From lampreys to salamanders: evolving neural controllers for swimming and walking

Auke Jan Ijspeert*, John Hallam*, David Willshaw**

* Dept. of Artificial Intelligence, U. of Edinburgh
5 Forrest Hill, Edinburgh EH1 2Q, UK
{aukei, john}@dai.ed.ac.uk

** Centre for Cognitive Science, U. of Edinburgh
2 Buccleuch Place, Edinburgh EH8 9LW, UK
david@cns.ed.ac.uk

Abstract

This paper presents how neural swimming controllers for a lamprey can be adapted for controlling both the swimming and the walking of a salamander-like animat. Using a Genetic Algorithm (GA), we extend a connectionist model of the biological Central Pattern Generator (CPG) controlling the swimming of a lamprey (Ekeberg, 1993) to control the locomotion of a 2D mechanical simulation of a salamander.

We first summarize experiments on the evolution of alternative swimming controllers for the lamprey (Ijspeert et al., 1998). The aim of that work was to study whether there exists other neural configurations than that found in the lamprey which could control swimming with the same efficiency and to develop a method for developing neural locomotion controllers using a GA. We then present how that method, namely a staged evolution of the neural configuration of a connectionist model, can be used to extend swimming controllers to control both swimming and walking. Controllers which, similarly to CPGs of animals, can produce complex oscillations when receiving simple excitatory signals are thus developed. In particular, we generate a controller which can switch from swimming to walking and produce different speeds of motion depending on its excitation.

1. Introduction

Although there exists a variety of different locomotor movements among vertebrates, their control systems appear relatively similar across different species (Grillner et al., 1991). Locomotion is controlled by networks of interneurons located in the spinal cord which produce the complex patterns of oscillations necessary for motion. As demonstrated in the 1960s by Orlovsky's classical experiment on the cat (as reported in (Grillner, 1996)), these networks, called Central Pattern Generators, need only simple excitatory signals from the brain to produce the coordinated oscillations necessary for motion.

Our research focusses on biologically inspired neural locomotion controllers for autonomous agents and how to develop them using a Genetic Algorithm (GA). In particular, we are interested in which kinds of neural configuration can control the anguiliform swimming observed in lampreys and the swimming and walking of salamanders. Both lampreys and salamanders project themselves in water by undulation of the body, without use of fins or limbs. The undulation is a traveling wave propagating from head to tail. When the salamander switches from swimming to walking, its trunk ceases to propagate an undulation and, instead, performs an S shaped standing wave with the nodes at the level of the girdles (Frolich and Biewener, 1991). The bending of the trunk helps the salamander to increase the reach of its limbs which are attached laterally to the trunk.

The work presented here follows experiments in which we used a GA to evolve swimming controllers for a simulated lamprey with alternative neural configurations to the observed biological configuration (Ijspeert et al., 1998). The work was inspired by a biological connectionist model of the lamprey's CPG (Ekeberg, 1993). We developed artificial controllers using an incremental approach where increasingly complex control mechanisms are developed using elements of the previous evolutionary stage. Here, as the method proved to be a useful design technique, we apply it again to study whether controllers for swimming can be extended to control both swimming and walking of a salamander-like animat. Walking controllers based on oscillatory networks of the swimming controllers are generated for the control of a 2-dimensional mechanical simulation of the salamander.

We are interested in the development of control mechanisms which, similarly to the CPGs of animals, can produce complex oscillations when receiving simple input signals. A potential application of these controllers could be the control of locomotion of an amphibian robot. Another motivation is to gain some insights on how CPGs function in real animals. Note that the evolution from swimming to walking controllers and its application to robotics has been studied before (Lewis, 1996), but at a more abstract level than the connectionist approach taken here.[1]

In this paper, we firstly present, in Section 2, Ekeberg's connectionist model of the lamprey's CPG (Ekeberg, 1993). We then summarize our work on the incremental evolution of alternative swimming controllers based on neuron models similar to those of Ekeberg (Ijspeert et al., 1998) (Section 3). An example of how the same method could potentially be used as a tool for developing biological models is also given (Section 3.4). Finally, in a further evolutionary stage, we show how the controllers can be extended to control both the swimming and the walking of a salamander-like animat (Section 4).

