

# Locomotion, Vertebrate

Auke Jan Ijspeert

Department of Computer Science, 3641 Watt Way, Hedco Neuroscience Building  
University of Southern California, Los Angeles, CA 90089, USA. Email: ijspeert@usc.edu

## 1 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. Vertebrate locomotion can take various forms including swimming, crawling, walking, flight, as well as some more idiosyncratic gaits 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 antagonist muscles at the joints of articulated systems composed of rigid bones. All types of vertebrate locomotions rely on some kind of rhythmic activity to move forward: undulations or peristaltic contractions of the body, and/or oscillations of fins, legs or wings. By rhythmically applying forces to the environment (ground, water, or air), reaction forces are generated which move the body forward.

This type of locomotion is in contrast to most man-made machines which usually rely 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 indeed to be well coordinated to generate efficient locomotion. However, as can be observed from the swimming of a dolphin or from the running of a goat in irregular terrain, animal locomotion presents many interesting features, such as energy efficiency (for swimming) and agility. The next sections will review the neural and mechanical mechanisms underlying vertebrates' fascinating locomotor abilities.

## 2 Neural control of locomotion

Despite the diversity in types of locomotion, the general organization of vertebrate locomotor circuit appears to be well 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).

### 2.1 Central pattern generators

Central pattern generators are circuits which can generate rhythmic activity without rhythmic input (see HALF-CENTER OSCILLATORS and MOTOR PATTERN GENERATION). The rhythms can often be initiated by simple tonic (i.e. non-oscillating) electric or pharmacological stimulation. In vertebrates, the CPGs are located in the spinal cord, and distributed in different oscillatory centers. In lamprey, for instance, the swimming CPG is a chain of approximately 100 segmental oscillators distributed from head to tail (see CHAIN OF COUPLED OSCILLATORS and SPINAL CORD OF THE LAMPREY). In tetrapods, the locomotor CPG appears to be composed of different centers, one for each limb, which are themselves decomposed into different oscillatory sub-centers for each joint (Grillner, 1981). Recent evidence from intracellular recordings in the mudpuppy suggests that joint sub-centers 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.

### 2.2 Sensory feedback

While not necessary for rhythm generation, sensory feedback is essential for shaping and coordinating the neural activity with the 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 decerebrated 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 sprawling postures like certain amphibians and reptiles), because the limbs of those vertebrates play an important role in posture control (i.e. supporting the body) in addition to locomotion.

A whole set of reflexes exist 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 to maintain a posture. The reflex pathways often share many of the interneurons which participate to 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 & Gordon, 2000) and *SENSORIMOTOR INTERACTIONS* for reviews.

### 2.3 Descending supraspinal control

Locomotion is initiated and modulated by descending pathways from diencephalic and mesencephalic locomotor centers. For reviews, see (Donkelaar, 2001) and Rossignol, Chapter 5, pp 173-216, in (Rowell & Shepherd, 1996). Some of these pathways are direct, e.g. 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 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 feet placement in uneven terrain.

Interestingly, the input signals to the brainstem do not need to be complex to generate locomotion. Since the 60s, we know that simple electrical stimulation of the brainstem initiates the walking gait in a decerebrated cat, and progressively increasing the amplitude of the stimulation leads to an increase of the oscillation frequency accompanied by a switch from walking to trotting and eventually to galloping (Shik, Severin, & 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*).

## 3 The biomechanics of locomotion

Locomotion is the result of an intricate coupling between the neural dynamics and the body dynamics, and many fundamental aspects of locomotion control including gait transition, control of speed and direction, cannot be fully understood by investigating the locomotor circuit in isolation from the body it controls. A body has indeed its own dynamics and intrinsic frequencies with complex non-linear properties, to which the neural signals must be adapted for efficient locomotion control. As observed by roboticist Marc Raibert, the central nervous system 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 coactivation 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 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) which 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 (see work by Tad McGeer and others).

