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Locomotion, Invertebrate

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Introduction

Locomotion can be defined as an animal's ability to move its body along a desired path, making it fundamental to many other animal behaviors (Dickinson et al., 2000). Given the diversity of ecological niches that animals inhabit, and the variety of body plans that they possess, it is not surprising that their modes of locomotion are equally diverse. Types of locomotion include walking, swimming, flying, crawling, and burrowing.

Despite this diversity, certain common principles can be discerned. All locomotion systems must solve the twin problems of *support* and *progression*. The problem of support arises because in many modes of locomotion (e.g., flight), the gravitational attraction of the earth must be overcome. The problem of progression arises because an animal must generate propulsive forces that overcome not only its body's inertia, but also any drag from the density and viscosity of the medium or the friction of the substrate.

Both support and progression involve the generation of forces. This is accomplished by the contraction of muscles attached to either flexible hydrostatic skeletons or rigid skeletons. In addition, many animals have specialized body structures and appendages that facilitate locomotion, such as fins, wings, and legs. Thus, the detailed design of an animal's body is a crucial component of its locomotion system. As a result of the nature of these specializations, the problems of support and progression are rarely independent. Wings, for example, are used to generate both lift and propulsion in flying animals.

In order to provide support and progression, the movements of these specialized body structures must be coordinated by an animal's nervous system. The diverse modes of locomotion and the variety of body plans lead to equally diverse neural circuitry mediating locomotion. However, once again, certain basic principles can be discerned. Underlying many forms of locomotion are basic oscillatory patterns of movement generated by neural circuits that are referred to as *motor pattern generators* (MOTOR PATTERN GENERATION). Even when these circuits contain dedicated neurons that autonomously produce rhythmic outputs (so-called *central pattern generators*), this central pattern is often strongly shaped by sensory feedback, fundamentally involving the body and environment in the generation of a locomotor pattern. In fact, sensory feedback can play such a fundamental role that it sometimes makes no sense to speak of a distinct central pattern generator.

Researchers have begun to use computer modeling to understand the neural basis of locomotion. In contrast to most work in computational neuroscience, models of animal bodies are playing an important role in understanding locomotion systems. Increasingly, experimental evidence suggests that motor systems cannot be fully understood without considering the biomechanical properties of the bodies in which they are embedded (Chiel and Beer, 1997). Modeling of both an animal's body and the neural circuitry underlying its behavior has been termed *computational neuroethology* (NEUROETHOLOGY, COMPUTATIONAL). This chapter will focus on invertebrate locomotion systems for which quantitative modeling has been done, reviewing computer models of swimming, flying, crawling, and walking.

Swimming

In swimming, support is less of a problem than it is in other modes of locomotion. However, unless an animal is neutrally buoyant, it must still make efforts to keep from either sinking or rising. Progression requires much more effort as a result of the drag from water's density and viscosity. Thus, the bodies of swimming animals are streamlined. Swimming invertebrates utilize one of two mechanisms, either hydraulic propulsion or rhythmic undulations of the body.

Although models of swimming in leeches, mollusks, and nematodes have been constructed (Pearce and Friesen, 1988; Niebur and Erdös, 1991), perhaps the most modeled swimming system is not that of an invertebrate but that of a primitive vertebrate known as the lamprey. Lampreys swim using coordinated contractions of muscles on each side of the body. These contractions produce a traveling wave along the body, with a wavelength of approximately one body length across a wide range of swimming speeds. Although the lamprey possesses much of the basic vertebrate neural architecture, the experimental accessibility of its nervous system has allowed a level of neurophysiological analysis that is more typically applied to invertebrate systems. Earlier work used mathematical analysis and simulation of chains of model oscillators to study intersegmental coordination in the lamprey spinal cord (SPINAL CORD OF LAMPREY: GENERATION OF LOCOMOTOR PATTERNS; CHAINS OF OSCILLATORS IN MOTOR AND SENSORY SYSTEMS). Recent work has focused on more realistic models of the underlying

neuronal circuit and models of the relevant mechanics of the lamprey body and the water through which it swims.