2. Connectionist model of the lamprey's Central Pattern Generator

The swimming controller of the lamprey has been extensively studied and is probably one of the best known vertebrate locomotion controllers. The controller is a Central Pattern Generator which can produce the patterns of oscillation necessary for locomotion without oscillating input either from the brain or from sensory feedback. The complete CPG is located along the spinal cord of the lamprey and, as small parts of the spinal cord can be made to oscillate when isolated, is thought to be composed of interconnected segmental oscillators. During swimming, each segment oscillates with a small phase lag compared to its rostral neighbour which leads to a wave of neural activity, and hence an undulation of the body, to travel from head to tail. The lamprey usually maintains a constant wavelength corresponding to approximately the length of the body and changes speed of swimming by changing the frequency of oscillation.

Physiological observations have allowed neurobiologists to make a model of the neural circuitry of the CPG (Buchanan and Grillner, 1987; Grillner et al., 1988) whose capacity to produce most of the observed patterns of oscillations has been demonstrated through simulations both at a neurobiological (Ekeberg et al., 1991; Wallén et al., 1992) and a connectionist level (Buchanan, 1992; Williams, 1992; Ekeberg, 1993). The biological circuitry connects four type of neurons: motoneurons MN, excitatory interneurons (EIN), contralateral inhibitory interneurons (CIN) and lateral inhibitory interneurons (LIN) (Figure 1).

We have reproduced Ekeberg's connectionist model of the biological controller (Ekeberg, 1993). In this model, populations of functionally similar neurons are represented by single neuron units which are modeled as leaky

[1] Lewis evolved abstract structures called Ring Rules representing explicitly the frequency and the phase of different oscillators and applied them to control the swimming of a simulated lamprey and the walking of a robot with a one-joint flexible spine.

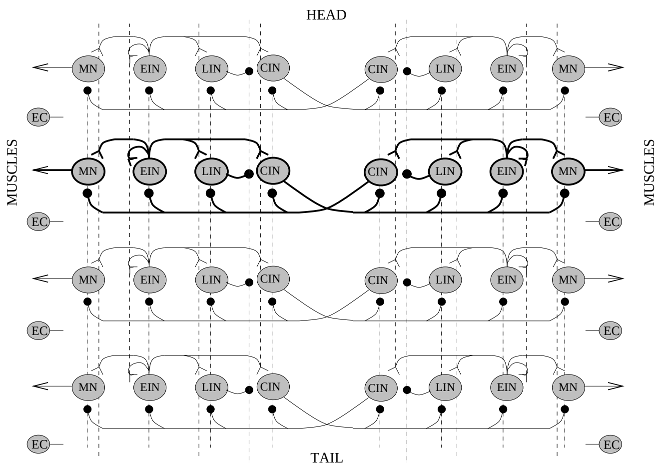

Figure 1 Model of the lamprey's CPG (based on (Buchanan and Grillner, 1987)). The controller is made of interconnected segmental oscillators (only 4 segments shown). Each segmental oscillator is composed of populations of neurons of four different types: 3 types of interneurons EIN, CIN and LIN and the motoneurons MN (one neuron unit represents a whole population of similar neurons in the lamprey). Inhibitory and excitatory connections are ended by • and ∨ respectively. The controller receives feedback from the stretch sensitive edge cells EC (connections not shown).

integrators with a saturing transfer function. The output u of a neuron corresponds to the mean firing frequency of the population it represents ($\in [0,1]$) and is calculated as follows:

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

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

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

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

where w_i are the synaptic weights, Ψ_+ and Ψ_- represent the groups of pre-synaptic 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 controller is made of 100 interconnected segmental oscillators. The segmental oscillators have the observed biological connectivity as shown in Figure 1 and the interconnections between segments are obtained through extending the connections from one neuron to another in one segment to the corresponding postsynaptic neuron in neighbouring segments. Because the interconnections in the lamprey are not well known, Ekeberg has simplified them by chosing a symmetric extension (in the rostral and caudal direction) for all connections (but not necessarily with the same extent) except for the extensions from CIN which project more caudally.

