

- Dickinson, M. H., Lehmann, F.-O., and Sane, S. P., 1999, Wing rotation and the aerodynamic basis of insect flight, *Science*, 284:1954–1960.
- Ekeberg, O., and Grillner, S. 1999, Simulations of neuromuscular control in lamprey swimming, *Phil. Trans. R. Soc. Lond. B*, 354:895–902.
- Kristan, W. B., Jr., Skalak, R., Wilson, R. J. A., Skierczynski, B. A., Murray, J. A., Eisenhart, F. J., and Cacciatore, T. W., 2000, Biomechanics of hydroskeletons: Studies of crawling in the medicinal leech, in *Bio-mechanics and Neural Control of Posture and Movement* (J. M. Winters and P. E. Crago, Eds.), New York: Springer-Verlag, pp. 206–218.
- Niebur, E., and Erdős, P., 1991, Theory of the locomotion of nematodes: Dynamics of undulatory progression on a surface, *Biophys. J.*, 60:1132–1146.
- Pearce, R. A., and Friesen, W. O., 1988, A model for intersegmental coordination in the leech nerve cord, *Biol. Cybern.*, 58:301–311.
- Quinn, R. D., and Ritzmann, R. E., 1998, Construction of a hexapod robot with cockroach kinematics benefits both robotics and biology, *Conn. Sci.*, 10:239–254.
- Webb, B., 2000, What does robotics offer animal behaviour? *Anim. Behav.*, 60:545–558. ♦
- Wilson, D. M., 1966, Insect walking, *Annu. Rev. Entomol.*, 11:103–122.

# Locomotion, Vertebrate

Auke Jan Ijspeert

## 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

SENSORIMOTOR INTERACTIONS AND CENTRAL PATTERN GENERATORS for reviews).

### *Descending Supraspinal Control*

Locomotion is initiated and modulated by descending pathways from diencephalic and mesencephalic locomotor centers. (For reviews, see Donkelaar, 2001, and Rossignol in Rowell and Shepherd, 1996, chap. 5). Some of these pathways are direct; an example is the pathway from the vestibular nuclei and the cerebellum to the spinal neurons. Other pathways are relayed by centers in the brainstem, in particular the red nucleus and the reticular nuclei. In all vertebrates, the reticulospinal tract plays a crucial role in generating the drive for the basic propulsive body and limb movements. In the lamprey, for instance, reticulospinal neurons control both the speed and direction of locomotion (Grillner et al., 1995). In mammals, additional direct pathways exist between the motor cortex and the spinal cord—the corticospinal tracts. These tracts are unique to mammals and play an important role in visuomotor coordination, such as accurate foot placement in uneven terrain.

Interestingly, the input signals to the brainstem do not need to be complex to generate locomotion. It has been known since the 1960s that simple electrical stimulation of the brainstem initiates the walking gait in a decerebrate cat, and progressively increasing the amplitude of the stimulation leads to an increase in the oscillation frequency, accompanied by a switch from walking to trotting and eventually to galloping (Shik, Severin, and Orlovsky, 1966). This demonstrates that the brainstem and the spinal cord contain most of the circuitry necessary for locomotion, including complex phenomena such as gait transitions (see GAIT TRANSITIONS).

### **The Biomechanics of Locomotion**

Locomotion is the result of an intricate coupling between neural dynamics and body dynamics, and many fundamental aspects of locomotion control, including gait transition, control of speed, and control of direction, cannot be fully understood by investigating the locomotor circuit in isolation from the body it controls. A body has its own dynamics and intrinsic frequencies with complex nonlinear properties, to which the neural signals must be adapted for efficient locomotion control. As observed by roboticist Marc Raibert, the central nervous system (CNS) does not control the body, it can only make suggestions.

The body is a redundant system, with many muscles per joint and several muscles acting on more than one joint. Muscles serve as actuators, brakes, stiffness regulators, and stores of elastic energy. During locomotion, the frequencies, amplitudes, and phases of the signals sent to the multiple muscles must be well orchestrated. In most vertebrates, complex coordination is required not only between different joints and limbs but also between antagonist muscles, which combine periods of co-activation for modulating the stiffness of the joint and periods of alternation for actuating the joint.