Ekeberg and Grillner (1999) have reviewed much of the recent work in this area. The rhythm-generation circuit consists of populations of motor neurons, excitatory interneurons, and two distinct types of inhibitory interneurons repeated in each segment. Models of this circuitry have demonstrated that oscillations are relatively easy to generate, but details of the pattern (e.g., burst termination) depend on biophysical details of the nerve cells. The generation and propagation of the traveling wave along the segments has been studied by coupling chains of model segmental oscillators. This work revealed that if the rostral segments receive stronger excitation, they become the source of the traveling wave, and variation of this extra excitation allows the spatial wavelength of the swimming pattern to be controlled separately from its temporal frequency.

Mechanical aspects of swimming have been investigated by coupling pattern-generation circuitry to a segmented body model actuated by linear viscoelastic model muscles and embedded in a model of the static drag force produced by the surrounding water. By varying the level and asymmetry of tonic input, this neuromechanical model could produce swims at a range of speeds, turns, and rolls. In addition, two kinds of sensory feedback have been modeled. Incorporating feedback from intraspinal stretch receptors led to improved robustness of the swim pattern against unpredictable changes in water flow. Feedback from vestibular receptors was incorporated in order to model roll and pitch stabilization.

Flying

In many ways, flying is similar to swimming. However, because of the much lower density of air, considerably faster motions are required for powered flight than for swimming. While quasi-steady-state aerodynamic analyses of the sort used to understand aircraft have been successfully applied to larger animals, they have not been very successful for small flying insects. According to steady-state theory, many insects should be unable to generate sufficient lift to hold themselves aloft!

A recent model by Dickinson and colleagues has begun to shed considerable light on insect flight (Dickinson, Lehmann, and Sane, 1999). Because of the delicate size and high speed of insect wings, direct measurement of the forces involved is extremely difficult. For this reason, a robotic model was used to explore unsteady flows during hovering by the fruit fly *Drosophila melanogaster*. The model was submerged in mineral oil and scaled both in space and time so as to reproduce the Reynolds number (ratio of inertial to viscous forces) relevant to small insects flying in air. Dickinson and colleagues found that three major mechanisms contributed to lift generation in the model. First, vortices formed at the leading edge of the wing produce lift during much of the power stroke. Second, additional lift is produced by circulation of air around the wings resulting from rapid rotation at the beginning and end of each stroke. Third, further forces are produced at the start of each upstroke and downstroke as a result of collisions of the wings with the swirling wake produced by the previous stroke, a mechanism termed *wake capture*. Because of the sensitivity of the latter two mechanisms to the timing of wing rotation, the model suggests that the control of small details of wing motion can be used in steering flight.

Crawling

In crawling, locomotion occurs along the bottom surface of an aquatic environment or the surface of the earth via rhythmic contact between the body and the substrate. Invertebrates generate propulsive forces for crawling by changing body shape in one of three

ways: contract-anchor-extend (as in the leech), pedal locomotion (as in molluscs), or peristaltic locomotion (as in earthworms). Crawling invertebrates typically utilize either hydrostatic skeletons or muscular hydrostatic structures to accomplish these movements.

A detailed neuromechanical model of crawling in the leech has been constructed by Kristan et al. (2000). This model assumes that the cross-sectional geometry of each body segment is elliptical, that the volume of body segments remains constant during movement, and that the animal's shape minimizes total potential energy. Kristan et al.'s simulations incorporate relatively realistic models of the circular and longitudinal muscles found in the leech body wall. Driving the model body with activation patterns deduced from the kinematics of intact animals produces crawling movements that are considerably more realistic than those produced by activation patterns derived from reduced preparations. These results suggest that sensory feedback plays a critical role in providing appropriate timing of activation of longitudinal and circular muscles.

