Evolution of neural controllers for salamander-like locomotion

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ABSTRACT

This paper presents an experiment in which evolutionary algorithms are used for the development of neural controllers for salamander locomotion. The aim of the experiment is to investigate which kind of neural circuitry can produce the typical swimming and trotting gaits of the salamander, and to develop a synthetic approach to neurobiology by using genetic algorithms as design tool.

A 2D bio-mechanical simulation of the salamander’s body is developed whose muscle contraction is determined by the locomotion controller simulated as continuous-time neural networks. While the connectivity of the neural circuitry underlying locomotion in the salamander has not been decoded for the moment, the general organization of the designed neural circuits corresponds to that hypothesized by neurobiologists for the real animal. In particular, the locomotion controllers are based on a body central pattern generator (CPG) corresponding to a lamprey-like swimming controller as developed by Ekleberg, and are extended with a limb CPG for controlling the salamander’s body. A genetic algorithm is used to instantiate synaptic weights of the connections within the limb CPG and from the limb CPG to the body CPG given a high level description of the desired gaits. A set of biologically plausible controllers are thus developed which can produce a neural activity and locomotion gaits very similar to those observed in the real salamander. By simply varying the external excitation applied to the network, the speed, direction and type of gait can be varied.

1. INTRODUCTION

Tools and methodologies developed in artificial intelligence and artificial life offer the possibility to take a new — synthetic — approach towards computational neurobiology.

At a high — behavioral — level, fields such as computational neuroethology, or also synthetic psychology, investigate how behavior results from neural circuits through the development of neural controllers for artificial animals (robots or simulations). Models of escape and feeding behaviors in frog, insect locomotion, fly vision, cricket phototaxis, classical conditioning have, for instance, been simulated and/or implemented in real robots. These studies investigate hypotheses on central nervous systems by embedding neural models into bodies (simulated or real) in interaction with an environment. An interesting aspect of these investigations, compared to more traditional computational neurobiology, is therefore that they test the completeness of a model, that is, they verify whether all elements necessary for the production of an observed behavior have been taken in account. They are also useful for analyzing the effect of having a real body in terms of sensory feedback and body dynamics. Finally, their synthetic essence, i.e. the fact that, although biologically plausible, the developed neural models do not necessarily correspond to existing mechanisms, is interesting for investigating possible control mechanisms and, potentially, inspiring new neurobiological measurements.

At a lower level, techniques from artificial neural networks can be used as tools for completing neurobiological models. Backpropagation algorithms have been used for instantiating synaptic weights of a connectionist model of the escape reflex in a leech, and the locomotor circuit of the stick insect, for instance. More recently, evolutionary algorithms are being used for setting parameters of compartmental models of single neurons, or for defining synaptic weights in a model of the salamander’s visual system. The interesting outcome of these approaches is the development of tools which automatically instantiate multiple parameters of complex non-linear systems modeling biological circuits, given a description of their observed output.

The work reported here was realized while the author was at the University of Edinburgh, Department of Artificial Intelligence.
This paper presents experiments—situated at the behavioral level described above—in which an artificial evolution approach is taken to develop potential neural controllers for salamander locomotion. Salamanders are capable of both aquatic and terrestrial locomotion. They swim using an *anguiform* swimming gait, i.e. by propagating a traveling wave of constant wavelength along their body, and, on ground, they switch to a trotting gait in which the body makes an S-shaped standing wave coordinated with the movements of the limbs. Electromyographic recordings along the salamander's trunk and tail have shown that these two gaits are produced by two distinct axial motor programs, with a traveling neural wave for swimming and a standing wave for trotting. The neural circuitry underlying this locomotion has not been decoded for the moment, but it has been hypothesized that it is a *central pattern generator* (CPG) —a circuitry capable of producing oscillatory activity without oscillatory input from sensory feedback or from higher control centers—with a similar organization to that of the lamprey. The lamprey, one of the earliest vertebrates, also uses an anguiform swimming gait, and its relatively simple swimming CPG has been found to be made of approximately 100 interconnected segmental oscillators located along the spinal cord (see for a review).

