Synthetic approaches to neurobiology: review and case study in the control of anguiliform locomotion

Auke Jan Ijspeert**

LAMI-EPFL, IN-F Ecublens, CH-1015 Lausanne, Switzerland
ijspeert@lamisun1.epfl.ch,
WWW home page: http://diwww.epfl.ch/w3lami/team/ijspeert/

Abstract. This paper briefly reviews synthetic approaches to neurobiology and presents results of two experiments on the use of evolutionary algorithms for the design of neural controllers for locomotion. The first experiment consists in using the evolutionary algorithm for instantiating low level parameters of a connectionist simulation of the lamprey's locomotor circuitry. The second experiment develops potential neural circuits for the swimming and trotting of the salamander; an animal whose locomotor circuitry has currently not been decoded. In both cases, biologically plausible control circuits are developed which produce a neural activity with many similarities to that measured in the real animals.

1 Synthetic approaches to neurobiology

The fields of artificial life and artificial intelligence have developed tools and methods which have the potential to significantly help computational neurobiology. Synthetic approaches to neurobiology can indeed increase our understanding of the central nervous system, and this at two levels.

At a high —behavioural— level, fields such as *computational neuroethology* [1, 2], or also *synthetic psychology* [3], investigate how behaviour results from neural circuits through the development of neural controllers for artificial animats (robots or simulations). Models of escape and feeding behaviours in frog [4], insect locomotion [1, 5], fly vision [6, 7], cricket phonotaxis [8], classical conditioning [9] 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 behaviour have been taken in account. They are also useful for analysing 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

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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 [10], and the locomotor circuit of the stick insect [5], for instance. More recently, evolutionary algorithms are being used for setting parameters of compartmental models of single neurons [11], or for defining synaptic weights in a model of the salamander's visual system [12]. The interesting outcome of these approaches is the development of tools which automatically instantiate multiple parameters of complex non-linear systems modelling biological circuits, given a description of their observed output.

We will next present two experiments in which a genetic algorithm is used for generating part of control circuits for anguiliform locomotion. In the first experiment, the genetic algorithm is used to instantiate synaptic weights of a neural circuit whose general structure is well known —the locomotor circuitry of the lamprey— while in the second experiment it is used for generating potential neural controllers for the locomotion of the salamander, an animal whose locomotor circuitry has not been decoded for the moment.

2 Design of the lamprey's swimming controller

2.1 Ekeberg's connectionist model

The lamprey —one of the earliest vertebrates— swims using an anguiliform swimming gait, i.e. by propagating a travelling undulation from head to tail. Its locomotor circuitry has been studied in detail by neurobiologists (see [13] for a review), and is known to be a *central pattern generator* (CPG) made of a chain of approximately 100 segmental oscillators located in the spinal cord (Figure 1).

Several models of that circuitry have been developed, and this research is based, in particular, on the connectionist model developed by Ekeberg [14]. That model simulates the complete 100-segment CPG of the lamprey organised as illustrated in Figure 1. It is composed of neuron units modelled as leaky integrators with a saturating transfer function which represent populations of functionally similar neurons in the real lamprey. The output u of a neuron unit corresponds to the mean firing frequency of the population it represents ($\in [0,1]$) and is calculated as follows:

$$\dot{\xi_+} = \frac{1}{\tau_D}(\sum_{i \in \Psi_+} u_i w_i - \xi_+) \tag{1}$$

$$\dot{\xi_-} = \frac{1}{\tau_D}(\sum_{i \in \Psi_-} u_i w_i - \xi_-) \tag{2}$$

$$\dot{\vartheta} = \frac{1}{\tau_A}(u - \vartheta) \tag{3}$$

$$u = \begin{cases} 1 - \exp\{(\Theta - \xi_+)\Gamma\} - \xi_- - \mu\vartheta & (u > 0) \\ 0 & (u \leq 0) \end{cases} \tag{4}$$

