Introduction

Insects are among the most agile and adaptable animals in the world. In addition to stable movements on relatively flat, horizontal substrates, they can readily walk through tortuous terrain that requires climbing, tunneling, or turning movements to deal with obstacles. Beyond that, many insects can also walk on water or fly through the air. What is it about insects that make them so successful? Certainly, much of their success in locomotion is due to mechanical factors. The hexapod body plan allows insects to maintain passive stability over a variety of movements, and a sprawled leg posture adds to that stability. However, beyond their body plan, insects take advantage of a remarkable array of sensors that provide a wealth of information to a sophisticated central nervous system (CNS) that in turn acts through an efficient neuromuscular system to alter movements appropriately. These neural and muscular systems, working with their lightweight exoskeletons, allow them to adjust to a wide range of terrain.

Sensors fall into two groups. Local sensors located on appendages such as legs and wings monitor immediate properties of the limb such as joint position and load. These proprioceptors contribute to reflex circuits in the thoracic ganglia and also impact pattern generators that control the timing of joint movements. Exteroceptors located primarily on the head are associated with a sophisticated brain. These sensors provide a remarkable amount of information on the insect's surroundings (e.g., chemical, mechanical, auditory, and visual cues). The sensory information gained by these structures is processed in primary sensory regions, and then used by association centers to generate descending commands, which in turn alter local movement parameters in the thoracic ganglia. Many researchers have learned a tremendous amount about the local reflex circuits of the thoracic ganglia and the primary sensory regions of the brain. However, we are only beginning to examine the brain circuitry that influences locomotion.

Interestingly, this hierarchical locomotion control scheme parallels that of vertebrate animals, in spite of the fact that they evolved legged locomotion independently. In vertebrates, local control similar to that found in insect thoracic ganglia is found in the spinal cord. Vertebrate exteroceptors are also processed in sophisticated brain regions, leading to descending commands. The convergence between insect and vertebrate control systems underscores the notion that the hierarchical design used by both these successful animal groups represents a particularly good system that was selected for at least twice for negotiating a range of complex terrains.

An Overview of Walking

Before examining the neural basis of walking, it is important to understand the leg structures and the basic walking movements that are made by most insects. Insect legs are made up of a series of leg segments surrounded by hard cuticle and connected by soft joints. Starting with the first leg segment that attaches to the thorax and moving distally, the leg segments are the coxa, trochanter, femur, and tibia (Figure 1). Beyond that, a series of tarsal segments make up the foot, which typically ends in a segment containing claws and/or attachment pads. Most of these joints are simple hinges that flex in one plane. In contrast, the most proximal thoracic-coxal (ThC) joint that connects the leg to the thoracic cuticle is a mechanical wonder, a compound joint that allows rotation around three different axes. Effective leg movements that propel the body forward require coordination of these joints, both within a single leg and between the various different legs of the body.

Being hexapods, adult insects typically walk in a tripod gait, in which the front and rear legs on one side of the body step simultaneously with the middle leg on the opposite side. This tripod alternates with the remaining three legs, maintaining continuous static stability under most conditions. The period of the walking cycle during which legs are in contact with the ground and propel the body forward is called the stance phase. This period alternates with the swing phase when the legs are lifted off the ground to either return to their starting position or move to a new starting position in anticipation of a turn or other maneuver. At slower speeds, legs move in a metachronal pattern with one leg stepping at a time on each side of the body, starting from the rear and moving forward. This can grade into a tripod gait if, for example, the hind leg begins another step before the front leg finishes moving.

Although the three legs of a tripod set down and lift off together, their actions are not the same. Rather, the rear, middle, and front legs move through very different joint actions and interact differently with the ground, generating unique ground-reaction forces. The rear legs make piston-like movements, with the two distal joints extending through similar angles to produce a powerful
Local Control Circuits in Thoracic Ganglia

Insects require a sophisticated neural control system to coordinate the movements of each of these legs. Recent neurobiological studies in several laboratories are beginning to describe the local control circuits that lead to these movements.

A technical advantage to studying insect motor control stems from the relatively small number of motor neurons that control each muscle. Indeed, at several joints, one can monitor motor activity with simple electromyogram wires anchored to the cuticle and thereby examine activity from a specific, identified motor neuron. For example, in the cockroach, the main muscle that extends the femur-tibia (FTi) joint is controlled by only two motor neurons (the slow and the fast extensors of the tibia or SETi and FETi, respectively), and FETi is only active when the insect is running at relatively high speed.