Following this assumption, we develop locomotion controllers simulated as continuous-time neural networks which are based on a lamprey-like body CPG extended by a limb CPG composed of two interconnected oscillators. The locomotion controllers are connected to a 2D mechanical simulation of a salamander. Both the lamprey-like swimming CPG and the mechanical simulation are inspired by Ekeberg's neuromechanical model of the lamprey. This paper follows initial experiments in which an artificial evolution approach was taken to develop neural controllers for the swimming of the lamprey. We found that the approach could be useful for both the low level and high level synthetic neurobiology described above. At the low level, it was demonstrated that the genetic algorithm could be very useful for automatically instantiating the synaptic weights of Ekeberg's model given a description of the desired behavior of the controller. In particular, one night of computation on a Sun Ultra 1 was sufficient to find sets of synaptic weights* which could produce swimming gaits closer, in terms of frequency range, to those observed in the real lamprey. At a higher level, when controllers were evolved without being restricted to have the connectivity observed in the real lamprey, a whole variety of different control architectures were evolved which were capable of producing an anguiform swimming very similar to that of the lamprey.

The next sections describe how a similar approach is used to develop neural controllers for the salamander. First the mechanical simulation is presented (section 2.1), section 2.2 presents the general organization of locomotion controller, section 3 describes the genetic algorithm, and finally sections 4 and 5 present and discuss the results of ten different evolutions.

## 2. SIMULATION OF A SALAMANDER-LIKE ANIMAT

### 2.1. Mechanical simulation

The 2D mechanical simulation of the salamander is an extension of Ekeberg's simulation of the lamprey. The body is made of ten rigid links representing the trunk and the tail, and four links representing the limbs (Figure 1). The links are connected by one-degree-of-freedom joints, and the torques on each joint are determined by pairs of muscles simulated as springs and dampers. The signals sent by the motoneurons contract muscles by modifying (increasing) their spring constant.

The accelerations of the links are due to three forces: the torques due to the muscles, inner forces linked with the mechanical constraints due to the joints, and the forces due to the environment. The forces due to the environment depend on whether the salamander is in water or on the ground. 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). On ground, all trunk links are subjected to a friction force, representing the fact that the trunk of the salamander slides on the ground when the salamander is trotting. As only the accelerations in the horizontal plane are calculated, we represent the contact of a limb with the ground as a constant friction force applied to the extremity of the limb link. We assume that the contact in itself is determined by the signals sent to the horizontal extensor and flexor muscles. The limb is assumed to be in the air when the signal of the extensor is larger than that of the flexor, and on the ground otherwise. The motoneurons for the flexor and extensor therefore not only determine the torque of the limb, but also its stand and swing phases.

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*It took Ekeberg a long time to set these weights by hand (personal communication).*
2.2. Neural simulation

The neural controllers developed in this paper have a general organization which is predetermined by the experimenter, while some of their main parameters—the synaptic weights of the circuitry involved in the trotting gait—are instantiated by the genetic algorithm, given a description of the desired behavior of the controllers.

2.2.1. Hypothesized neural organization

The hypothesized organization of the salamander’s locomotor circuit is shown in Figure 2. The circuit is composed of a lamprey-like body CPG and a limb CPG made of two oscillators. The body CPG has a similar organization to the lamprey CPG with 100 coupled segmental oscillators, and its motoneurons determine the muscular activity in the trunk and the tail. The limb CPG controls the fore and hind limb motoneurons, and project unilaterally to the body CPG, with the anterior oscillator projecting to the trunk segments and the posterior oscillator projecting to the tail segments.

![Figure 2. Organization of the evolved controllers for the salamander.](image)

In this paper, a body CPG is used which corresponds exactly to that of Ekeberg’s model of the lamprey.\textsuperscript{11} The chain of 100 interconnected segmental oscillators is able to produce the following behaviors observed in the real lamprey: 1) when tonic (i.e. constant) excitation is applied to the neurons of the different segmental oscillators, the segmental circuits develop an oscillatory activity with a frequency proportional to the level of excitation; 2) applying extra excitation to segments closest to the head leads the system to oscillate with small phase lags between segments.