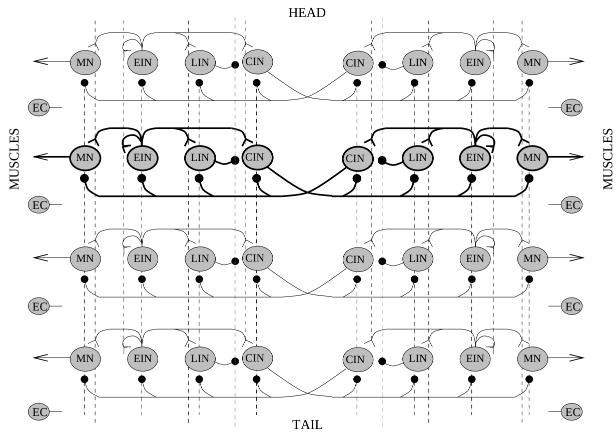

Fig. 1. Lamprey's swimming controller. The controller is made of 100 interconnected segmental oscillators (only 4 segments shown) composed of 8 neurons each. Four types of neurons are present in the oscillators: 3 types of interneurons EIN, CIN and LIN and the motoneurons MN. Sensory feedback is provided by stretch sensitive *edge cells* EC. The dashed lines indicate the projections from segmental connections to neighbouring segments.

where w_i are the synaptic weights, Ψ_+ and Ψ_- represent the groups of presynaptic excitatory and inhibitory neurons respectively, ξ_+ and ξ_- are the delayed 'reactions' to excitatory and inhibitory input, and ϑ represents the frequency adaptation observed in some real neurons.

The model is able to produce the following behaviours observed in the real lamprey: 1) when 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 which are constant over the spinal cord, therefore producing the typical wave of neural activity observed in anguiliform swimming; 3) for a given level of extra excitation, the wavelength of the undulation is independent of the oscillation frequency. Furthermore, when the motoneuron signals are used to determine the muscular activity of the simple mechanical simulation of the lamprey that Ekeberg developed, a swimming gait is produced which is very similar to that of real lampreys.

2.2 Parameter instantiation using a genetic algorithm

The implementation of a model such as Ekeberg's requires a significant amount of time for the setting of a large number of parameters, including the neuron parameters and the synaptic weights of all connections (Ekeberg, personal communication). We will here present how a genetic algorithm can be used as a tool for automatically instantiating those parameters, given a description of the desired behaviour of the system. This experiment follows evolutions of "artificial" controllers for swimming [15], i.e. controllers without the lamprey's connectivity. For a more detailed description of the results, see [16].

The evolved controllers are composed of the same type of neurons as those of Ekeberg and their connectivity corresponds to that observed in the lamprey. The design process is made in three stages, with first the development of segmental oscillators, then the development of intersegmental coupling and finally the development of sensory feedback connections from stretch sensitive cells.

Genetic algorithm. The same real number genetic algorithm is used for the three stages. Genes are real numbers between 0.0 and 1.0 which directly encode parameters of the neural controller (see below). Parents chromosomes are chosen with a rank-based probability, and children chromosomes are created with a 2-point crossover and a mutation operator. Mutation consists of modifying the old gene value by a small random value.

Stage 1: segmental oscillators. In this stage, the synaptic weights of the 26 connections within one segment are evolved. Because a left-right symmetry is assumed, chromosomes have 13 genes, which directly encode a synaptic weight through a linear transformation. The fitness function is defined to reward solutions which 1) produce regular motoneuron oscillations, and 2) have a frequency and an amplitude of oscillations which increase with the level of external excitation (for the mathematical definition of the function see [16]).

Ten runs were carried out with populations of 100 chromosomes for 500 generations. All populations converged to best solutions oscillating regularly and covering a large range of frequencies. Interestingly, the range of frequencies of the evolved oscillators (e.g. from 0.9 to 11.0 Hz) is much closer to that observed in the real lamprey (from 0.25 to 10.0 Hz) than Ekeberg's segmental oscillator (from 1.7 to 5.6 Hz).

