A neuromechanical investigation of salamander locomotion

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Abstract

Understanding biological control of locomotion requires not only good models of the neural mechanisms of pattern generation, but also of the interaction of these neural circuits with the body. In this article, we investigate the neural mechanisms underlying the locomotion of the salamander, an animal capable of both aquatic and terrestrial locomotion. A 3D biomechanical simulation of the salamander's body is developed whose muscle contraction is determined by a locomotion controller simulated as a leaky-integrator neural network. While the connectivity of the neural circuitry underlying locomotion in the salamander has not been decoded for the moment, the neural circuit designed in this article has a a general organization which corresponds to that hypothesized by neurobiologists for the real animal. In particular, the locomotion controller is based on a body *central pattern generator* (CPG) corresponding to a lamprey-like swimming controller, and is extended with a limb CPG for controlling the salamander's limbs. A genetic algorithm is used to instantiate parameters of the neural circuit (e.g. synaptic weights and time parameters) in three stages, with first the evolution of segmental oscillators, second the evolution of intersegmental coupling for making a body CPG, and third, the evolution of the limb CPG and its connections to the body CPG. A controller is developed which can produce a neural activity and locomotion gaits very similar to those observed in the real salamander. By varying the tonic excitation applied to the network, the speed, direction and type of gait can be varied. Movies of the simulations can be found at http://rana.usc.edu:8376/~ijspeert/ .

1 Introduction

Locomotion is a fundamental skill for animals, which need it for a variety of actions such as finding food, encountering a mate for reproduction, escaping predators, and moving to a more friendly environment. Similarly, efficient locomotion is essential in mobile robotics if we want robots to carry out useful tasks. As wheeled robots are limited in the type of environments in which they can move, there is an increasing interest to develop robots which use more animal-like types of gaits. This usually means that more complex means of locomotion than powered wheels are needed, involving a greater number of actuators generally used in a rhythmic way. Very quickly, the engineer is then faced with the same control problems faced by biological systems, namely the control of multiple actuators which only produce the desired behavior when appropriately coordinated. The problem is to find the right control mechanism which can translate commands concerning the speed and direction of motion into the set of rhythmic signals sent to the multiple actuators. Biologically inspired robotics may therefore not only gain from inspiration from biology for the structure of the robot (e.g. legged robots) but also for its control system (e.g. neural based central pattern generators). Examples of such an approach include [20, 2, 19].

In this work, we investigate control of locomotion in vertebrates using biomechanical and neuronal simulations. We are, in particular, interested in the locomotion of the salamander, an animal capable of both aquatic and terrestrial locomotion. The salamander makes axial movements during locomotion. It swims using an anguiliform swimming gait, in which the whole body participates to movement creation, and in which a wave of neural activity is propagated from head to tail, with an approximately constant wavelength along the spinal cord [9, 3]. On ground, the salamander switches to a trotting gait, in which the body forms an S-shaped standing wave with the nodes at the girdles, which is coordinated with the movements of the limbs such as to increase their reach during the swing phase. EMG recordings have shown that two different motor programs underly these typical gaits, with a traveling of neural activity along the body for swimming and a mainly standing wave during trotting [9, 3]. The locomotor circuitry responsible for these motor programs has, however, not been decoded for the moment.

This article presents a potential control circuit capable of producing these two types of gaits in a biomechanical simulation of the salamander. The control circuit is a central pattern generator (CPG) whose circuitry is based on a lamprey-like organization, with a lamprey-like CPG for the body segments extended by a limb CPG for controlling the limbs as hypothesized in [1, 3]. Similarly to other works which have investigated biological locomotion control using neuromechanical simulations [21, 5, 6], a simple 3D mechanical simulation of the salamander's body in interaction with water or ground is developed whose muscular activity is determined by the locomotor circuit simulated as a leaky-integrator neural network. The work presented here follows preliminary experiments on the control of a 2D salamander simulation [17, 13, 15], and uses the same methodology as that used to develop potential swimming controllers for the lamprey [18]. This article presents, in particular, how the locomotor circuit for the 2D simulation can be extended to control a 3D salamander with more realistic limbs.