\textsuperscript{11}In,\textsuperscript{22} salamander controllers are developed based on evolved lamprey-like swimming controllers, but the types of gaits they produce are not significantly different from those produced by the controllers developed here.
which are constant over the spinal cord, therefore producing the typical wave of neural activity observed in anguilliform swimming; 3) the wavelength of the undulation is independent of the oscillation frequency when the level of extra excitation is kept constant. The connectivity (set of synaptic weights) of the CPG is given in Table 1. Because the body (i.e., the trunk and the tail) is composed of 10 links in the mechanical simulation, only the motoneurons in segments 5, 15, ..., 95 are connected to the simulated muscles.

<table>
<thead>
<tr>
<th>from:</th>
<th>EINl</th>
<th>CINl</th>
<th>LINl</th>
<th>EINr</th>
<th>CINr</th>
<th>LINr</th>
<th>BS</th>
</tr>
</thead>
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<tr>
<td>EINl</td>
<td>0.4</td>
<td>[2, 2]</td>
<td>-</td>
<td>-</td>
<td>-2.0</td>
<td>[1, 10]</td>
<td>-</td>
</tr>
<tr>
<td>CINl</td>
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<td>[2, 2]</td>
<td>-</td>
<td>-1.0</td>
<td>[5, 5]</td>
<td>-2.0</td>
<td>[1, 10]</td>
</tr>
<tr>
<td>LINl</td>
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<td>[5, 5]</td>
<td>-</td>
<td>-</td>
<td>-1.0</td>
<td>[1, 10]</td>
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<td>-</td>
<td>-</td>
<td>-2.0</td>
<td>[5, 5]</td>
<td>-</td>
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<tr>
<td>EINr</td>
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<td>[1, 10]</td>
<td>0.4</td>
<td>[2, 2]</td>
<td>-</td>
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<td>[1, 10]</td>
<td>13.0</td>
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<td>-</td>
<td>5.0</td>
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<tr>
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<td>[5, 5]</td>
<td>1.0</td>
<td>[5, 5]</td>
<td>-</td>
<td>-</td>
<td>5.0</td>
</tr>
</tbody>
</table>

Table 1. Connectivity of the body CPG (corresponds to the Ekeberg’s lamprey configuration). Each segmental oscillator is composed of 8 neurons of 4 different types (EINl, CINl, LINl, and MNI, the motoneurons). Left and right neurons are indicated by l and r. BS stands for brain stem, that is, for the connections through which the external excitation is applied. The extension of the segmental connection to neighbor segments (i.e., the intersegmental coupling) is given in brackets (extensions to the rostral and caudal direction, respectively).

The two oscillators composing the limb CPG are copies of the body segmental oscillator. This choice is motivated by the hypothesis that the natural evolution from fin-less swimming to swimming using fins and finally terrestrial locomotion, which has seen morphological changes of the bones and the musculature of some parts of the trunk to become fins and then limbs, has been accompanied by similar specialization of the corresponding trunk segmental oscillators for the control of the new limbs (see\textsuperscript{16} for a discussion). From a control point of view, having the same oscillators as those of the body CPG has the advantage that all these oscillators have the same intrinsic frequency when the same level of excitation is applied to them.

As will be described in the next section, the genetic algorithm will be used to instantiate the synaptic weights of the following connections: 1) the connections between the limb oscillators, 2) the connections from the limb oscillators to the segments of the body CPG, and 3) the connections from the limb oscillators to the limb motoneurons. The goal is to develop a controller which can produce the swimming and trotting gaits depending on how external excitation is applied to the network. The swimming gait should be produced when excitation is only applied to the body CPG, while the trotting gait should be produced when excitation is applied to both the body and the limb CPGs.