In legged locomotion, the dynamics of a leg can be approximated by a pendulum model during walking and by a spring-mass model during running. These models allow one to relate several features, such as resonance frequencies, to the length and stiffness of the legs, and are able to describe the mechanics of legged locomotion surprisingly well in many animals.

The importance of the mechanical properties of the body is illustrated by research on passive walkers. Passive walkers are legged machines (some with knees and arms) that transform potential energy from gravity into kinetic energy when walking down a gentle slope. When correctly designed, these machines do not require any actuation or control for generating a walking gait, which in some cases can be strikingly human-like.

### **Numerical Simulations of Locomotor Circuits**

Although the general organization of the vertebrate locomotor circuit is known, much work remains to be done to elucidate how its different components are implemented and how they interplay to generate the complex patterns underlying locomotion. This is a complex task because (1) these patterns are due to the interaction of the CNS and the body in movement, (2) numerous neurons in the brainstem and the spinal cord are involved, and (3) in most vertebrates, the same circuits appear to be involved in generating very different patterns of activity (e.g., different gaits in tetrapods). For the moment, the best decoded locomotor circuits are probably the swimming circuits in the lamprey and the frog embryo. For other vertebrates, in particular tetrapods, significant parts of the structure and functioning of the locomotion circuitry remain unknown.

Numerical simulations have an important role to play in evaluating whether a potential model of a neural circuit is adequate and sufficient to reproduce the rhythmic patterns observed through intracellular and/or EMG measurements. Several important issues can be investigated in simulation, such as the general stability of the patterns and the effect of modulating the tonic drive on the frequencies and phases of the oscillations. Simulations do not need to be restricted to the CNS. An interesting approach to understanding locomotion control is to couple the simulations of the locomotor circuits to physics-based simulations of the body (or to a robot). Such *neuromechanical* simulations are particularly useful because they embed the neural circuits in a body in interaction with the environment, therefore allowing one to close the sensing-acting loop and to investigate the complete resulting motor patterns (as opposed to only the patterns produced by the isolated CPGs).

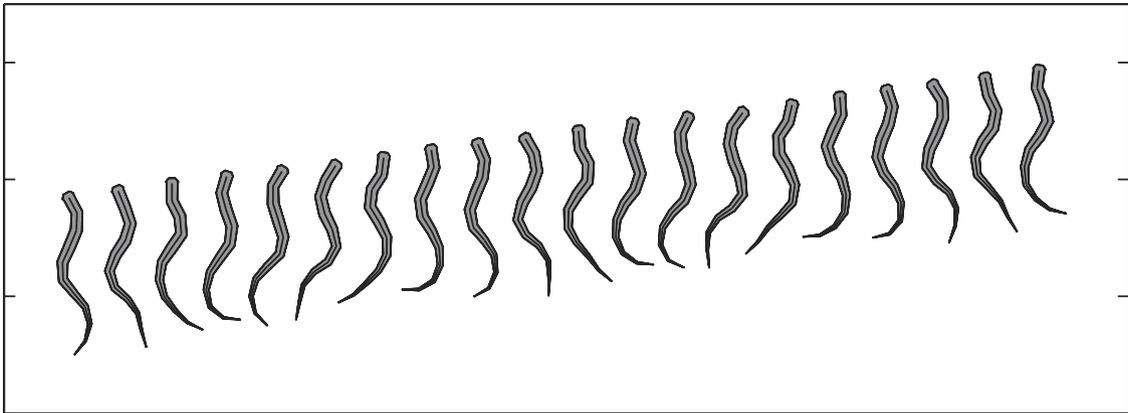
### **Some Models of Vertebrate Locomotor Systems**

This section presents some results of modeling of vertebrate locomotion, with a special focus on neuromechanical simulations.