2 Mechanical simulation

The 3D mechanical simulation is composed of ten rigid links representing the trunk and the tail, and eight links representing the limbs (Figure 2). The tail and trunk links are connected by one degree-of-freedom (DOF) joints, while the limb joints have 2 DOF at the shoulder/pelvis and 1 DOF at the knee. The torques on each joint are determined by pairs of muscles simulated as springs and dampers, whose spring constant are modified by the signals sent from the motoneurons.

The simulation is implemented in a dynamical simulation package from Mathengine,[1] which handles the internal forces necessary for keeping the links connected, as well as the contacts of the body with the ground. During terrestrial locomotion, friction forces are applied to all links in contact with the ground (e.g. the trunk and tail links slide on the ground while the salamander is trotting), and in water, it is assumed that each link (limbs included) is subjected to inertial forces due to the water (with forces proportional to the square of the speed of the links relative to the water). A more detailed description of the biomechanical simulation can be found in [14]. The simulation is only a first approximation of a salamander, and does not attempt to reproduce in detail the biomechanical properties of any specific salamander species.

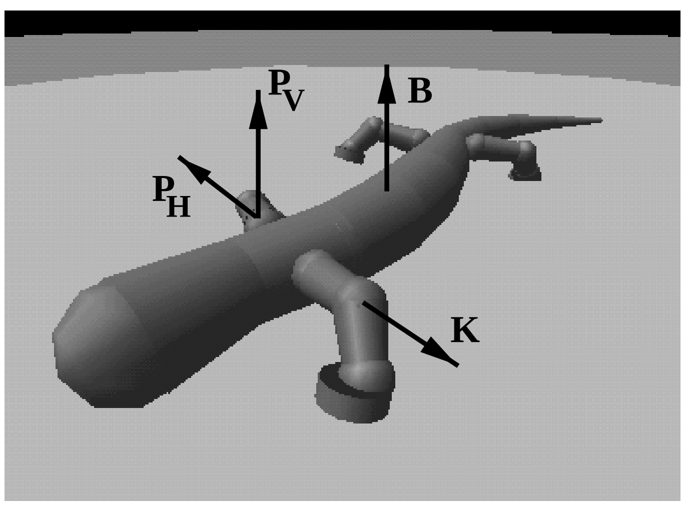

Figure 1: Mechanical simulation. The body is composed of 18 rigid links. Body (trunk and tail) links are connected by one-DOF hinge-joints, with vector B as axis of rotation. Limbs are attached to the body by two-DOF joints with one vertical axis of rotation P_V and one horizontal P_H. Finally, knee joints have one DOF and they rotate around axis K.

[1] MathEngine PLC, Oxford, UK, www.mathengine.com

3 Neuronal simulation

The locomotion controller is simulated as a leaky integrator neural network. It is composed of a body CPG and a limb CPG (Figure 2). The body CPG is lamprey-like with an interconnection of 40 segmental networks for the generation of traveling waves of neural activity. The limb CPG is made of two interconnected oscillators projecting to the limb motoneurons and to the body CPG segments, creating a unilateral coupling between the two CPGs. While the general organization of the controller is set by hand, the time parameters, biases and synaptic weights of the neurons are instantiated using a genetic algorithm. This is done in three stages, with first the evolution of segmental oscillators, second, the evolution of intersegmental coupling for the body CPG, and finally the evolution of the limb CPG connectivity.

In this article, only a summary of the different design stages will be given. For a detailed description of the design of neural controllers for a 2D simulation of the salamander, see [17, 13, 15]. This paper mainly investigates how the 2D neural controller developed in [15] can be extended to control the locomotion of a 3D body.