\subsection*{2.2.2. Neuron model}

The type of neurons used for implementing the neural controllers corresponds to those used by Ekeberg to simulate the lamprey’s swimming circuit.\textsuperscript{1} Neurons are modeled as leaky integrators with a saturating transfer function. The output $u$ of a neuron unit corresponds to the mean firing frequency of a real neuron ($\in [0, 1]$) and is calculated as follows:

\begin{align}
\xi_+ &= \frac{1}{\tau_D} \left( \sum_{i \in \Psi_+^+} u_i w_i - \xi_+ \right) \\
\xi_- &= \frac{1}{\tau_D} \left( \sum_{i \in \Psi_-^+} u_i w_i - \xi_- \right) \\
\dot{\vartheta} &= \frac{1}{\tau_A} (u - \vartheta) \\
u &= \begin{cases} 1 - \exp\{ (\Theta - \xi_+ \Gamma) \} - \xi_- - \mu \vartheta & (u > 0) \\
0 & (u \leq 0) \end{cases}
\end{align}

where $w_i$ are the synaptic weights, $\Psi_+^+$ and $\Psi_-^+$ represent the groups of pre-synaptic excitatory and inhibitory neurons respectively, $\xi_+$ and $\xi_-$ are the delayed ‘reactions’ to excitatory and inhibitory input, and $\vartheta$ represents the frequency
adaptation observed in some real neurons. The parameters of the four neuron types used in this paper are given in Table 2.

### 3. EVOLUTION OF NEURAL CONTROLLERS

#### 3.1. Genetic algorithm

A real number genetic algorithm is used for instantiating the synaptic weights. Each solution (i.e. a set of synaptic weights) is represented by a chromosome (a string of genes which are real numbers in [0.0,1.0]) and given a fitness value determining how “good” it is (see below). The algorithm starts with a randomly generated population of 100 chromosomes, and at each generation, 30 chromosomes are generated using a cross-over and a mutation operator. The crossover operator chooses 15 couples of chromosomes with a rank-based probability (chromosomes with the best fitness values have the highest chance to be chosen). Couples of new chromosomes are then created by either applying a 2-point crossover (0.5 probability) or by simply copying the 2 parent chromosomes. Next, mutation is applied to the new chromosomes with each gene having a 0.4 probability to be mutated, and a mutation consisting in adding or subtracting a small value within a 0.2 range. At the end of each generation, the population size is kept constant by rejecting the 30 worst solutions (i.e. with the lowest fitness values) of the increased population (old population and new chromosomes).

#### 3.2. Encoding

A direct encoding scheme is used in which each gene corresponds, through a linear transformation, to one of the synaptic weights to be determined in the neural configuration (see above). Synaptic weights of connections coming from inhibitory and excitatory neurons are limited to the ranges [-5.0;0.0] and [0.0;15.0], respectively; except for the connections between limb oscillators for which they are limited to the ranges [-2.0;0.0] and [0.0;6.0]. A left-right symmetry is assumed. All evolved connections are encoded into 104 genes (Figure 3).

#### 3.3. Fitness function

The fitness of a controller depends on its capacity to control the motion of the mechanical simulation. The fitness function is defined to reward solutions which:

1. trot as fast as possible,
2. can change the speed of the trot when the excitatory drive is varied (excitation of both the limb and body CPGs), with a monotonic relation between the level of excitation and the speed,
3. can change direction when left-right asymmetrical drive is applied,
4. maintain, most of the time, one foot on the ground on each side of the body. This factor was added to prevent the emergence of gaits which would tend to roll in a 3D simulation, and is an indirect way to reward trotting gaits.