#### *Swimming*

Vertebrate swimming has been most studied in the lamprey (see SPINAL CORD OF LAMPREY: GENERATION OF LOCOMOTOR PATTERNS), an eel-like fish using *anguilliform* swimming, in which a traveling wave is propagated along the whole elongated body. Ekeberg developed a neuromechanical simulation composed of a connectionist neural network representing the lamprey's 100-segment spinal locomotor circuit and a simplified model of the body in interaction with water (Ekeberg, 1993). The neural network produces oscillating activity when tonic input is provided to the neurons, with the frequency of oscillation being proportional to the level of excitation. When extra excitation is provided to the most rostral (i.e., closest to the head) segments, a traveling wave is propagated from head to tail. The extra excitation determines the wavelength, independent of the frequency. With these settings, the model therefore replicates the fact that a swimming lamprey can cover a large range of frequencies while maintaining the wavelength constant at approximately one body length.

The mechanical simulation is a two-dimensional articulated rigid body actuated by muscles simulated as spring and dampers. Although the hydrodynamics of the model is simplified, it produces swimming gaits very similar to those of lamprey swimming (Figure 1). The mechanical simulation allowed Ekeberg to investigate the effect of modulating the locomotor pattern on the speed and direction of locomotion, as well as the effect of sensory feedback from spinal stretch-sensitive cells. The model demonstrated that the speed of swimming can be varied by changing the frequency of oscillation through the level of tonic input, whereas the direction



**Figure 1.** Neuromechanical simulation of lamprey swimming. (Reimplementation by the author of the model presented in Ekeberg, Ö, 1993, A combined neuronal and mechanical model of fish swimming, *Biol. Cybern.*, 69:363–374.)

of swimming can be varied by applying asymmetric tonic drive between left and right sides of the locomotor circuit.

Vertebrate swimming has inspired several underwater vehicles, such as eel-like robots that use anguilliform swimming (REEL, at the University of Pennsylvania) and a lamprey-based undulatory robot (at the Marine Science Center of Northeastern University), and caranguiform swimming in the RoboTuna (at the Massachusetts Institute of Technology).

### *From Swimming to Walking*

One of the most important changes during vertebrate evolution has been the transition from aquatic to terrestrial habitats. Our own work investigated the transition from swimming to walking in the salamander, an animal that is believed to be one of the modern animals closest to the first vertebrates that made this transition during evolution.

The salamander swims like a lamprey by propagating an undulation from head to tail. On ground, it switches to a stepping gait, usually with the phase relation of a trot. Although the locomotor circuit of the salamander has not yet been decoded, it has been found to share many similarities with the swimming circuit of the lamprey (Cohen, 1988; Delvolvé, Bem, and Cabelguen, 1997).

Our work sought to demonstrate that a lamprey-like swimming circuit could be extended to produce the swimming and stepping gaits of the salamander, with, in particular, a traveling wave along the body during swimming and a standing wave during stepping. The neural configuration of the model is illustrated in Figure 2. It is composed of a lamprey-like body CPG, extended by forelimb and hindlimb CPGs (Ijspeert, 2001). These limb centers have been identified just rostral to the anterior and posterior girdles, respectively. The mechanical simulation was an extension of Ekeberg's model of the lamprey (see Ijspeert, 2001, for a detailed description).

The model is able to (1) generate stable traveling waves and standing waves, depending on simple tonic input, (2) quickly switch between them, and (3) coordinate body and limb movements so as to produce swimming and walking gaits very similar to those recorded in salamanders. Gait transition is obtained as follows: when only the body CPG receives tonic input, the limb CPGs remain silent (limbs are maintained tonically against the body) and the body CPG produces a traveling wave that propels the salamander forward in water, whereas when tonic input is applied to both the body CPG and the limb CPGs, the body CPG is forced by the limb CPGs to produce a standing wave for stepping. The body then makes a standing S-shaped wave with the nodes at the girdles that

is coordinated with the movements of the limbs so as to increase the reach of the limbs during the swing phase (Figure 3, bottom).

Much as in Ekeberg's model of the lamprey, the speed and direction of locomotion can be modulated by respectively varying the level and the asymmetry (between left and right) of tonic input applied to the CPGs. Experiments involving the tracking of a randomly moving target show that locomotion is stable even when the input signals change rapidly and continuously (Ijspeert and Arbib, 2000). In collaboration with Richard Woesler and Gerhard Roth, we are currently extending this work to investigate visuomotor coordination (see VISUOMOTOR COORDINATION IN SALAMANDER).