Walking

In legged animals, the body is raised above the ground and propelled by a sequence of leg movements. During walking, each leg cycles between a *stance phase*, in which the leg is providing support and propulsion, and a *swing phase*, in which the leg is off the ground and swinging forward. Swing phase duration is often nearly constant, while stance phase duration varies considerably with the speed of progression. Because the legs provide both support and propulsion and must be lifted after each stance, their movements must be coordinated so that the center of mass of the body remains within a polygon of support formed by the stancing legs (static stability). Otherwise, the animal must dynamically stabilize its body. Another coordination problem arises because adjacent legs must not interfere with one another. In many-legged animals, avoiding interference between adjacent legs is the crucial coordination problem, whereas the maintenance of stability is more important for animals with fewer legs.

Insect locomotion is remarkably flexible and robust. Insects can walk over a variety of terrains, as well as vertically and upside-down. In addition, they can also adapt their gait to the loss of up to two legs without severe degradation of performance (Delcomyn, Chapter 2 in Beer, Ritzmann, and McKenna, 1993) and sometimes even utilize dynamically stable gaits (Full, Chapter 1 in Beer et al., 1993). Most modeling has focused on statically stable walking across flat, horizontal surfaces. Even under these conditions, insects exhibit different gaits depending on their speed of locomotion.

Slowly walking insects show distinct *metachronal waves* on each side of the body: each leg begins its swing immediately following the termination of the swing of the leg behind it, with a 180° phase relationship between the pair of legs in each segment. Fast-walking insects utilize a *tripod gait*, in which the front and back legs on each side of the body step in unison with the middle leg on the opposite side. In one of the earliest theoretical models of insect walking, Wilson (1966) suggested that the entire range of observed insect gaits could be explained by assuming that fixed, antiphase metachronal waves on each side of the body increasingly overlap as walking speed increases.

We developed a neural network model based on work by Pearson and colleagues on the neural organization of the American cockroach's walking system (Beer and Chiel, Chapter 12 in Beer et al., 1993). In this model, each leg controller has a pacemaker neuron whose output rhythmically oscillates due to a voltage-dependent intrinsic current. These pacemakers implement the swing burst-generators that Pearson hypothesized. A pacemaker burst initiates a swing by inhibiting the foot and backward swing motor neurons and exciting the forward swing motor neurons, causing the foot to lift and the leg to swing forward. Between bursts, the foot is down

and tonic excitation from a command neuron moves the leg backward. Feedback from two sensors that signal when a leg is nearing its extreme forward or backward position fine-tunes pacemaker output. Forward angle sensor inhibition encourages burst termination, whereas backward angle sensor excitation encourages burst initiation. The forward angle sensor also makes direct connections to the motor neurons, modeling leg reflex pathways described by Pearson.

In order to generate statically stable gaits, the swings of the individual legs must be coordinated in some way. Following Pearson, we inserted mutually inhibitory connections between the pacemaker neurons of adjacent legs. We also added an entrainment mechanism for generating metachronal waves: slightly increasing the angle ranges of the rear legs lowers the burst frequency of the rear pacemakers, causing the pattern generators on each side of the body to phase-lock into a stable metachronal relationship.

In simulations of this circuit in a kinematic hexapod body model, a continuous range of statically stable gaits similar to those described by Wilson (1966) were observed. This range of gaits was produced simply by varying the tonic level of excitation of the command neuron. Smooth transitions between gaits could be generated by continuously varying this excitation. We found that the ability of this circuit to generate statically stable gaits was quite robust to lesions. For example, removing any single sensor or interpacemaker connection did not generally disrupt locomotion. These studies also demonstrated that sensory feedback was crucial for the maintenance of the slower metachronal gaits, but was relatively unimportant in the tripod gait.

The stick insect *Carausius morosus* has also been a major focus of legged locomotion research. Cruse (1990) reviewed leg coordination influences in both the stick insect and the crayfish *Astacus leptodactylus*. In the stick insect, there are three major influences: (1) a swinging leg inhibits the swing of a more anterior leg; (2) when a leg begins its stance phase, it excites the swing of a more anterior leg; and (3) as a stancing leg nears the end of its stance, it increasingly excites the swing of a more posterior leg. Some of these influences also operate between pairs of legs in the same segment.