The mathematical definition of the fitness function is the following:

$$
\text{fitness} = \text{fit}_{\text{max speed}} \cdot \text{fit}_{\text{speed range}} \cdot \text{fit}_{\text{turning slow}} \cdot \text{fit}_{\text{turning fast}} \cdot \text{fit}_{\text{feet ground}} \in [(0.05)^5, 1.0]
$$
Figure 3. Encoding of genes 1 to 52. Genes 53 to 104 similarly encode the projections from the posterior oscillator.

where $\text{fit}_\text{max speed}$, $\text{fit}_\text{speed range}$, $\text{fit}_\text{turning slow}$, $\text{fit}_\text{turning fast}$ and $\text{fit}_\text{feet ground}$ are functions which are limited between 0.05 and 1.0 and which vary linearly between these values when their corresponding variables vary between two boundaries, a bad and a good boundary. The variables for each function and their corresponding boundaries are given in Table 3. An evaluation consists of several simulations (1000ms) with different levels of excitatory drive for determining the range of speeds which can be obtained. If the speed range includes the chosen speeds of 0.15 and/or 0.30 m/s, the capacity to induce turning is measured at the corresponding level of excitation and $\text{fit}_\text{turning slow}$ and/or $\text{fit}_\text{turning fast}$ is measured. Turning is induced by applying a symmetrical excitation for 1200ms (straight motion), followed by a left-right asymmetrical excitation ($\pm 20\%$) for 600ms, followed by 1200ms of symmetrical excitation. The angle of deviation corresponds to the difference of headings before and after the asymmetrical excitation. The factor $\text{fit}_\text{feet ground}$ depends on the minimal time left or right foot have spent on the ground in all the simulations of the evaluations.\(^1\) The lower this variable is, the more likely it is that the corresponding simulation would roll to a 3D simulation, as it indicates that the body is insufficiently supported on one side during a part of the cycle. A value of 1.0 means that, in all simulations, a leg (either the fore- or the hindlimb) was kept on the ground on each side of the body at all times.

<table>
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<th>Function</th>
<th>Variable</th>
<th>Bad, Good Boundaries</th>
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<tr>
<td>$\text{fit}_\text{max speed}$</td>
<td>Maximum speed</td>
<td>[0, 0.6] m/s</td>
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<tr>
<td>$\text{fit}_\text{speed range}$</td>
<td>Relative speed range</td>
<td>[0, 1.0]</td>
</tr>
<tr>
<td>$\text{fit}_\text{turning slow}$</td>
<td>Deviation angle</td>
<td>[0, $\pi$]</td>
</tr>
<tr>
<td>$\text{fit}_\text{turning fast}$</td>
<td>Deviation angle</td>
<td>[0, $\pi$]</td>
</tr>
<tr>
<td>$\text{fit}_\text{feet ground}$</td>
<td>Minimum time on ground</td>
<td>[0.5, 0.9]</td>
</tr>
</tbody>
</table>

Table 3. Variables and boundaries for the fitness function. The speed range is measured relative to the maximum speed.

\(^1\) For each simulation, the time $t_{\text{left foot}}$ (and $t_{\text{right foot}}$) an anterior or posterior foot has been in contact with the ground on the left (and right) side of the body is calculated (as a ratio of the duration of the simulation). The variable minimum time on ground is then the minimum of all $t_{\text{left foot}}$ and $t_{\text{right foot}}$.  

4. RESULTS

Ten evolutions of 50 generations were carried out starting with different random populations of 100 chromosomes each. The fitness and maximum speed of the best evolved controllers of each run are given in Table 4. These best controllers are analyzed below. In section 4.3, it is also investigated how one of the evolved CPGs could be used by higher control centers for a simple tracking behavior.

| Table 4. Fitness and maximal speed during trotting. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Run             | 1   | 2   | 3   | 4   | 5   | 6   | 7   | 8   | 9   | 10  |
| Fit             | 0.05| 0.01| 0.07| 0.02| 0.02| 0.07| 0.01| 0.03| 0.11| 0.01|
| Spd m/s         | 0.64| 0.40| 0.52| 0.38| 0.54| 0.65| 0.25| 0.45| 0.75| 0.34|