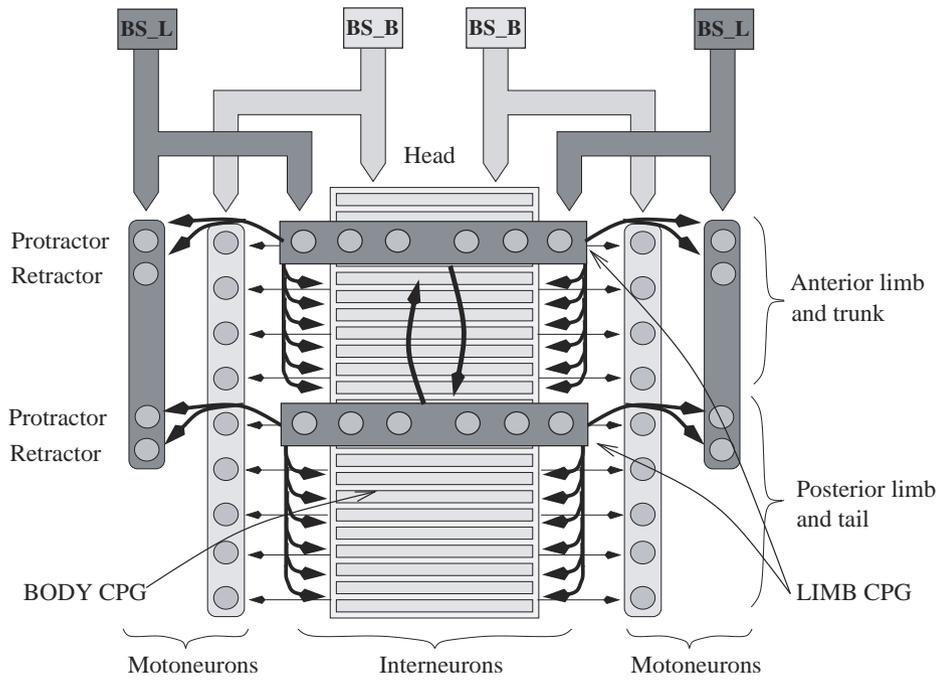
### *Quadruped Locomotion*

Quadruped locomotion in vertebrates has evolved from the sprawling posture found in salamanders and lizards to the upright posture found in mammals. During that evolution, the limbs gradually moved under the body, and movements in the body evolved from lateral to mainly sagittal (i.e., ventrodorsal) undulations.