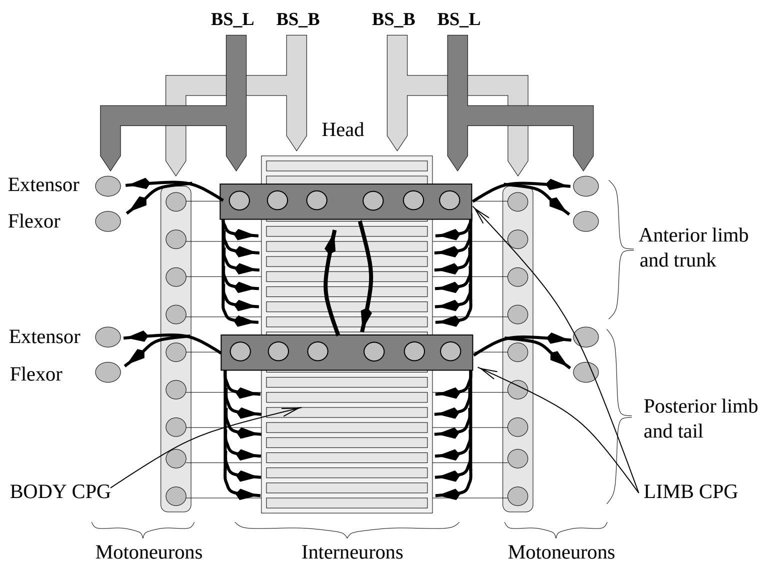

Figure 2: Proposed organization of the salamander's locomotor circuitry. The circuitry is composed of a body CPG and a limb CPG which can be activated by four pathways from the brainstem (BS). Each limb is activated by 3 pairs of flexor-extensor neurons (only one pair per limb shown here).

3.1 Neuron model

Leaky-integrator neurons, i.e. neurons of intermediate complexity between abstract binary neurons used traditionally in artificial neural networks and detailed compartmental models used in computational neuroscience, are used for implementing the neural controllers. Instead of simulating each activity spike of a real neuron, a neuron unit computes its average firing frequency [12]. According to this model, the mean membrane potential m_i of a neuron N_i is governed by the equation:

$$\tau_i \cdot dm_i/dt = -m_i + \sum w_{i,j} x_j$$

where $x_j = (1 + e^{(m_j + b_j)})^{-1}$ represents the neuron's short-term average firing frequency, b_j is the neuron's bias, τ_i is a time constant associated with the passive properties of the neuron's membrane, and $w_{i,j}$ is the synaptic weight of a connection from neuron N_j to neuron N_i.

4 Staged evolution of the central pattern generator

4.1 Segmental oscillators

In the first design stage, segmental oscillators are developed by using the genetic algorithm (GA) to instantiate neural (b_i,τ_i) and network parameters (the synaptic weights $w_{i,j}$) in a network composed of 8 neurons. For this stage, the fitness function of the GA is defined to reward networks which can produce stable oscillations and whose frequency of oscillation can be modulated by the level of tonic (i.e. non-oscillating) input applied to the network.

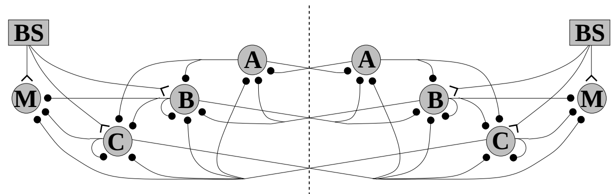

Figure 3: Connectivity of the segmental oscillator. The oscillator is composed of three types of inhibitory interneurons (A, B, and C) and of excitatory motoneurons (M). The neurons receive tonic input coming from the brainstem (BS).

Figure 3 illustrates one of these evolved networks. This network produces stable oscillations over a large range of frequencies (from 0.75 to 8.75Hz). It starts to oscillate when it receives sufficient tonic input (which can be viewed as the descending signals coming from the brainstem), with the frequency of oscillation increasing with the level of input. Note that the oscillations are due to the connectivity and the time-delayed reaction of the neurons to their synaptic input rather than to intrinsic oscillatory properties of the neurons (i.e. the circuit has no pacemaker cells).[2]

4.2 Intersegmental coupling

The aim of this stage is to develop a complete body CPG which can propagate a traveling rostro-caudal wave for swimming. The body CPG is made of 40 segments like the number of segments found in salamanders (instead of the 100 segments of lampreys). One of the best oscillators of the previous stage is chosen as template segmental oscillator. The coupling between segments is obtained using *synaptic spreading* [22], in which a connection between two neurons in a segmental oscillator is projected to corresponding neurons in neighboring segments. The extent of the projections in both rostral and caudal directions are instantiated using the GA, with a fitness function rewarding networks which produce regular oscillations in all segments, and which propagate a traveling wave from head to tail with a constant phase lag along the spinal cord.