4.1. Performance of the controllers

All runs converged to solutions exhibiting a trotting gait, and all evolved controllers, except three (runs 7, 8 and 10), exhibit a body-limb coordination very similar to that of the salamander. The three exceptions have the trunk and tail segments of the body oscillating in phase which leads to the body making C-like undulations. The resulting movements are not well coordinated with the limbs, and the maximal speed of these solutions is therefore relatively low. For the other controllers, the trunk and the tail are approximately out of phase leading to the typical standing S-wave undulation (see Figure 4, left). Similarly to the real salamander, the body movements are coordinated with the limb movements such as to increase their reach when they are in the swing phase. The controller 9 presents, a body-limb motoneuron coordination very similar to data of the real salamander.15

Note that the limb oscillators project to the interneurons of body segments and therefore influence the body motoneurons only indirectly. The S-wave undulation is obtained because the limb oscillators force the trunk and tail segments to oscillate out of phase. The neural activity within the body segments is therefore the result of the interaction between the lamprey-like coupling between segments which tends to make neighboring segments oscillate with a similar phase, and the projections from the limb oscillators which leads to a steep change of phase at the level of segment 50. The effect of the coupling is, for instance, illustrated in Figure 5, right.

A general observation about the activity of the body circuitry is that there is less variability in the signal shapes and phases in the trunk segments than in the tail segments. In all controllers, the first 40 segments (in the trunk) oscillate with identical phases and signal shapes.5 There is then an area between segment 40 and segment 60 (i.e. around the transition from anterior to posterior limb oscillator influences) in which signal shapes and phases change significantly. The rest of the tail segments then tend to oscillate with identical signal shapes, either in synchrony (controllers 1, 2, 3, 6, 7) or with caudally-directed phase lags (controllers 4, 5, 8, 10). In some controllers such as 4 and 9 (Figure 5), the signal shapes also change along the tail segments. The fact that, for all controllers, trunk rather than tail segments oscillate in synchrony is probably due to the caudal asymmetry of Ekeberg’s intersegmental coupling.

The gaits produced by the evolved controllers can be modulated by the excitatory drive, and the speed of trotting increases with the level of excitation applied to the body and limb CPGs. Turning can also be induced by a left-right asymmetry of input (to both the limb and the body CPGs), and controller 9, in particular, can exhibit sharp turning movements because of large differences in the contraction between the left and right sides of the trunk, in addition to differences in the amplitude of the limb motoneurons (see section 4.3). Finally, when external excitatory drive is applied only to the body CPG with some extra excitation of the most rostral segments, the lamprey-like swimming gait can be produced (see Figure 4, right). Tonic drive is then also applied to the flexor muscles in order to hold the limbs against the body.

5Note that with Ekeberg’s intersegmental coupling, there is no lag between segments as long as no extra excitation is given to the first segments, and therefore both the intersegmental coupling and the projections from the anterior oscillator tend to make segmental networks in the trunk oscillate in phase.
Figure 4. Trotting (left) and swimming (right) salamander with the fittest controller (run 9). Notice the typical standing wave of the body during trotting compared to the traveling wave during swimming. See also animated gifs at http://www.dai.ed.ac.uk/students/aulef/, in particular the gifs illustrating the transition from swimming to trotting.

Figure 5. Neural activity during trotting. Left: Neural activity in the limb oscillators ($M_a$ and $M_p$ represent the motoneuron activity of body segments 5 and 95, respectively). Right: Motoneuron activity along the left side of the body. Remember that interneurons of segments 1 to 50, i.e. the trunk segments, receive projections from the anterior limb oscillator, while segments 51 to 100, the tail segments, receive projections from the posterior limb oscillator.

4.2. Configurations of the controllers

There is no identical neural structure between the different controllers, but rather a variety of different neural configurations, which however produce relatively similar gaits. The coupling between the two limb oscillators leads to several phase relations between them, depending on the controllers. In controller 4, for instance, the two oscillators are almost out of phase while, in controller 9, they are close to synchrony.

The fact that the phase relation between the oscillators varies significantly from one run to another means that the connections from the oscillators to the limb- and, to a less extent, body motoneurons also vary significantly in order to produce the trotting gait observed in all solutions. In order words, the projections from the oscillators to the motoneurons compensate the different phases between the two oscillators observed in the different controllers in order to produce a similar limb motoneuron output for all controllers.

