circuit that controls any leg movement has been described in detail similar to that of the stomatogastric ganglion, nor is there any direct evidence for the kind of circuit reorganization it exhibits. Nevertheless, based on the similarities and differences among the

movements of the legs when an insect walks, grooms, and searches for a foothold (Reingold and Camhi, 1977; Delcomyn, 1987), plus the demonstrated ability of certain neurochemicals to induce or strengthen the rhythmic output associated with locomotion (Sombati and Hoyle, 1984; Büschges et al., 1995), it is likely that similar reconfiguration of neural networks controlling leg movements occurs in insects. The consequence, for both neurobiologists and engineers, is that simply knowing “the circuit” controlling walking will not give the complete story.

Sensory signals themselves may also be modulated. Either coincident with the start of a behavior or in time with some rhythmic component of it, sensory input can become effective where it was not before, ineffective where it was effective before, or exhibit an increase or decrease in effectiveness. For example, sensory input may be modulated in association with a repetitive activity. In flying locusts, input from mechanically sensitive sense organs in the wing hinges impinges on the motor neurons that control the flight muscles. The strength of this input, which helps provide an extra boost to the motor neurons at appropriate phases of wing movement, is modulated continually in time with the wing beat so that it is strongest at the phase when it should be most effective (Büschges and Wolf, 1999). In walking locusts, terminals of certain sensory neurons from the leg continually receive input that modulates output to their target neurons (Wolf and Burrows, 1995) in relation to the ongoing stepping of the leg from which they originate.

It may seem counterproductive for sensory signals to be disabled entirely (or at least ignored), but this phenomenon has been shown to be an essential component in generation of the stepping patterns used by fast moving cockroaches. For insects that never walk very fast, it is adequate to say that amputation causes a dramatic change in the insect’s gait, as described previously. In the American cockroach, however, it has been found that the effects of amputating a middle leg are speed-dependent (Fig. 3). During slow walking in an insect missing a middle leg, the timing of muscle activity in the front and rear legs on one side of the body is quite different than that during walking in an intact insect. However, the faster the insect walks, the closer to the normal timing is observed, until during quite rapid walking/running, there may be no significant change in the timing of muscle activity in the front and rear legs compared to normal—they are still lifted more or less together (Delcomyn, 1991a), even though

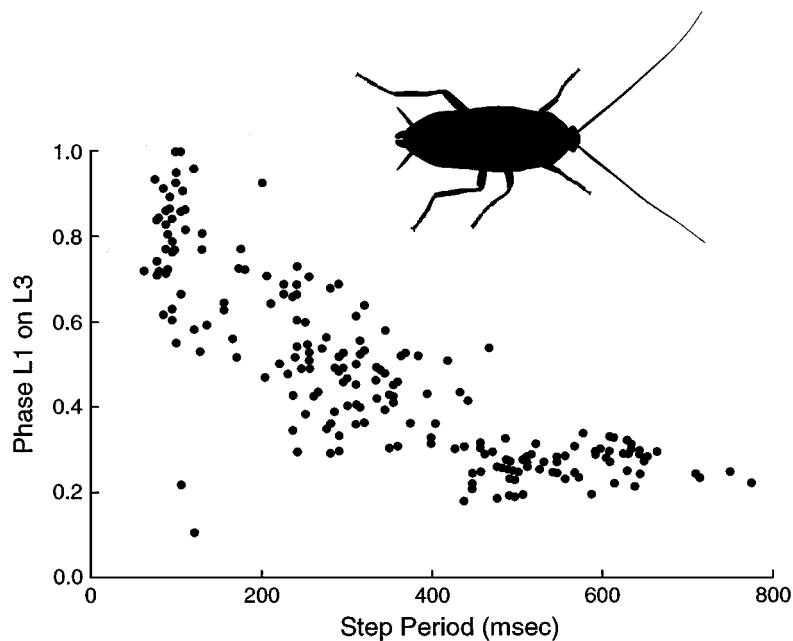


Figure 3. Graph showing the shift in timing of motor activity in the left front leg relative to motor activity in the left rear leg of a cockroach in which the left middle leg has been amputated (outline drawing above graph) as a function of step period (i.e., walking speed). Phase is calculated as the ratio of the lag between the end of a burst of motor activity in an extensor muscle in the rear leg and the end of a burst of motor activity in an extensor muscle in the front leg divided by the period (measured from burst end to burst end) of the cycle of rear leg motor activity. A phase of 1.0 or 0.0 means the bursts of activity in the two legs end at the same time. The graph shows that as the insect walks faster and faster, motor activity in the two legs (and hence the movements of the legs) drift closer to the muscle and movement synchrony (phase about 0.9–1.0) seen in intact insects. Adapted from Delcomyn (1991a).

this leaves one side of the body without any physical support during part of the stepping cycle.