The model is able to produce patterns of oscillations which are very similar with those observed in the lamprey. When the segmental networks receive adequate excitation from the brainstem, they oscillate regularly with the left and right neurons out of phase. The frequency of oscillations increases with the level of excitation. The interconnections between segments lead to traveling waves of oscillations when the most rostral segments receive extra excitation compared to the others. The lag between segments relative to the period of oscillation is then constant over the whole spinal cord, except for the first and last ten segments at the extremities where it decreases towards zero. The value of the lag can be varied with the amount of extra excitation, and the higher the extra excitation, the larger the lag (or the shorter the wavelength). Interestingly, the frequency of oscillation and the wavelength of the undulation can be changed nearly independently. The model can therefore reproduce the capacity of the real lamprey to cover a whole range of different frequencies of oscillations while keeping the wavelength of the undulation constant.

We have also reproduced Ekeberg's mechanical model of the lamprey's body interacting with water (Ekeberg, 1993).[2] The body is made of 10 rigid links connected through one-degree of freedom joints. Muscles are connected to each link and are modeled as a combination of springs and dampers whose spring constants are determined by the motoneurons' signals (from every tenth neural segment). Propulsion through water is obtained when the traveling waves of neural activity are transformed into traveling undulations of the body. The mechanical simulation allows a direct evaluation of the efficiency of the CPG to control swimming (in terms of speed of swimming, for instance). It also allows study of the effect of sensory feedback from stretch sensitive cells (the edge cells) located on both sides of the spinal cord (Viana Di Prisco et al., 1990).

Our simulations produce frequencies of oscillations between 1.6 and 5.5 Hz, phase lags per segment and relative to the oscillation period between 0.0% and 2.4% and speeds of swimming between 0.0 and 0.50 m/s. Because of the correction of some mechanical parameters, we obtain speeds of swimming which are approximately 40% smaller for the two quantitative examples given in (Ekeberg, 1993).

3. Evolution of swimming controllers

In (Ijspeert et al., 1998), we developed alternative swimming controllers by using a GA to define suitable connections and synaptic weights between neurons similar to those of Ekeberg's model. Our motivations were to evaluate how efficient GAs could be for the design of neural controllers and to investigate whether there exist alternative neural configurations to the biological one found in the lamprey. The controllers were evolved in three stages. First, segmental oscillators were evolved; then multi-segmental controllers were generated by evolving the couplings between copies of a chosen segmental oscillator; and, finally, connections providing sensory feedback from stretch sensitive cells were added. A similar real number GA was used for the three stages and will be described in Section 4.2. We briefly summarize here the results of the experiments.

3.1 Evolution of segmental oscillators

Segmental oscillators were generated by evolving both the connectivity between the 8 neurons composing the biological segment and the *sign* (excitatory and inhibitory) of each interneuron. The evaluations were based on the neural activity of the oscillators, and the fitness function was defined to reward the following characteristics:

1. The production of regular oscillations of the motoneurons, with one peak of activity per period and with the left and right neurons out of phase.
2. A frequency of oscillation which can be varied and which increases monotonically with the level of external excitation.
3. A minimal set of connections.

We evolved 10 populations of 100 chromosomes for 500 generations. All runs converged to final populations composed of networks producing regular oscillations with variable frequency. Although the fittest oscillator of one of the runs had a similar structure to the biological one, a variety of different segmental oscillators were produced which differed not only in their connectivity, but also in the sign of the interneurons and in the number of neurons active in the creation of oscillations (a majority of solutions use only four interneurons). All fittest oscillators covered a larger range of frequency than Ekeberg's segmental network (largest range: between 1.1 and 11.3 Hz).