## 4 Numerical simulations of locomotor circuits

While the general organization of the vertebrate locomotor circuit is known, much work remains to be done on elucidating how its different components are implemented and how they interplay to generate the complex patterns underlying locomotion. This is a complex task because (a) these patterns are due to the interaction of the central nervous system and the body in movement, (b) numerous neurons in the brainstem and the spinal cord are involved, and (c) in most vertebrates, the same circuits ap-

pear 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 central nervous system. An interesting approach to the understanding of 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 into 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).

## 5 Some models of vertebrate locomotor systems

We will next review some results on the modeling of vertebrate locomotion, with a special focus on neuromechanical simulations. The review is far from exhaustive.

### 5.1 Swimming

Vertebrate swimming has been most studied in the lamprey (see SPINAL CORD OF THE LAMPREY), 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, independently of the frequency. With these settings, the model therefore replicates the fact that a swimming lamprey can cover a large range of frequen-

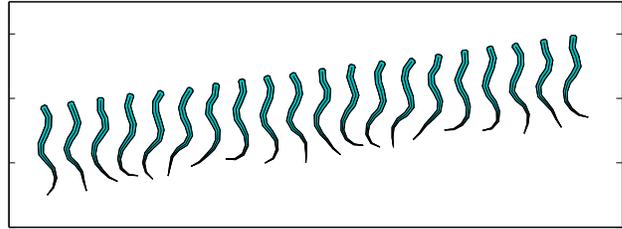


Figure 1: Neuromechanical simulation of lamprey swimming. Reproduction by the author of Ekeberg's model presented in (Ekeberg, 1993).

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

Vertebrate swimming has inspired several underwater vehicles, for instance, anguilliform swimming in eel-like and lamprey-like robots at, respectively, the University of Pennsylvania and the Marine Science Center of the Northeastern University, and caranguiform swimming in the RoboTuna at the Massachusetts Institute of Technology.

### 5.2 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 which is believed to be one of the modern animal closest to the first vertebrates having 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. While the locomotor circuit of the salamander has not been decoded yet, it has been found to share many similarities with the swimming circuit of the lamprey (Cohen, 1988; Delvolvé, Bem, & Cabelguen, 1997).

This work aimed at demonstrating that a lamprey-like

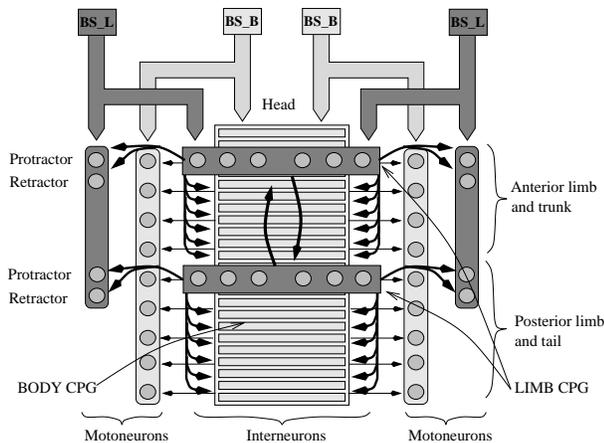


Figure 2: Potential model for the salamander locomotion central pattern generator (Ijspeert, 2001).

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 fore- 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 (1) to generate stable traveling waves and standing waves depending on simple tonic input, (2) to quickly switch between them, and (3) to coordinate body and limbs movements such 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 which 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 which is coordinated with the movements of the limbs such as to increase the reach of the limbs during the swing phase (Figure 3 bottom).