Functional considerations make this result more understandable than it might be at first glance. At stepping rates of upwards of 20 steps per second and assuming a leg spends half its time on the ground, any one leg will be in stance phase for a maximum of only 25 msec. During this period, if the body were entirely unsupported on the side of the amputated leg the body would fall only 3 mm. Since cockroaches typically maintain a height of 8–10 mm from the walking surface, this is only about a third of the distance that the body could fall. Furthermore, since at high walking speeds stance is a bit shorter than swing and slight differences in liftoff time occur for the front and rear legs, the actual time during which the body is unsupported is significantly less than 25 msec, reducing the distance the body would fall. A final consideration is that cockroaches generally run at top speed in response to some threat, and under these circumstances it makes better biological sense for the insect to keep its legs churning without regard to the possibility of stepping in a hole than to slow down to be sure of solid footing.

The physiological basis of this shift in behavior is not yet clear. However, experiments have shown that reflexes elicited by campaniform sensilla activity that might provide information about weight on the legs and hence help adjust the stepping of legs after an amputation are too slow to provide any useful information when the insect is moving its legs rapidly (Zill and Moran, 1981). In fact, at top speeds, the reflex activation of some muscles would occur at the very time when they should be relaxing while their antagonists move the leg in the opposite direction. For this reason, it is inferred that the sensory input is suppressed or dampened so as not to interfere with leg movements, thereby allowing an intrinsic pattern of coordination to emerge (Delcomyn, 1991a).

A third type of modulation is modulation of motor output. This may not be mutually exclusive from sensory modulation since a change in the strength of some sensory input can and usually does result in a change in a resulting movement, but movements such as reflexes can be modulated without any change in sensory input. To take one instance, insects, like other arthropods, show resistance reflexes in their legs. That is, forced

flexion of a limb will activate extensor motor neurons to resist the movement, and forced extension will activate flexor motor neurons. However, the magnitude of this reflex may be dependent on the behavioral state of the animal. For example, immediately after cessation of flight, resistance reflexes in the legs of a locust may be decreased by as much as 70% (Büschges and Wolf, 1996) as measured by the amplitude of the motor response, compared to insects that have been standing still. And in stick insects, the gain of the tibia control loop, which regulates the angle between the tibia and the femur, depends on whether the insect is in the active or inactive state (Bässler, 1993b).

Reflexes such as resistance reflexes in the legs can show another form of modulation as well—they can be reversed. During walking, when such reflexes would impede normal movement, these resistance reflexes become assistance reflexes so that flexion of a limb activates flexion motor neurons, and extension activates extensor motor neurons (see Pearson, 1995). In other words, a negative feedback effect of a sensory input on a motor output is switched to a positive feedback effect. These and the other circuit, sensory, or motor modulations mentioned here considerably complicate efforts of neurobiologists to understand the neural basis of walking and of engineers to reproduce the mechanisms in hardware.

6. Mechanisms

The modulatory effects discussed above are brought about by a variety of neural mechanisms. Although the precise cellular mechanisms have not been fully described in every case, it might be helpful to outline the general principles by which they are thought to operate to at least provide ideas about how similar features might be built into a robot control system.

The effects of sensory input on the timing of rhythmic movements is well understood in principle. Sensory input, or neurons that receive sensory input, must make direct connections with one or more of the neurons that constitute the CPG. Any external input that is received by one of these neurons will have an effect on the ongoing rhythm that will depend on when during the cycle of activity the input is received. At some phases of the cycle the input can cause the cycle to speed up (advance), whereas at other phases it can cause the cycle to slow down (delay) (Fig. 4(A)). Plotting the effects of the input at all phases yields a phase response curve (Fig. 4(B)), which shows the predicted effect of sensory input to the CPG at all possible times relative

to the ongoing activity of the pattern generator. It is through a combination of inappropriately timed input from some sense organs, missing input from others, and coupling between CPGs, that the amputation of a middle leg is believed to change the gait of a slowly walking insect.