Dean (1991) simulated these and other coordination mechanisms. The pattern generator for each leg was modeled as a relaxation oscillator with two states corresponding to stance and swing. The positions of each of the six legs were the state variables for a kinematic model of walking. The coordination mechanisms modified the position at which an affected leg began its swing, with inhibitory influences producing a posterior shift and excitatory influences producing an anterior shift. Dean's simulations demonstrated that these coordination mechanisms were sufficient to generate a continuous range of gaits, including the wave gait at low stepping frequencies and the tripod gait at high stepping frequencies. The model also exhibited distinct asymmetries in stepping pattern observed in the stick insect, in which the phase relationship between legs in the same segment is consistently lower or higher than 180°. A good review of earlier models of stick insect walking can also be found in Dean (1991).

Dean also explored the robustness of these coordinating mechanisms to various perturbations, including variations in starting configurations, perturbations of individual leg velocities, and obstructions to the swing of individual legs. He found that the gaits generated by these mechanisms were quite robust to such perturbations and that, in most cases, the model's responses were similar to those of the insect. Discrepancies between the model and the insect could be traced to the need for dynamic variables in addition to kinematic ones. Dean varied the strength and form of the coordination mechanisms. He found that influence (3) was the most important to maintaining proper coordination due to its graded na-

ture, though the model was quite robust to substantial variations in the strengths of individual mechanisms.

Biorobotics

The remarkable flexibility and robustness of animal locomotion has intrigued roboticists. Biologically inspired locomotion controllers offer a number of advantages over more classical approaches, including their distributed nature, their robustness, and their computational efficiency. Likewise, robots can serve as an important new modeling methodology for testing biological hypotheses. Thus, a number of researchers have begun to explore the interface between biology and robotics (Beer et al., 1998; Webb, 2000). Raibert and Hodgins (Chapter 14, in Beer et al., 1993) have argued for the importance of leg and actuator design in locomotion, designing a series of dynamically stable hopping and running robots based on the biomechanical design of animal limbs. For example, we implemented both the locomotion circuit and the stick insect coordination mechanisms described previously in hexapod robots and found that they could generate a range of gaits similar to those observed in simulations and were equally robust to perturbations (Beer et al., 1997), and more recent work has successfully incorporated significantly more biological realism into the latest robot (Quinn and Ritzmann, 1998). Thus, models of animal locomotion may not only yield insights into the neural control of motor behavior, but may also have significant technological applications.

Discussion

We have touched on several successful examples of quantitative modeling of locomotion. It is notable that the different simulations utilize very different neural models. More fundamentally, it is striking that very different neural architecture can be utilized to generate locomotion. Undoubtedly, this variety is a result of the diverse body plans of animals and the many different ecological niches that they occupy. One consistent theme that does emerge, however, is the complex interplay of sensory input and central circuitry in the generation of locomotion. This complex interplay is responsible for the adaptive flexibility of animal locomotion.

Road Map: Motor Pattern Generators

Related Reading: Biologically Inspired Robotics; Chains of Oscillation in Motor and Sensory Systems; Half-Center Oscillators Underlying Rhythmic Movements; Locomotion, Vertebrate; Locust Flight: Components and Mechanisms in the Motor; Spinal Cord of Lamprey: Generation of Locomotor Patterns

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Locomotion, Vertebrate

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Introduction

Locomotion is a fundamental skill for animals. It is required for a large variety of actions, such as finding food, encountering a mate, and escaping predators. Among the various forms of vertebrate locomotion are swimming, crawling, walking, flying, and the more idiosyncratic movements such as hopping, brachiation, and burrowing.