Successful swimming controllers are thus created which, when connected to the mechanical simulation, produce the typical anguiliform swimming observed in salamanders and lampreys (Figure 4). Note that during swimming, tonic signals are also sent to the horizontal flexors of the limbs in order to keep the limbs against the body. The phase lag between neighboring segments is almost constant, leading to a neural wave of constant wavelength along the spinal cord (Figure 5, left). The speed of swimming can be modulated by varying the level of tonic input applied the whole body CPG, with the frequency of oscillation and therefore the speed of swimming increasing with the level of input. Interestingly, while the frequency of oscillation depends significantly on the level of tonic input, the wavelength of the neural wave remains more or less constant for any level of input, similarly to what is observed in the lamprey [10]. Finally, this body CPG has also the interesting property of being able to induce turning when asymmetrical input is applied between left and right sides of the spinal cord. If the asymmetry is permanent, the salamander swims in a circle, and if it is temporary it can be used to change the heading of swimming.

[2] In the lamprey, several mechanisms of rhythmogenesis have been found, with cellular properties playing an important role for low frequencies of oscillation, while higher frequencies are mainly generated by network properties [11, 10].

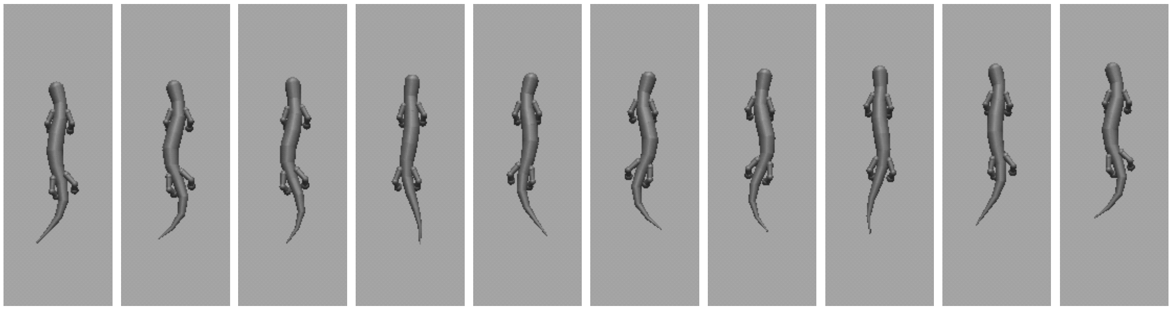

Figure 4: Swimming.

4.3 Complete CPG

The aim of this last stage is to develop a complete CPG able of producing both the swimming and the trotting gaits of the salamander. A limb CPG is therefore developed on top of the body CPG. The limb CPG is composed of two oscillators which are copies of the segmental oscillator. The GA is used to instantiate the synaptic weights of all connections represented as thick arrows on Figure 2, that is, the coupling connections between the limb oscillators, the connections from the limb oscillators to the limb motoneurons, and the connections from the limb oscillators to the segmental oscillators of the body CPG. The GA is also used to instantiate the neural parameters for the flexor and extensor limb motoneurons. The aim is to be able to switch between the swimming and the trotting gaits, by either applying tonic input only to the body CPG for swimming (by the left and right *BS_B* pathways in Figure 2), or applying tonic input to *both* the body and the limb CPGs for trotting (i.e. by both the *BS_B* and *BS_L* pathways). For this stage, the fitness function is defined to reward complete CPGs which have their limb oscillators oscillating out-of-phase and which can produce a trotting gait whose speed can be modulated by the level of tonic input applied to both the body and the limb CPGs.