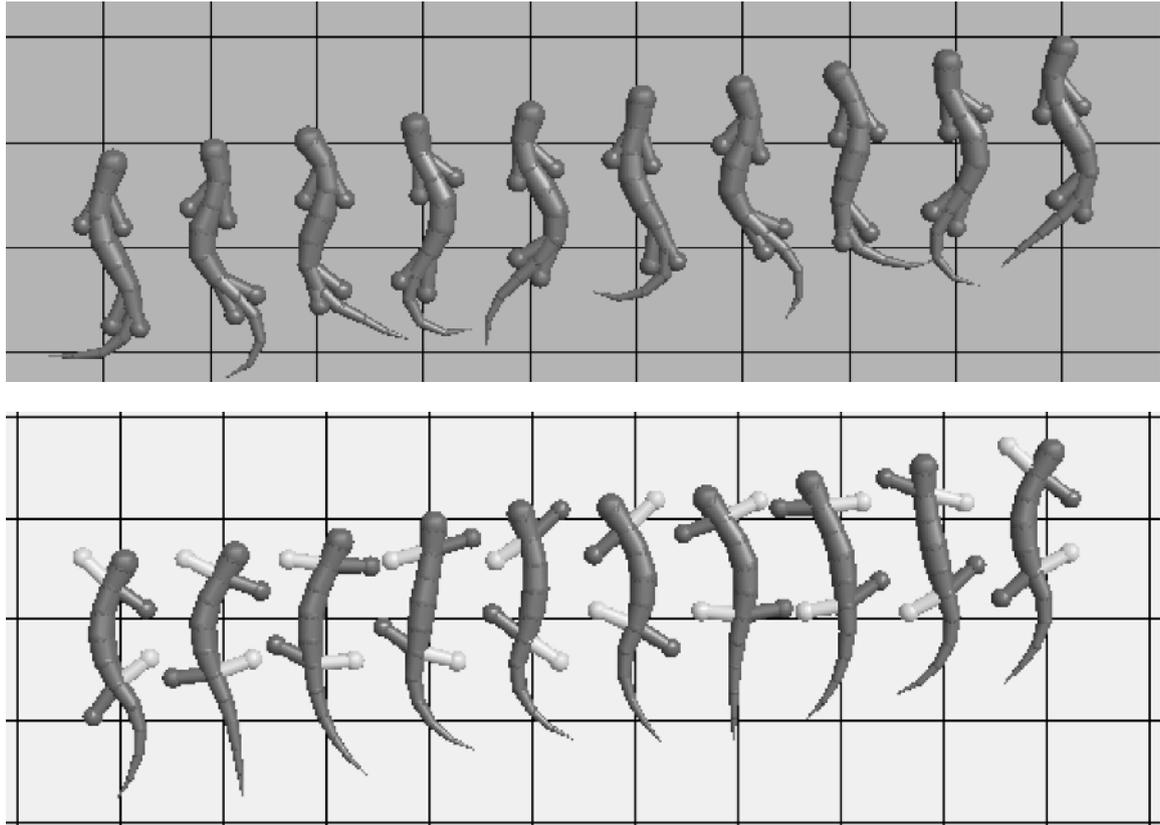
The upright posture means that limbs serve both for locomotion and for maintaining balance. Gaits can either be *statically stable*, in which the center of mass is maintained at all times above the polygon formed by the contact points of the limbs with the ground, or *dynamically stable*, when this rule is not maintained at all times and stability is achieved as a limit cycle that balances moments, gravitational forces, and inertial forces over time. Depending on the phase relation between limbs, a large variety of gaits can be distinguished, such as the walk, the trot, the pace, and the gallop. Mammals can usually switch between these gaits very quickly (see GAIT TRANSITIONS).

The neural mechanisms underlying quadruped locomotion have not yet been decoded, but investigations in the cat have shown that the rhythmic patterns for locomotion are generated by spinal CPGs, while control of posture and accurate placement of feet are under control of the cerebellum and motor cortex. Decerebrate cats, for instance, can produce normal-looking gaits on a treadmill, but need to be supported to do so. The mechanisms underlying intra- and interlimb coordination, however, are still far from understood, especially in relation to gait transition.

Kimura, Akiyama, and Sakurama (1999) present a model of quadruped locomotion that emerges from the coupling of a neural controller with a quadruped robot with 12° of freedom. The neural controller is composed of four coupled oscillators, one for each limb, and several types of reflexes. Kimura and colleagues investigated several schemes of how feedback from load sensors, touch



**Figure 2.** Potential model for the central pattern generator responsible for locomotion in the salamander. (From Ijspeert, A., 2001, A connectionist central pattern generator for the aquatic and terrestrial gaits of a simulated salamander, *Biol. Cybern.*, 85:331–348. Reprinted with permission.)



**Figure 3.** Neuromechanical simulation of salamander locomotion. *Top*, swimming; *bottom*, stepping. (From Ijspeert, A., 2001, A connectionist central pattern generator for the aquatic and terrestrial gaits of a simulated salamander, *Biol. Cybern.*, 85:331–348. Reprinted with permission.)

sensors, and a vestibular system (a rate gyro) could be coupled to the CPG. The schemes in which the feedback was fed into and gated by the CPGs (as opposed to being independent of the CPGs) were found to generate significantly more stable gaits on irregular terrain. This strongly resembles the modulation of reflex signals by CPGs found in vertebrates and described earlier under Sensory Feedback. Other examples of impressive running and hopping robots can be found in Raibert and Hodgins (1993), for instance.