The timing of extension and flexion in each joint is controlled by a separate pattern generator located within the thoracic ganglia. These small neural circuits are found throughout the animal kingdom and can act independent of sensory activity to provide basic timing commands for oscillatory behaviors. However, in normal behavioral situations, pattern generators typically act in concert with associated sensory structures to produce specific actions that are appropriate for the conditions that the animal is experiencing at any given moment. In insects, the transitions between extension and flexion of individual joints are influenced by sensory signals from leg proprioceptors. These sensors include chordotonal organs that monitor angle and direction of movement in each joint, strain detectors called ‘campaniform sensilla’ that provide information on load and muscle forces, and hair plates that detect maximal joint flexion. Thus, for example, a transition between stance and swing movements typically requires both pattern-generator activity and unloading of the leg.

How do leg proprioceptors exert their influence on leg movements? Their activation typically evokes reflex responses in specific motor neurons. In the simplest situation, these are resistance reflexes. For example, stretch of a chordotonal organ that normally occurs when the FTi joint is flexed will excite the motor neuron that, in turn, activates the muscle that counteracts the movement (SETi). Increases in load are detected by the campaniform sensilla and evoke similar reflexes to counteract imposed load and maintain posture.

When the insect is walking, these reflexes become more complex. Many reflexes are both quantitatively and qualitatively altered from the situation found in a standing insect. Moreover, they must now interact with the pattern generators that control timing of joint behavior in order to produce different leg movements that are appropriate for walking on horizontal surfaces, inclines, walls, or ceilings. Changes in joint coordination can also lead to movements associated with turning, climbing, or backward walking.

A particularly interesting finding from Ansgar Büschges’ laboratory in Cologne, Germany, revolves around the roles of proprioceptors in coordinating joint movements. After eliminating sensory signals from leg proprioceptors, the outputs of the pattern generators continue to burst, but their individual phase patterns are unrelated, indicating independence among the actual pattern generation circuitry. That is, there does not appear to be a master pattern generator present for each leg that would coordinate the various joints of that leg. However, coordination of joints can occur via interjoint reflexes. It is now apparent that proprioceptors project to neurons that control adjacent joints as well as those that control the joint that they monitor. These weaker interjoint reflexes influence transitions between flexion and extension of adjacent joints.

The interjoint reflexes that control stick insect legs have now been documented in great detail. Moreover, the pattern of these reflexes was used by Ekeberg, Blümel, and Büschges to control a sophisticated, dynamic simulation of a stepping leg. By simply progressing through the various chains of reflexes, the simulated leg moves realistically through stance and swing phases of walking. Interestingly, hind legs tend to move very differently than front
and middle legs, yet the simulation can replicate those movements also by simply reversing some of the reflexes. Similar alterations in leg movement occur in cockroach middle legs when they transition between forward walking and turning behaviors. Robotic models of both the stick insect and the cockroach leg, developed in the Ritzmann laboratory based upon the Ekeberg model, have confirmed that a transition from forward walking to turning can occur through changes in reflex sign.

These observations and models suggest a hypothetical mechanism for redirecting leg movement. Under this model, descending commands from the brain alter locally coordinated actions in each leg by modifying various opposing reflex circuits in the thoracic ganglia. Laiyong Mu, working in the Ritzmann laboratory, demonstrated that proprioceptive leg reflexes could, in fact, be influenced by activity that descends from the brain. His experiments examined an interjoint reflex generated by stretching and relaxing the femoral chordotonal organ (FCo) that monitors the position of the FTi joint. In addition to the intra-joint reflex described earlier for SETi, this organ also excites the slow depressor motor neuron that controls extensor muscles of the coxa-trochanter joint (Ds). In intact animals, relaxation of the FCo inhibits Ds. However, in animals with descending activity from the brain eliminated by cutting both cervical connectives, the reflex reverses and FCo stretch generates excitation in Ds. Similarly, Turgay Akay, working in the Büschges laboratory, has demonstrated that reflexes in stick insects reverse sign when the animal changes from forward to backward walking.

In addition to coordination within each leg, effective movements must also be coordinated among all six legs. The manner in which this occurs has been formalized by a set of rules described by investigators in Holk Cruse’s laboratory in Bielefeld, Germany. These rules stem from examination of various insect locomotion behaviors. They describe effects that the state of one leg has upon adjacent leg movements. For example, one rule states that a leg should not be lifted off the substrate for return while the next posterior leg is still in swing. Another rule states that as an anterior leg progresses through the stance power stroke, it increasingly influences the next posterior leg to enter into its swing return phase.

The total set of ‘Cruse rules’ can explain much of the interleg coordination that is seen in insect locomotion. They have also been used to control several robotic devices and to guide neurobiological studies that seek to understand the neural basis of these properties.