Figure 6 illustrates the trotting gait of one of the evolved complete CPGs. Interestingly, the evolved coupling from the limb CPG to the body CPG induces a body-limb coordination very similar to that observed in the real salamander. The body makes an S-shaped movement which is coordinated with the movements of the limbs to increase their reach when they are in the swing phase. The effect of the coupling can be observed in Figure 5 (right). The unilateral coupling from the limb oscillators forces the chain of segmental oscillators of the body CPG (which would normally propagate a traveling wave) to be in perfect synchrony in the upper part of the body and in the tail, with an abrupt change of phase at the level of the posterior girdle (i.e. where the influence of the anterior limb oscillator stops and that of the posterior limb oscillator begins).

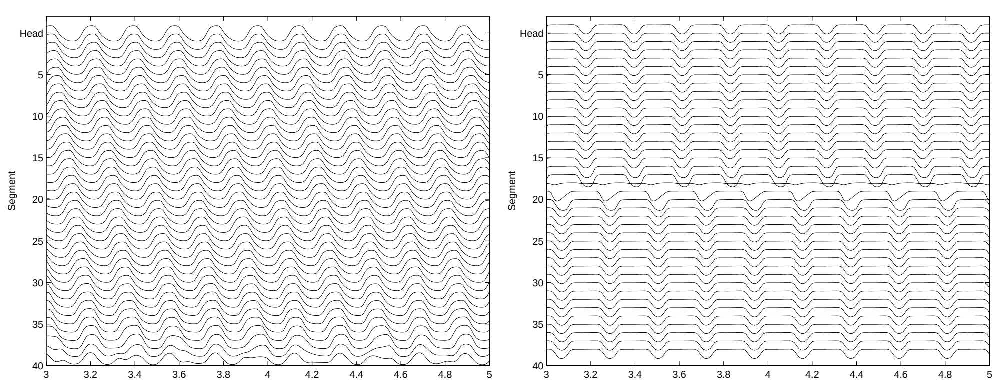

Figure 5: Neural activity in left motoneurons of the body CPG during swimming (*left*) and trotting (*right*).

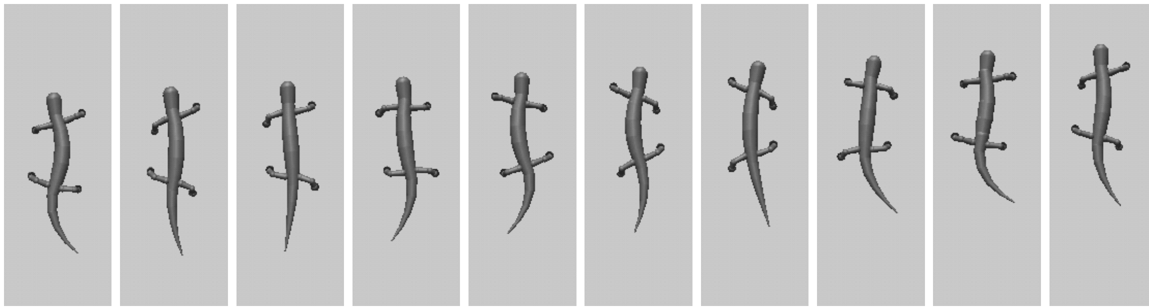

Figure 6: Trotting.

The activity of the limb CPG is shown in Figure 7. Note that this limb CPG was initially developed for a 2D simulation of the salamander. Two motoneurons F_V and E_V, for the vertical flexor and extensor muscles at the shoulder/pelvis, were added by hand to the network. These motoneurons oscillate with a phase of approximately 90 degrees compared to the horizontal motoneurons, so that the limbs perform approximate circles. Also the signals from the F_H and E_H motoneurons are sent to both the horizontal muscles at the shoulder/pelvis and to the knee muscles. Turning during trotting can be induced by applying asymmetrical input to both the limb and the body CPGs. Turning is then mainly due to the extra bending of the body which enables the simulated salamander to make relatively sharp turns.