### Biped Locomotion

Biped locomotion, such as human locomotion, is usually a dynamically stable gait. Humans use mainly two gaits: walking, in which at least one foot is in contact with the ground during the whole locomotor cycle, and running, which has a flight phase without foot contact.

The control of posture is essential in biped locomotion because of the erect posture. In humans, the motor cortex and the cerebellum play a crucial role in locomotion, much more so than in lower vertebrates. As in other vertebrates, there seems to be good evidence that the locomotor pattern can be generated at the spinal level, most likely driven from reticulospinal pathways. Clearly, the postural problem involves an important role of the cerebellum for behaviorally successful locomotion, with the corticospinal pathway playing, in addition, a role in the step-to-step modification (e.g., visually guided) of the locomotor cycle. See Horak and MacPherson in Rowell and Shepherd (1996, chap. 7) for a review.

In a series of papers, Gentaro Taga developed an interesting two-dimensional model of human locomotion (motion in the sagittal plane) in which stable locomotor patterns emerged from the interaction of a set of neural oscillators coupled to a musculoskeletal system composed of eight rigid segments (e.g., Taga, 1998). Taga's work was seminal in showing potential mechanisms of global entrainment between two highly nonlinear systems, the neural oscillators and the body. Balance in the model is maintained by a posture controller that regulates the impedance of the joints in parallel to the oscillators. The patterns are sufficiently stable to generate gaits even in unpredictable environments. In the latest version of the model, the locomotion controller is extended with a discrete movement generator for anticipatory adaptation for stepping over obstacles. The discrete movement generator modifies the stepping by generating a sequence of discrete motor signals, changing the gains of specific muscles. The functional role of the discrete movement generator is therefore comparable to the modulatory effect of the motor cortex observed during obstacle avoidance tasks in cats and humans.

### Discussion

Vertebrate locomotion control is organized such that neural networks in the spinal cord generate the basic rhythmic patterns necessary for locomotion, and higher control centers interact with the spinal circuits for posture control and accurate limb movements. This means that, in general, the control signals sent to the spinal cord do not need to specify all the details of when and how much the muscles must contract, but rather specify higher-level commands such as stop and go signals, speed, and heading of motion. This type of distributed control has provided an interesting inspiration for robotics, as it implies (1) a reduction in the amount of information that has to be communicated back and forth, and (2) a reduction in the time delays between sensing, command generation, and acting.

Locomotor circuits are the result of evolution, which means that there exists a chain of changes from the ancestral vertebrate to all vertebrates. An important question that remains open is to determine which modifications have occurred in the locomotor circuits

from the generation of traveling waves for swimming (the most ancestral vertebrates were close to the lamprey) to the generation of standing waves for walking, to the generation of multiple gaits for quadruped locomotion, and finally to the generation of biped locomotion (not to forget all the other forms of vertebrate locomotion mentioned in the Introduction). This is an important issue, since the mechanisms of locomotion in modern vertebrates are strongly shaped by this evolutionary heritage and might not be fully understood without taking evolution into account. In particular, we will need to determine to what extent the three components of locomotion control—CPGs, sensory feedback, and supraspinal descending commands—have changed. It is clear that important morphological changes have significantly modified the patterns of sensory feedback. However, for lower vertebrates, it is likely that most of the changes are due to modifications of the CPGs, since CPGs are able to generate relatively normal gaits without sensory feedback, and comparative studies show that descending pathways are in general strikingly conserved (Donkelaar, 2001). In higher vertebrates such as mammals, changes of the CPGs have been accompanied by important modifications of the descending pathways under the requirements of complex posture control and accurate limb movements, although the extent of the respective changes remains unknown. In addition to neurophysiological experiments and comparative studies, computer models, in particular models that combine neural models with biomechanical models, have an important role to play in answering these fascinating questions.