Stage 2: intersegmental coupling. The second stage consists of developing the coupling connections between segmental oscillators. In the lamprey, oscillators are coupled through projections of segmental connections towards neighbouring segments. The extent of the projections are currently not known in detail, and for that reason Ekeberg chose a simplified coupling in which all segmental connections project symmetrically in the rostral and caudal directions except for the connections from the CIN neurons which project more caudally.

Here the GA is used to investigate potential coupling configurations between 100 copies of a chosen segmental oscillator. The chromosome encodes the extent of the projections of each segmental connection for both the rostral and caudal direction. The fitness function is defined to reward solutions which are able 1) to produce regular oscillations of the motoneurons in all segments, 2) to produce a travelling wave whose wavelength can be modulated by the extra excitation applied to the segments closest to the head, and 3) to produce swimming gaits covering a large range of speeds.

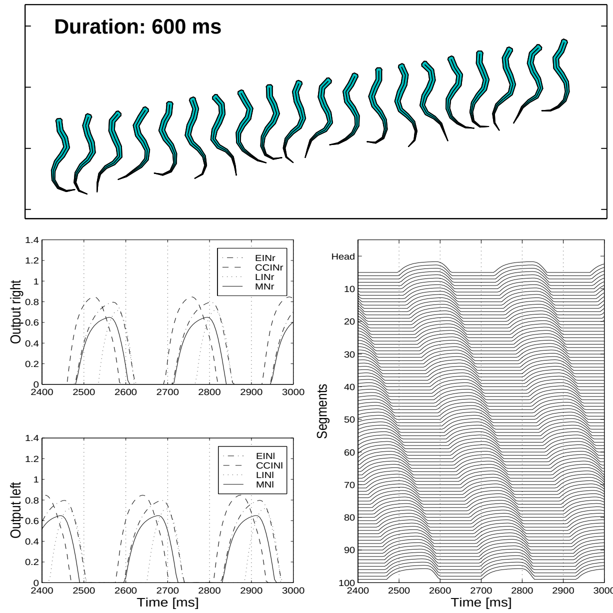

Fig. 2. *Top*: swimming gait produced by the optimised lamprey's controller. *Bottom*: Corresponding neural activity in the 50th segmental oscillator (*left*) and in the motoneurons along the left side of the spinal cord (*right*).

Five runs were realised with populations of 40 chromosomes for 100 generations. All five runs converged to controllers with similar performances to Ekeberg's biological model, in particular they cover larger ranges of lags and can reach slightly higher speeds. The range of lags of the best solution, for instance, varies between 0.0 and 3.5% of the oscillation period, which corresponds to the lags observed in the real lamprey (up to 3.0%) when local concentrations of excitatory bathes are varied [17]. Figure 2 illustrates the swimming gait produced by one of the evolved controllers.

Stage 3: sensory feedback from stretch sensitive cells. The last evolutionary stage consists of evolving the synaptic weights of sensory feedback connections from stretch sensitive cells. The lamprey has a series of inhibitory and excitatory stretch sensitive cells —the edge cells— located on both sides of the body which project to the segmental oscillators [18]. In [19], Ekeberg demonstrated that these cells could be useful for crossing a speed barrier (a local area with an increase of the speed of the water).

In order to further investigate how sensory feedback could be best used by the swimming CPG, the GA was used to generate weights for these feedback connections, given a fitness function rewarding the capacity to progress against the speed barrier with as small deviation as possible.

In all 5 runs tested (populations of 100 chromosomes, 100 generations), controllers were generated capable of crossing the chosen speed barrier (15 cm wide with a speed 40% higher than the lamprey's swimming speed). Interestingly, the evolved sensory feedback pathways correspond very closely to those observed in [18]: for all established (inhib. and excit.) biological connections, the evolved controllers have developed sensory feedback connections with the same sign.

3 Design of the salamander's locomotor controller

This second experiment concerns the salamander, an animal whose locomotor circuitry has not been decoded for the moment. The aim of the synthetic approach is here to investigate which kind of neural circuits can produce the observed gaits of the salamander.