Interestingly, the simulated trotting salamander did not present rolling problems in this 3D simulation. This is partly due to the fact that, in this first approximation of a salamander, joints connecting body links have been simulated as hinges (i.e. with only 1 DOF) therefore preventing torsion, but also to the intrinsic property of the salamander's trotting gait in which the whole body slides on the ground with a stabilizing S-shape, therefore significantly reducing postural instability compared to other, supported, quadrupedal gaits.

5 Discussion and conclusion

This article presented a potential locomotor circuit for salamander locomotion, based on a lamprey-like body CPG extended by a limb CPG. The limb CPG is based on two oscillators which are copies of the segmental oscillators of the body CPG. This could be seen as being the result of the evolution from a lamprey-like ancestor with two body oscillators having gradually specialized to control fins and then limbs. As the salamander has kept a partially aquatic habitat, it has kept the control circuitry for aquatic locomotion and developed a new motor program for terrestrial locomotion. In our model, we hypothesize that the salamander is able to switch between gaits by varying how tonic (i.e. non-oscillating) input is applied to the locomotor circuit through four different pathways from the brainstem.

The coupling from the limb CPG to the body CPG explains the capacity of the locomotor circuit to produce two different types of waves: when activated, the body CPG tends to produce traveling waves for swimming, unless it is forced by the unilateral coupling from the activated limb CPG to produce a standing wave for trotting. In agreement with the first assumption, it has recently been found out that the completely isolated spinal circuit of the salamander tends to spontaneously propagate traveling waves when submitted to an excitatory bath [4]. Further anatomical and physiological studies may test the validity of the model by investigating whether two distinct limb oscillatory circuits exist, and whether these circuits project through relatively long range projections to each other and to the body segments.

The mechanical simulation, even if it was just a first approximation, allowed an investigation of what phases and shapes the signals sent to the muscles should have for efficient locomotion. As biomechanical systems have complex nonlinear dynamics, including models of the body is important to fully understand the neural mechanisms underlying locomotion. Furthermore, having a representation of the body becomes necessary if one wants to investigate the effect of sensory feedback on the pattern generation. The controller presented in this article works in an open loop, i.e. without proprioceptive feedback. In future work, we intend to integrate such a feedback, as it is important for "shaping" the neural signals and coordinating

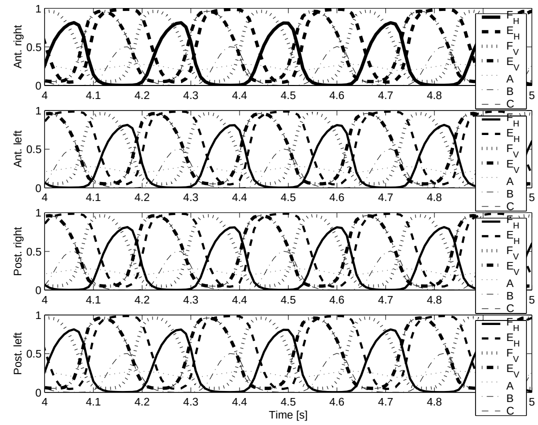

Figure 7: Neural activity in the limb CPG during trotting.

them with the actual mechanical activity. In models of lamprey swimming, for instance, it has been shown that sensory feedback enables the crossing of zones of non-stationary water which would be impossible to cross without [6, 18].

We are currently investigating how the locomotor circuit presented in this article can be integrated into a more comprehensive model of the salamander's central nervous system. Several models of the salamander's visual system have, for instance, been designed [7, 8], but a comprehensive model which interconnects sensory and motor systems remains to be developed. In [16], we present a first experiment in that direction in which a simple control circuit is designed to implement a tracking behavior based on two simple retinas and a "water" sensor. It is found 1) that the pattern generation of the locomotor circuit is robust against constantly varying inputs, 2) that the simulated salamander can robustly switch between swimming and trotting, and 3) that it can successfully track a randomly moving target.

To conclude, biologically inspired CPGs may be interesting for controlling robots using animal-like type of gaits, that is, machines which require control mechanisms for efficiently coordinating multiple actuators for locomotion. The CPG presented in this paper has the interesting property that the generated gait can be modulated by simple input signals. By simply varying how tonic input is applied to the different parts of the network, the speed, direction, and type of gait can be modulated.

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