Modulation of sensory signals and of reflexes may have several causes. One such mechanism is presynaptic inhibition, in which input from elsewhere in the CNS to the terminals of the sensory neurons reduces their influence on the neurons with which they synapse (review: Clarac and Cattaert, 1996). The mechanism of this reduction may be different in different cases, but the functional means by which it works is a reduction in the amount of neurotransmitter released by the sensory nerve terminal and a consequent reduction in the effectiveness of the excitation that is delivered to its target neuron. It has also been shown that the sensitivity of a sense organ to a particular stimulus may be modified by modulatory chemicals that are released by neurons from the CNS (Matheson, 1997), indicating that modulation can occur at the periphery as well as within the CNS.

Changes in reflex gain may be due to variation of the effective strength of a synapse, such as that between a sensory neuron and its target, according to the behavioral state of the animal. The sensory neuron may synapse directly with one or more motor neurons, in which case the effect is localized (e.g., Kittmann, 1997), or the neuron may synapse with what are called premotor neurons. These are neurons that themselves control groups of motor neurons, and hence control not just the contraction of a single muscle but perhaps the movement of an entire leg. Hence, modulation of the effect of sensory input to a premotor neuron can affect the efficacy of the sensory input on a complex movement (e.g., Stein and Sauer, 1998). Another possible mechanism of gain change is to alter the threshold for firing of a motor neuron (Kittmann, 1997).

7. Can Roboticians Learn Anything from Insect Neurobiology?

Does our imperfect understanding of the neural basis of insect walking provide any useful guidelines for the design of controllers for legged robots? This question does not yet have a clear answer, in part because it has proven difficult to transfer important elements of insect locomotor control into robot controllers. Furthermore, it is also not clear which elements of insect locomotor control are actually critical for the extraordinary agility