**Road Maps:** Motor Pattern Generators; Neuroethology and Evolution

**Related Reading:** Evolution of Artificial Neural Networks; Spinal Cord of Lamprey: Generation of Locomotor Patterns; Visuomotor Coordination in Salamander

### References

- Cheng, J., Stein, R., Jovanovic, K., Yoshida, K., Bennett, D., and Han, Y., 1998, Identification, localization, and modulation of neural networks for walking in the mudpuppy (*Necturus maculatus*) spinal cord, *J. Neurosci.*, 18:4295–4304.
- Cohen, A., 1988, Evolution of the vertebrate central pattern generator for locomotion, in *Neural Control of Rhythmic Movements in Vertebrates* (A. H. Cohen, S. Rossignol, and S. Grillner, Eds.), New York: Wiley.
- Delvolvé, I., Bem, T., and Cabelguen, J.-M., 1997, Epaxial and limb muscle activity during swimming and terrestrial stepping in the adult newt, *Pleurodeles waltl*, *J. Neurophysiol.*, 78:638–650.
- Donkelaar, H. ten, 2001, Evolution of vertebrate motor systems, in *Brain Evolution and Cognition* (G. Roth and M. Wullmann, Eds.), New York: Wiley Spectrum, pp. 77–112.
- Ekeberg, Ö., 1993, A combined neuronal and mechanical model of fish swimming, *Biol. Cybern.*, 69:363–374.
- Grillner, S., 1981, Control of locomotion in bipeds, tetrapods and fish, in *Handbook of Physiology: The Nervous System, 2, Motor Control* (V. Brooks, Ed.), Bethesda, MD: American Physiology Society, pp. 1179–1236. ♦
- Grillner, S., Degliana, T., Ekeberg, Ö., El Marina, A., Lansner, A., Orlovsky, G., and Wallén, P., 1995, Neural networks that co-ordinate locomotion and body orientation in lamprey, *Trends Neurosci.*, 18:270–279.
- Ijspeert, A., 2001, A connectionist central pattern generator for the aquatic and terrestrial gaits of a simulated salamander, *Biol. Cybern.*, 85:331–348.
- Ijspeert, A., and Arbib, M., 2000, Visual tracking in simulated salamander locomotion, in *Proceedings of the Sixth International Conference of the Society for Adaptive Behavior (SAB2000)* (J. Meyer, A. Berthoz, D. Floreano, H. Roitblat, and S. Wilson, Eds.), Cambridge, MA: MIT Press, pp. 88–97.
- Kimura, H., Akiyama, S., and Sakurama, K., 1999, Realization of dynamic walking and running of the quadruped using neural oscillators, *Auton. Robots*, 7:247–258.
- Pearson, K., and Gordon, J., 2000, Spinal reflexes, in *Principles of Neural*

Science, 4th ed. (E. Kandel, J. Schwartz, and T. Jessel, Eds.), New York: McGraw-Hill. ♦

Raibert, M., and Hodgins, J., 1993, Legged robots, in *Biological Neural Networks in Invertebrate Neuroethology and Robotics* (R. Beer, R. Ritzmann, and T. McKenna, Eds.), San Diego, CA: Academic Press, pp. 319–354.

Rowell, L., and Shepherd, J., Eds., 1996, *Handbook of Physiology*, sect.

12: *Exercise: Regulation and Integration of Multiple Systems, Neural Control of Movement*. New York: Oxford University Press. ♦

Shik, M., Severin, F., and Orlovsky, G., 1966, Control of walking by means of electrical stimulation of the mid-brain, *Biophysics*, 11:756–765.

Taga, G., 1998, A model of the neuro-musculo-skeletal system for anticipatory adjustment of human locomotion during obstacle avoidance, *Biol. Cybern.*, 78:9–17.