Similarly to 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 & Arbib, 2000). This work is currently being extended to in-

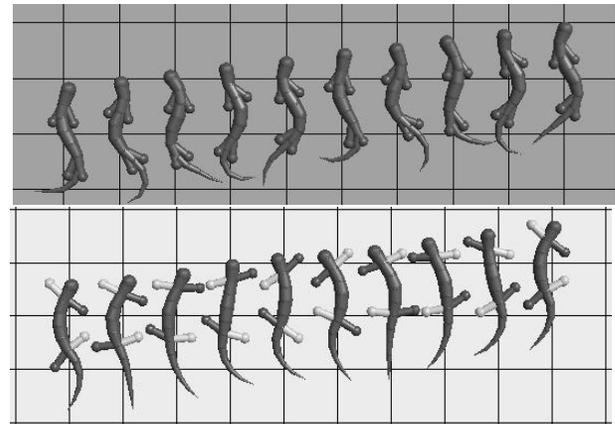


Figure 3: Neuromechanical simulation of salamander locomotion. *Top*: swimming. *Bottom*: stepping.

vestigate visuomotor coordination in collaboration with Richard Woesler and Gerhard Roth (see VISUOMOTOR COORDINATION IN SALAMANDERS).

### 5.3 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 have gradually moved under the body, and movements in the body have evolved from lateral to mainly sagittal (i.e ventro-dorsal) undulations.

The upright posture means that limbs serve both for locomotion and for keeping balance. Gaits can either be *statically stable*, when 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 which balances the moments, the gravitational forces, and the inertial forces over time. A large variety of gaits can be distinguished depending on the phase relation between limbs, such as the walk, the trot, the pace, and the gallop. Mammals can usually switch very quickly between these gaits (see GAIT TRANSITIONS).

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

(Kimura, Akiyama, & Sakurama, 1999) presents a

model of quadruped locomotion which emerges from the coupling of a neural controller with a quadruped robot with 12 degrees of freedom. The neural controller is composed of four coupled oscillators, one for each limb, as well as several types of reflexes. Kimura and colleagues investigated several schemes of how feedback from load sensors, touch 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 independent of the CPGs) were found to generate significantly stabler gaits in irregular terrain. This strongly resembles the modulation of reflex signals by CPGs found in vertebrates and described in the Sensory Feedback section. Other examples of impressive running and hopping robots can be found in (Raibert & Hodgins, 1993), for instance.

## 5.4 Biped locomotion

Biped locomotion as, for instance, 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 for the (e.g. visually-guided) step to step modification of the locomotor cycle. See Horak and MacPherson, Chapter 7, pp 255-292, in (Rowell & Shepherd, 1996) 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 emerge from the interaction of a set of neural oscillators coupled to a musculo-skeletal system composed of 8 rigid segments (see for instance (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 regulating 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 dis-

crete motor signals changing the gains of specific muscles. The functional role of the discrete movement generator are therefore comparable to the modulatory effect of the motor cortex observed during obstacle avoidance tasks in cats and humans.

## 6 Discussion

Vertebrate locomotion control is organized such that neural networks in the spinal cord generate the basic rhythmic patterns necessary for locomotion, and that higher control centers interact with the spinal circuits for posture control and accurate limb movements. This means that the control signals sent to the spinal cord do, in general, not need to specify all the details of when and how much the multiple 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 of the amount of information which needs to be communicated back and forth, and (2) a reduction of the time delays between sensing, command generation, and acting.

Locomotor circuits are the result of evolution, which means that there exist a chain of changes from the ancestral vertebrate to all vertebrates. An important question which remains open is to determine which modifications have occurred in the locomotor circuits between the generation of traveling waves for swimming (the most ancestral vertebrates were close to the lamprey), followed by the generation of standing waves for walking, followed by the generation of multiple gaits for quadruped locomotion, and finally biped locomotion (not to forget all the other forms of vertebrate locomotions mentioned in the introduction). This is an important issue since the locomotor mechanisms 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 which extent the three components of locomotion control (CPGs, sensory feedback, and supraspinal descending commands) have changed. Clearly, the important morphological changes have significantly modified the patterns of sensory feedback. However, for lower vertebrates, it is likely that the largest part 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 conservative (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 remain unknown. In addition to neuro-

physiological experiments and comparative studies, computer models, in particular models which combine neural models with biomechanical models, have an important role to play in answering these fascinating questions.

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