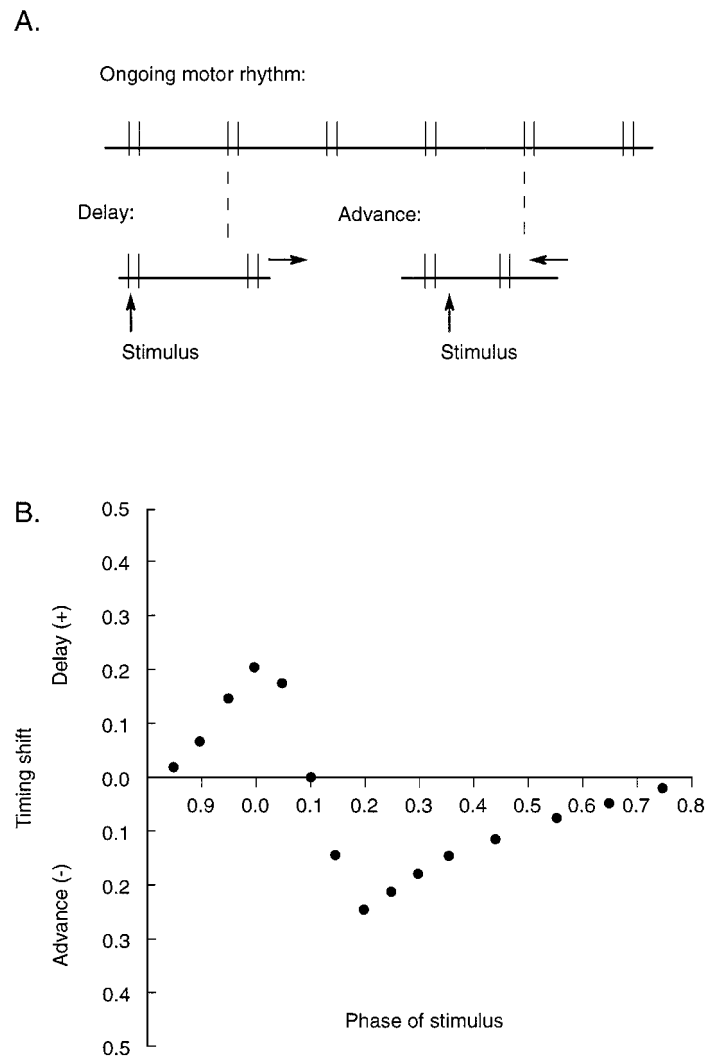


Figure 4. Phase shifting of an ongoing rhythm (pairs of spikes, upper part of panel A) in response to a stimulus to one of the neurons comprising the CPG. A. Diagrammatic representation of the effects of a stimulus at two different phases of the rhythmic cycle. Stimulating one of the neurons in the CPG just after the start of a cycle (phase close to 0.0) delays the next burst. Stimulating one of the neurons in the CPG about 20% into the cycle (phase about 0.2) advances the next burst. B. Smoothed phase response curve showing the shape of the delay or advance produced by stimulus at any phase. Delay and advance are computed as the ratio of the difference between the expected and actual cycle periods to the expected period. Data obtained from stimulation of a member of the CPG for flight in a locust. See Robertson and Pearson (1985) for more detail.

and adaptability exhibited by insects as they traverse rugged terrain. Nevertheless, several points can be made.

First, insects exhibit hierarchical control of walking and use a modular organization of control elements during walking. The brain is responsible for decisions about what behavior is to be selected and the overall elements of its execution, such as speed and direction in the case of walking. The actual activation of the appropriate muscles in the legs and the coordination of these

muscles is made locally by groups of neurons functionally organized in modules such as central pattern generators. Using a similar hierarchical and modular approach to control a legged robot may prove beneficial (see also Dean, 1999).

Second, there is an enormous redundancy of sense organs. In consequence, the loss of any single sense organ rarely has more than minor effects on walking (Cruse et al., 1984). This may aid adaptability as well as allowing an insect to compensate for damage to its

legs. Furthermore, the sensory input may help stabilize walking (Delcomyn, 1991b). Hence, plentiful sensors will almost certainly confer additional stability to the walking of a robot.

Third, neural circuits and the operation of their component parts can be modulated. This confers to insects an enormous versatility in the way in which particular neural circuits, sensory input, or motor output, is used. Sensory input and motor output can be fine tuned to operate within the best range for the behavior underway, and neural circuits can be selected and enhanced to provide the most efficient output. It is not clear whether it will be necessary for engineers to devise similar mechanisms in order, for example, to balance the needs of standing at rest with those of walking forward, but the necessity may have to be kept in mind.

Finally, at least some insects use a dual system of coordination and control. Fast moving insects like the American cockroach essentially ignore sensory input during fast running, but during slow or medium walking combine input from sense organs with the output from CPGs to produce the pattern of motor activity that will drive the leg. In contrast, it appears that in the much slower walking stick insect the centrally generated pattern is either extremely weak or nonexistent, so that the insect requires sensory input at all times to generate a proper pattern of motor output. Sensory signals certainly are returned to the central nervous system too late to be effective at high speeds of walking (Zill and Moran, 1981), while at the same time they appear to be essential to stabilize the gait during slow walking. The dual control system exhibited by American cockroaches may give those insects more adaptable control and enable the animal to achieve the high speeds of walking of which it is capable. As current robot actuators are still relatively slow, robots cannot yet achieve the stepping rates that many insects can achieve. Hence, it remains to be seen whether a dual control system is an absolute requirement for fast walking. Certainly it has not proved necessary for control of the relatively slow walking robots developed to date (Bachmann et al., 1997; Cruse et al., 1998a, 1998b).

One final caveat is necessary. Roboticists are interested in insect locomotor control because insects have evolved an extraordinarily flexible, adaptable, and for some insects, rapid locomotor capability. Using the information biologists provide about how the nervous system generates appropriate leg movements during walking may provide important clues for the design of a robust robotic controller. However, animals are subject

to many more evolutionary pressures than those that lead to efficient locomotor systems. Legs are used for grooming, searching for a foothold, fending off other animals, jumping, swimming, or other activities in addition to walking. Hence, the neural system for the control of leg movements found in an insect must be flexible enough to handle these other activities in addition to driving the leg through a stepping cycle. It certainly seems likely that understanding the neural basis of walking will provide information quite useful for the design of a controller for a legged robot, but it is unlikely that every neural mechanism is going to be beneficial for control of a robot that will have only a restricted set of uses for its legs. On the other hand, legs are inherently more flexible than wheels, which have little use except for locomotion. Hence, understanding the biology of leg controllers in all their complexity may make possible the construction of robots that have much richer possibilities of interactions with their environment than any yet built.

Acknowledgments

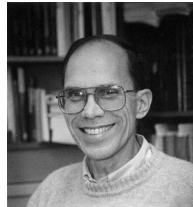
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