## Locust Flight: Components and Mechanisms in the Motor

R. Meldrum Robertson

### Introduction

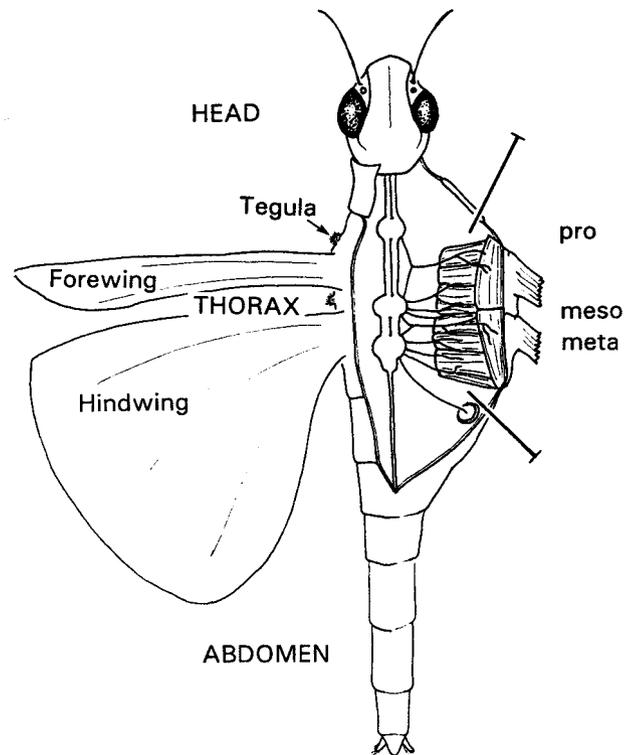
The locust flight motor provides an excellent model system for investigations of constraints and mechanisms of MOTOR PATTERN GENERATION at the neuronal level. In locusts the neural elements involved in generating the patterns of flight motor activity are individually identifiable (see Comer and Robertson, 2001, for a review of identified neurons controlling insect behaviors). It is thus possible to describe the operation of networks of identified neurons, connected by identified synapses, and to determine how these networks contribute to the computational task of producing rhythmical motor patterns capable of keeping the locust aloft in an unpredictable environment.

The flight systems of other insects have attracted research interest in their neural control mechanisms. Indeed, the visuomotor control of dipteran flight has received notable attention (VISUAL COURSE CONTROL IN FLIES). Nevertheless, it is only for the locust that enough is known of the circuitry underlying the form and timing of the wingbeat that it can be useful as a model of central nervous system function.

### The Motor Output

The locust flight system (Figure 1) creates a spatiotemporal pattern of electrical activity in about 80 flight motoneurons that activate muscles controlling the four wings (a pair of forewings and a pair of hindwings) and cause beating of the wings at around 22 cycles/s. Telemetric techniques now exist to monitor the activity of identified flight muscles during free flight under conditions that require the generation of different combinations of rotational and translational flight forces (Kutsch, 1999). Particular features of the motor pattern can be correlated with specific flight parameters that are modified to effect adaptive flight maneuvers (i.e., natural behaviors). It was originally demonstrated that a version of the motor pattern, albeit slower (around 12 cycles/s), could be generated by a central nervous system deafferented from phasic timing information emanating from wing proprioceptors and other sense organs. This discovery was influential in establishing the central pattern generator concept (MOTOR PATTERN GENERATION). An important question is to what extent the central pattern generator is responsible for controlling the *behavior*, particularly given that afferent input can change the set of active flight interneurons in the locust. There is no doubt that a rhythmic central pattern can be generated, but it is conceivable that this pattern is the output of a network artificially created by the act of deafferentation, i.e., a malformed, degenerate pattern that has no real bearing on the generation of the functional flight motor pattern. There is little evidence for this extreme position, and the extent to which sensory feedback supersedes the role of the central pattern generator in normal intact

flight remains unclear. Nevertheless, it is quite clear that proprioceptive feedback is necessary for appropriate timing of the wing-beat phase transitions. The tegulae are external sense organs stimulated by depression of each wing and they can initiate the subsequent elevator phase by excitation of elevator motoneurons and interneurons. The stretch receptors are internal, at the wing base, and activated by wing elevation. They promote the occurrence of the subsequent depression by opposing the hyperpolarization between the bursts of action potentials in depressor moto-



**Figure 1.** The locust flight system. Diagrammatic representation of a locust showing on the left side the form of the forewing and hindwing and the position of the fore and hind tegulae (only the forewing tegula is labeled). On the right side the thorax has been pinned open to reveal the bank of flight muscles that power the wings and the three thoracic ganglia (pro-, meso-, and metathoracic) that contain the motoneurons and interneurons involved in generating flight motor patterns.