3.1 Neurobiology of the salamander's locomotor circuitry

A salamander swims like a lamprey, and on ground it switches to a trotting gait with the body producing a standing wave coordinated with the movements of the limbs [20]. It has been hypothesised that the neural circuitry capable of producing both the travelling and the standing wave is based on a similar organisation to that of the lamprey [21, 22].

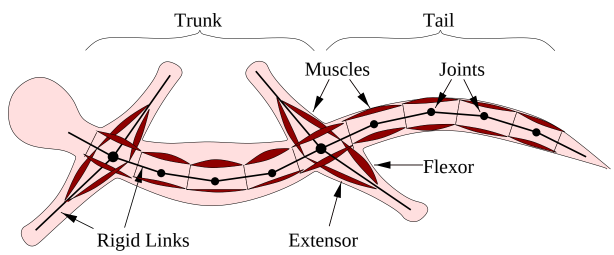

Fig. 3. Mechanical simulation of a salamander-like animat.

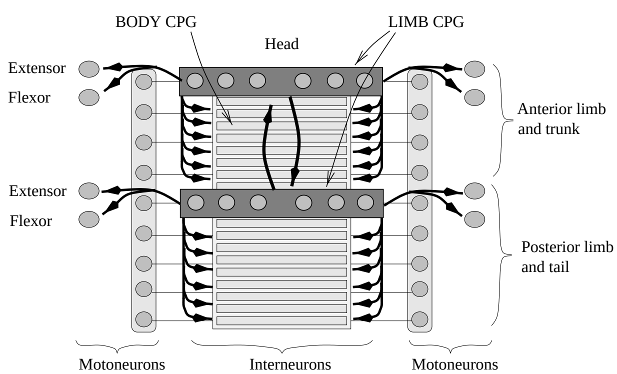

Fig. 4. Organisation of the evolved controllers for the salamander.

3.2 Evolution of potential locomotor controllers for the salamander

Following that assumption, we use a genetic algorithm to generate synaptic weights of a controller made of a lamprey-like body CPG and two limb oscillators which are copies of the body's segmental oscillators (Figure 4). The limb oscillators project to the motoneurons of the limbs and to the segmental oscillators of the body CPG, creating an unilateral coupling between them and the body CPG. [1] A simple 2D mechanical simulation of a salamander-like animat is developed for testing the swimming and trotting gaits (Figure 3, see [23] for a more detailed description). The aim is to be able to switch between the swimming and the trotting gaits by applying external excitation either to the body CPG or to both the body and the limb CPGs, respectively.

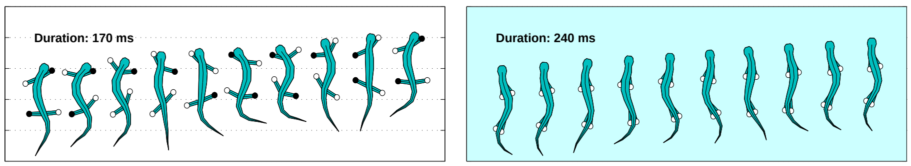

Fig. 5. Trotting (*left*) and swimming (*right*) salamander.

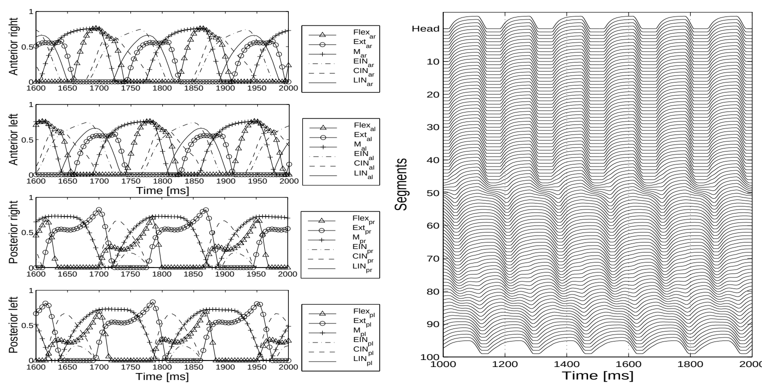

Fig. 6. Neural activity during trotting. *Left:* Neural activity in the limb oscillators (M_a and M_p represent the motoneuron activity of body segments 5 and 95, respectively). *Right:* Motoneuron activity along the left side of the body.