Influence of Brain Circuits on Locomotion

One might conclude from the previous section that walking movements are controlled exclusively by local circuits, with higher centers serving merely to initiate movement. However, the situation becomes more complex when considering movements through unpredictable, natural terrain. Upon encountering a block, a cockroach rears up to an appropriate height, so that it can place its front legs on the top surface, and then climbs over the barrier. A shelf-like obstacle can evoke either tunneling or climbing. Detailed behavioral analysis by Cynthia Harley in the Ritzmann laboratory indicates that this decision is largely dictated by the manner in which antennae contact the obstacle. Contact from above evokes climbing, while contact from below yields tunneling. Of course, other options are possible. Insects readily turn and walk around obstacles, follow complex walls, and span gaps in substrates, and several laboratories have described these behaviors in a variety of insect species.

Any of these obstacles requires a directed change in the actions that are typically made by the legs as the insect walks forward. While some barriers can be dealt with through local reflex effects, the redirection of leg movements associated with large barriers requires that the animal become aware of the barrier, evaluate it, and then redirect leg movements accordingly. In order to accomplish these adjustments, the insect takes advantage of the various sensory systems located on its head. These include tens of thousands of mechanoreceptors on each antenna and on the maxillary palps, chemoreceptors also on those structures, visual cues detected by either compound eyes or simple ocelli, and in some insects, auditory or vibration signals. Many of these sensors project to primary sensory regions and then to association regions of the brain. This neural processing of sensory information must ultimately lead to descending commands that interact with the local control circuits in the thoracic ganglia and thereby redirect leg movements appropriately. Indeed, insects that have experienced damage within various brain regions fail to negotiate barriers appropriately.

Two main association regions exist in the insect brain. They are the mushroom bodies (MB) and the central complex (CC). The MBs are perhaps the most studied region of the insect brain. They are involved in learning and memory as well as olfactory processing. The CC was originally described by Les Williams. It is made up of several midline neuropils, including the fan-shaped body, ellipsoid body, protocerebral bridge, and two paired nodules. The morphology of these neuropils has been described in detail for several insects. Several have a distinctly columnar organization, and fibers project between the left and right columns in the protocerebral bridge and columns of the fan-shaped body. This anatomy suggests that turning decisions may be made in the CC. In earlier experiments, Franz Huber found that stimulation within the CC of crickets evoked increases in locomotion and turning movements. More recently, both genetic and
mechanical lesions within the CC have been associated with motor deficits.

Physiological studies have only recently focused upon the CC. Perhaps the most remarkable finding is a topographic map of polarized light space that was described by Uwe Homberg’s laboratory. Observations in the Ritzmann laboratory describe multisensory CC units that respond to visual and antennal stimulation. Some of these units are biased to one antenna or to a preferred direction of movement of either antenna. Thus, it is possible that sensory information on barriers as well as surrounding ambient conditions acts through the circuits of the CC to ultimately influence the local control circuits of the thoracic ganglia.

Descending activity, influenced by sensory information processed in the CC, could represent the commands that are required to alter local reflexes and redirect leg movements, as described earlier. Neurons leaving the CC project to a region of the brain called ‘the lateral accessory lobe,’ and several neurons that ultimately descend to the thoracic ganglia also pass through this region. Thus, it is possible that the remarkable agility of insects in the face of complex terrain arises in large part from descending commands that are influenced by head-based sensors through the actions of CC circuits. Appropriate modifications on basic walking patterns would then occur when these descending commands alter local reflexes within the thoracic ganglia. By allowing the local reflex circuits to perform the moment-by-moment control of actual leg movements, insects achieve both remarkable stability and amazing flexibility.

Insect Flight

Of course, insect locomotion is not limited to walking and running. Many insects are among the most maneuverable flyers in the animal kingdom. How is the hierarchical control system modified to suit this form of locomotion? Conceptually, the issues faced by flying insects are similar to those confronted by walking ones. The wings beat up and down with an intrinsic rhythm, and descending commands from the brain based on sensory information must be processed and executed within the context of this ongoing locomotor pattern. In many ways, flight control can be viewed as an extreme example of terrestrial locomotor control, as many of the same sensors and neural circuits are involved. The extreme limits of a behavior, however, are often informative regarding what factors limit an animal’s ability to perform, survive, and thrive.

One prominent control problem, differing between walking and flying, is that flight is only dynamically stable, meaning that an insect cannot simply stop in place to gather or process more sensory information before implementing an action. Further complicating this situation is the fact that motor commands must be executed at an appropriate phase of the wing beat cycle, just as a walking animal must contract its muscles at the right times to influence movement. Because the wing beat frequencies are generally higher than stepping rates, this means that descending control mechanisms must include extremely precise methods for gating and synchronization with locomotor rhythms. To make matters even worse from a control standpoint, in some insects the powerful muscles which drive the wings up and down are not under direct control of the nervous system, as the upstroke and the downstroke muscles excite each other mechanically through stretch activation. Therefore, the animal must use sensory information to determine the state of its own muscles and body, combining this appropriately with information about the outside world to produce and execute a turning movement through precisely timed contractions of the wings’ small steering muscles.