4.3. Using the locomotor CPG: a simple tracking experiment

This section presents a preliminary experiment in which the capacity to sense its environment is given to the simulated salamander. Rather than aiming to simulate a realistic visual system, the main motivation is to investigate how the evolved CPGs cope with continuously changing commands by having the salamander tracking a randomly moving...
target. The experiment therefore investigates how “usable” the CPGs are by higher control centers for behaviors which require constant variations of the motor output.

![Figure 6. Salamander tracking the randomly moving target (controller 9).](image)

A very simple visual system is added on top of the locomotion CPGs composed of two retinæ which compute the bearing of the target. The outputs of the retinæ are proportional to that bearing (i.e. the more the target is on the left, the higher the output of the left retina) and determine the command signals (i.e. external excitation) sent to the locomotion CPG through crossed inhibitory connections and ipsilateral excitatory connections. The simple control mechanism is hand-coded to perform tracking behavior, and no evolution is therefore performed.

Equipped with this visual system, the salamander is capable of successfully tracking the target (Figure 6). The constant variations of command signals do not affect the capacity of the locomotor CPG to produce stable oscillations. Their effect is to simply modulate the amplitude of outputs of the trunk and limb motoneurons such as to induce turning by increasing the trunk bending towards one side and the step size of the limbs on the opposite side.

The tracking capacity is however slightly limited because of the strong head movements the simulated salamander makes during trotting. This is due to the fact that, in the mechanical simulation, there are no links representing the neck, which is unlike the real salamander which has several degrees of freedom in the neck and which actively compensates the movements of the trunk by having the neck muscles contracting in antiphase compared to the trunk muscles. This small problem could therefore be solved by improving the mechanical simulation.

5. DISCUSSION

5.1. Gaits

The best evolved CPGs produce a trotting gait similar to that of real salamanders with the fore- and hindlimbs out of phase and the body making S-shaped standing undulations which increase the reach of the limbs. Although the fitness function was defined to reward trotting gaits and therefore the emergence of trotting gaits is not surprising, it is interesting to see that optimizing the speed and the control of direction has led to a limb-body coordination very similar to that of the salamander.

The gaits do not produce, however, an exact reproduction of a salamander gait and, for instance, for many controllers, the body movements are significantly more accentuated than during trotting in the real salamander. The differences are mainly due to simplifications in the mechanical simulation (in particular, the fact that the limbs are represented by single rigid links), and also probably because energy efficiency was not taken into consideration by the fitness function. The evolved gaits may therefore be near optimal for the speed of locomotion (and the
control of direction), but suboptimal for the speed versus mechanical energy consumption ratio, with a large amount of mechanical energy being used for the body movements compared to the forward progression. An interesting extension of this work would be to include a factor in the fitness function rewarding such energy efficiency.

The speed of trotting of the evolved controllers can be modulated with the level of excitation applied to the trotting CPG (i.e., to both the limb and the body CPG). All these controllers have a range of levels of excitation in which the speed increases monotonically with the excitation. The increase of speed is mainly due to an increase of the frequency of oscillation, and in some cases also to an increase in the step size. Similarly, in the Ambystoma Tigrinum salamander, the speed of trotting is mainly due to an increase of the stepping frequency. In other salamander species which also use walking gaits, the increase of speed from walking to trotting is accompanied not only by an increase of frequency, but also an increase in step size and a decrease of contact interval.

Turning can be induced by the controllers when asymmetrical excitation is applied to the trotting CPG. The asymmetrical excitation leads to larger limb movements on one side of the body as long as the asymmetry lasts. The controllers which can induce the sharpest turning also use larger trunk contractions in the direction of turning, as controller 9, for instance. For this controller, it has also been shown that it can be used by a higher control center for a simple tracking behavior and that it can perfectly cope with continuously changing command signals. That experiment could be considered as a first step towards the development of a complete animat capable of sensing and behaving in an environment.