Chromosomes encode the synaptic weights of all possible connections from the two limb oscillators, as well as the connections from the brain stem to the limb motoneurons. The fitness function is defined to reward solutions which 1) trot as fast as possible, 2) can cover a large range of speeds when the excitation applied to both the body and the limb CPGs is varied, and 3) can change the direction of motion when left-right asymmetrical excitation is applied. The same real number genetic algorithm as for the experiment on the lamprey is used.

[1] This configuration is more biologically plausible than the one used in initial experiments in which there was no coupling between the swimming and the trotting CPGs [23].

Ten evolutions with populations of 100 chromosomes are carried out for 50 generations. All but 3 evolutions converged to controllers exhibiting a trotting gait with a trunk-limb coordination very similar to the real salamander (Figure 5, left). The speed of the trotting can be increased by increasing the amount of excitation, and applying a small asymmetry of excitation between the left and right sides of the CPGs leads to the salamander trotting in a circle. Finally, a lamprey-like swimming gait can be produced when excitation is applied only to the body CPG (Figure 5, right).

During trotting, the effect of the unilateral coupling from the limb oscillators on the body CPG is to force the anterior and posterior part of the body to oscillate in antiphase (Figure 6, right). Interestingly, the timing of the flexor and extensor limb motoneurons compared to the body motoneurons is very similar to that measured in the real salamander [22].

4 Discussion

These two experiments illustrated how a genetic algorithm could be used as a tool for neurobiological modelling. The interesting features of the method are:

1. GAs allow automatic instantiation of multiple parameters in complex non-linear models of central nervous systems. The evolution of controllers for the lamprey illustrate, for instance, that the GA can generate a significant part of the model that Ekeberg has designed by hand.
2. Specific characteristics specified by the user can be optimised. It was, for instance, possible to optimise the frequency range of Ekeberg's model and to obtain a better fit of biological data.
3. As illustrated with the salamander, the GA can also be used to investigate potential control mechanisms for biological systems whose structure is not known for the moment.

Compared to more traditional learning algorithms for artificial neural networks, such as variations of the backpropagation algorithm, for instance, a GA has the advantage that the fitness function does not need to be differentiable and that the desired output of the system can be described at a higher level. There is no need to provide a specific output cycle that the network should learn, and the desired behaviour of the system can, for example, be described in terms of a desired range of frequencies or the capacity of fast swimming. Note that the GA is here not used as a simulation of natural evolution, and that, similarly to [24, 25, 26], the staged evolution approach taken here rather corresponds to an "engineering" approach to artificial life.

It is hoped that, in the case of the salamander, this synthetic approach can provide news ideas for neurobiological measurements, and that a back and forth processus between modelling and measurements on the real animal will lead to a progressive improvement of the model by incorporating new neurobiological data when it becomes available.

Finally, the types of developed connectionist controllers may also be useful to robots using animal-like locomotion. The neural controllers are capable of transforming simple commands into the multiple rhythmic signals sent to the different actuators for efficient locomotion. They present the interesting property that by simply varying the amplitude of the commands, the speed, direction and type of locomotion can be modulated.

5 Conclusion

This paper briefly reviewed synthetic approaches to neurobiology and presented two experiments in the use of genetic algorithms for designing connectionist models for anguiliform locomotion. In these experiments, the genetic algorithm is used for instantiating synaptic weights of neural circuits whose structure corresponds to that decoded (for the lamprey) or hypothesised (for the salamander) in the real animal. It is found that 1) the GA is successful in automatically instantiating variables which require a long time to be set by hand, and 2) it can generate solutions which optimise high level characteristics specified by the user such as the speed of locomotion of a mechanical simulation.

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