The true (dipteran or two-winged) flies have specialized sense organs which are extremely well suited to monitor motions of their bodies. In these insects, the hind pair of wings has evolved into very small, club-shaped organs called ‘halteres’ (Figure 2). The halteres beat back and forth at the same time as the wings, but have no aerodynamic function and instead are tightly packed with mechanosensors. Most of the sensors on the halteres are dedicated to measuring the back-and-forth motions, which presumably serve to report the wings’ positions to the central nervous system. In combination with similar signals from the wings themselves, information from the halteres could be used to calculate not only the state of each wing power muscle, whether contracting or relaxing, but may also contain clues as to whether the wings are moving as they should be, in phase with the halteres, or if wind, load, or other external forces have derailed the wings from their normal pattern.

Beyond these uses, the halteres also have a more celebrated function as onboard gyroscopes, recently studied in depth by Michael Dickinson’s lab. Some of the halteres’ mechanosensors do not respond phasically to each stroke,
but rather are activated when the halteres are deflected from their stroke plane. Since the halteres are so tiny, such a deflection would not result from a swat or even from wind blowing the haltere, but only by Coriolis forces corresponding to a rotation of the fly's body, and then only during a particular part of the haltere's stroke phase. Afferent neurons from the deflection-sensitive fields are electrically coupled to motor neurons of the wing steering muscles, thereby producing very fast and precisely timed contractions designed to compensate for the imposed rotation of the body. This ability to sense body rotations seems to be very important to insect flight, possibly because the inherent instability of flight in small animals makes the maintenance of equilibrium a task of primary importance. Recent studies suggest that moths and butterflies may use their antennae as rotation sensors, in a similar manner to the halteres of flies.

In line with the hypothesis that ongoing patterns of movement are controlled by descending commands working indirectly through reflex arcs, the halteres are equipped with their own set of steering muscles. Thus, a neuron from the brain might cause a contraction in the haltere steering muscles, in addition to or instead of modifying the wing motions directly. These muscles could act to deflect the haltere from its stroke plane in the same way that Coriolis forces do, thus triggering a reflex cascade that leads to the fly turning. Work in the Dickinson laboratory has demonstrated that visual stimuli are capable of eliciting activity in the haltere steering muscles, but the rest of this pathway remains conjectural. One especially appealing part of this hypothesis is that the haltere reflexes, just like those acting through leg mechanosensors, normally have precise and effective influence over locomotor activity, so co-opting those mechanisms to produce directed movements takes advantage of this built-in robustness.

Mechanosensation is not the only way that insects detect the motions of their bodies during flight. Bees, beetles, ants, locusts, crickets, and even cockroaches can fly without any known mechanical ability to sense body rotations independently from their wings, but exceedingly few insect species can fly stably in complete darkness. Dragonflies, in fact, are so dependent on vision for flight control that they cannot fly in normal indoor lighting. Even nocturnal insects, such as moths, make extensive use of vision to navigate and to sustain flight. Many fundamental visual processes, such as the delay-and-correlate model for retinal motion detection, were derived from experiments on flies by Werner Reichardt and subsequent investigators. Karl Götz, in particular, advanced the use of what might now be called 'insect psychophysics' to probe the neural processes underlying visually mediated flight behaviors. These experiments involve tethering a fly to a sensitive torque meter and using the forces produced by the insect to close the feedback loop, rotating a patterned cylinder in place around the animal. This artificial-closed-loop sensory environment allows experimenters to manipulate parameters of both the stimulus and the feedback to determine how visual information is processed in a behaving animal. For example, researchers such as Axel Borst and Martin Egelhaaf have shown that, rather than parsing the world into collections of objects like trees or rocks, basic insect flight control is based only on optic flow – the amount and direction of movement seen by the retina. This is partially due to the poor spatial resolution of the insect eye (something like us viewing the world through a 40 × 40-pixel camera), but also reflects the minimum requirements to keep an insect airborne. Martin Heisenberg has suggested some forms of shape learning in flies and Mandyam Srinivasan has shown memory for color and texture in bees, but simply maintaining steady flight is a much lower-level goal and can seemingly be achieved using motion cues alone.

Summary

Insects take advantage of both local reflexes and sensors mounted on their heads to generate adaptable movements. Sensory information is processed both locally within the thoracic ganglia and in sophisticated brain regions. Interactions within this hierarchical neural control system then allow insects to quickly adjust their movements according to immediate demands. As a result, they can successfully navigate a wide range of terrestrial terrain and, for many insects, fly with an agility that is unmatched by manmade devices. These control systems, coupled with efficient body mechanics, certainly contribute to their unparalleled success within the animal kingdom.

See also: Insect Navigation; Nervous System: Evolution in Relation to Behavior; Robot Behavior; Robotics in the Study of Animal Behavior; Vision: Invertebrates.

Further Reading