Animal locomotion is characterized by rhythmic activity and the use of multiple degrees of freedom (i.e., multiple joints and muscles). In vertebrates, motion is generated by the musculoskeletal system, in which torques are created by antagonistic muscles at the joints of articulated systems composed of rigid bones. All types of vertebrate locomotion rely on some kind of rhythmic activity to move forward: undulations or peristaltic contractions of the body, oscillations of fins, legs, or wings. As the animal rhythmically applies forces to the environment (ground, water, or air), reaction forces are generated that move the body forward.

This type of locomotion is in contrast to the motion of most man-made machines, which usually relies on few degrees of freedom (e.g., a limited number of powered wheels, propellers, or jet engines) and continuous rather than rhythmic actuation. From a technological point of view, animal locomotion is significantly more difficult to control than most wheeled or propelled machines. The oscillations of the multiple degrees of freedom need to be well coordinated to generate efficient locomotion. However, as can be observed from the swimming of a dolphin or the running of a goat over irregular terrain, animal locomotion presents many interesting features, such as energy efficiency (for swimming) and agility. The next sections review the neural and mechanical mechanisms underlying vertebrates' fascinating locomotor abilities.

Neural Control of Locomotion

Despite diversity in types of locomotion, the general organization of the vertebrate locomotor circuit appears to be highly conserved. Locomotion is controlled by the interaction of three components: (1) spinal central pattern generators (CPGs), (2) sensory feedback, and (3) descending supraspinal control. The combination of these three components is sometimes called the motor pattern generator (MPG).

Central Pattern Generators

Central pattern generators are circuits that can generate rhythmic activity without rhythmic input (see HALF-CENTER OSCILLATORS UNDERLYING RHYTHMIC MOVEMENTS and MOTOR PATTERN GEN-

ERATION). The rhythms can often be initiated by simple tonic (i.e., nonoscillating) electrical or pharmacological stimulation. In vertebrates, the CPGs are located in the spinal cord and distributed in different oscillatory centers. In the lamprey, for instance, the swimming CPG is a chain of approximately 100 segmental oscillators distributed from head to tail (see CHAINS OF OSCILLATORS IN MOTOR AND SENSORY SYSTEMS and SPINAL CORD OF LAMPREY: GENERATION OF LOCOMOTOR PATTERNS). In tetrapods, the locomotor CPG appears to be composed of different centers, one for each limb, that are themselves decomposed into different oscillatory subcenters for each joint (Grillner, 1981). Recent evidence from intracellular recordings in the mudpuppy suggests that joint subcenters can be decomposed even further into distinct oscillatory centers for flexor and extensor muscles (Cheng et al., 1998).

Experiments in completely isolated spinal cords and in deafferented animals (i.e., animals without sensory feedback) have shown that the patterns generated by the CPG are very similar to those recorded during intact locomotion. This demonstrates that sensory feedback is not necessary for generating and coordinating the oscillations underlying locomotion during stationary conditions.

Sensory Feedback

Although sensory feedback is not necessary for rhythm generation, it is essential for shaping and coordinating neural activity with actual mechanical movements. The main sensory feedback to the CPGs is provided by sensory receptors in joints and muscles (see MOTOR CONTROL, BIOLOGICAL AND THEORETICAL). Rhythmically moving the tail or a limb of a decerebrate vertebrate is often sufficient to initiate the rhythmic patterns of locomotion. The frequency of oscillations then matches that of the forced movement, illustrating the strong influence of peripheral feedback on pattern generation.

Sensory feedback is especially important in higher vertebrates with upright posture such as mammals (as opposed to vertebrates with sprawling postures, like certain amphibians and reptiles), because the limbs of those vertebrates play an important role in posture control—supporting the body—in addition to locomotion.

A whole set of reflexes exists to coordinate neural activity with mechanical activity. One example is the stretch reflex, which generates the contraction of a muscle when the muscle is lengthened and which therefore helps maintain posture. The reflex pathways often share many of the interneurons that participate in locomotion control, and the action of reflexes is therefore not fixed. During locomotion, the action of reflexes can be modulated by central commands and in some cases even reversed, depending on the timing within the locomotor cycle (see Pearson and Gordon, 2000, and