5.2. Neural controllers

The neural configurations have the following similarities with the organization proposed by Delvotte et al.: they are made of two coupled limb oscillators which project to a lamprey-like body CPG, and which, during trotting, provide phasic inhibition and excitation to different parts of the body segments, forcing the anterior and posterior parts of the lamprey-like body CPG to oscillate in antiphase. The differences are that, in our model, the neural configurations do not have body segments representing the neck of the salamander, and that the posterior limb oscillator projects to all segments of the tail, while in they project only to the most caudal segment.

The production of S-shaped standing waves was also investigated in a chain of coupled mathematical oscillators. It was found that, in a chain with closest neighbor connections and with long connections from the extremities towards the middle, a S-shaped standing wave is a stable solution. That type of configuration is different from the neural configurations in our model in the sense that it does not have distinct limb oscillators which project unilaterally to a chain of oscillators and that only single oscillators of the chain receive long couplings instead of all oscillators of the anterior and posterior parts in the controllers presented here. The chain of mathematical oscillators and the evolved controllers are, however, similar in that, in both cases, a chain of oscillators, which would oscillate in synchrony if undisturbed, is forced to oscillate in antiphase above and below its middle.

5.3. Neural activity

The neural activity produced by the evolved controllers presents several similarities with reported EMG recordings. During trotting, most segments of the trunk (all segments from 1 to 40 in all controllers) oscillate in synchrony as observed. There is also a coordination between trunk motoneurons and limb motoneurons very similar to that measured in the real animal, with the trunk motoneurons being active just prior to and during the activation of the ipsilateral forelimb flexor and the ipsilateral hindlimb extensor. The evolved controllers do not, however, produce the double burst pattern observed in the tail of the salamander, with the first burst traveling in the rostral direction and the second burst traveling in the caudal direction.

5.4. About the approach

The use of a genetic algorithm to design part of a continuous time neural network proved to be very useful. Compared to more traditional gradient-based learning algorithms in neural networks, genetic algorithms present the advantages that the fitness function does not need to be differentiable or even continuous compared to error functions. Also, they do not require a specific limit cycle that the network should learn, and the desired output of the network can be described at a higher level, in this case, by a description of the desired characteristics of the locomotion gaits in the mechanical simulation. The main disadvantage of genetic algorithms compared to gradient-based learning algorithms is that they are time-consuming.
The combination of neural networks and genetic algorithms provides an interesting approach to the control of animal-like locomotion which could potentially be applied to robotics.\textsuperscript{25–27} Animal-like locomotion is characterized by a large number of actuators, a rhythmic activity, and the fact that efficient locomotion is only obtained when the actuators are well coordinated. The difficulty is therefore to develop control mechanisms which can transform simple commands concerning the direction and speed of motion into the rhythmic signals sent to the multiple actuators. As illustrated here, the artificial evolution of central pattern generators can produce control mechanisms which can modulate, when simple command signals are varied, the speed, direction and even the type of gait of the locomotion.

Finally, it is hoped that the synthetic approach to neurobiology described here can provide new ideas for neurobiological measurements, and that a back and forth process between modeling and measurements on the real animal will lead to a progressive improvement of the model by incorporating new neurobiological findings when these become available. The similarities between the neural activity and the gaits produced by our simulations with the EMG and kinematic recordings on the real animal lead to think that the proposed model is not too far from the circuitry used by the real salamander.

6. CONCLUSION

This paper presented a synthetic approach to neurobiology in which a genetic algorithm is used to develop potential neural controllers for the control of salamander locomotion, an animal whose locomotor circuitry has not been decoded. The developed neural controllers are partially predetermined by the experimenter with a general organization based on a lamprey-like body CPG and a 2-oscillator limb CPG, while the synaptic weights of the connections within and from the limb CPG are instantiated by the genetic algorithm, given a high level description of desired behavior of the controller. Biologically plausible locomotor circuits are developed capable of producing the typical swimming and trotting gaits of the salamander. By simply modulating the external excitation applied to the network, the speed, direction and type of gait can be varied.

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