3.2 Evolution of the coupling between oscillators

We generated complete CPGs by evolving the interconnections (i.e. the extents in the caudal and rostral direction of the projections of each segmental connection) between 100 copies of a segmental network. The fittest segmental oscillators of each evolution of the previous evolutionary stage were chosen. The evaluation was based on simulations of both the neural activity and the mechanical movements of the body. In order to obtain the same swimming characteristics as the biological controller, we defined the fitness function to reward:

[2] Our simulation is identical to Ekeberg's except for the correction of some mechanical parameters. See Table 2 in Appendix A.

1. generation of stable oscillations in the 100 segments with coordinated phase differences for the creation of traveling undulations of the body,
2. ability to change the speed of swimming by changing either the frequency of oscillation or the wavelength of the undulation,
3. ability to change the frequency and the wavelength independently, by changing, respectively, the global excitation level and the amount of extra excitation on the most rostral segments.

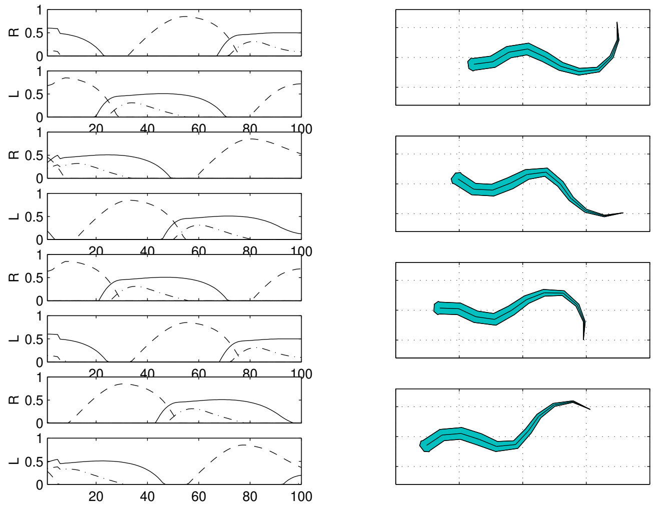

Figure 2 Simulation of one of the evolved artificial swimming controllers. The frequency of oscillations is 4.0 Hz, the phase lag between segments is 1.1% of a cycle duration and the speed of swimming is 0.41 m/s. *Left:* Neural simulation, the continuous line correspond to the MN, the dashed line corresponds to the CIN and dotted-dashed line to the EIN. *Right:* Mechanical simulation, the dotted vertical lines are separated by 100 mm, and there are 60 ms between each snapshot.

We evolved 10 populations of 40 chromosomes (each population based on one of the fittest evolved segmental oscillators). All runs developed couplings between the segmental oscillators which produce stable oscillations with the necessary phase lags for swimming (Figure 2 shows the simulation of one of them). Similary to the biological model, swimming at different speeds and with different wavelengths of undulations could be produced by varying simple external signals (the excitation applied to the CPG). Although it was not rewarded by the fitness function, turning could also be induced when one side of the controller receives more excitation than the other. The evolved controllers could generally cover larger ranges of frequency, phase and speed (maximum speed 0.60 m/s) than Ekeberg's model but with less independence in the control of the frequency and the phase between segments.

3.3 Evolution of sensory feedback from stretch sensitive cells

The CPGs evolved in the second stage did not receive feedback from the mechanical simulation. In the real lamprey, sensory feedback is provided to the CPG by stretch sensitive cells (the edge cells) situated on both sides of the spinal cord. There are both inhibitory and excitatory edge cells and they emit signals proportional to their elongation (Viana Di Prisco et al., 1990). Ekeberg showed (Ekeberg et al., 1995) that this sensory feedback is necessary for crossing a barrier of water with local speed opposite to the direction of swimming. We carried out a preliminary experiment on how to evolve this sensory feedback for the artificial controllers (i.e. the synaptic weights of excitatory and inhibitory connections from the stretch sensitive cells to the neurons of the segmental networks) in order to allow them to cross a similar speed barrier. The barrier was 150 mm wide (half the length of the simulated lamprey) and the speed of the water flow opposite to direction of swimming was set to be 40% higher than the speed of swimming of the lamprey. The fitness function was defined to reward:

1. progression through the barrier in the direction of swimming,
2. minimal deviation in the direction,
3. minimal difference of speed between swimming with and without sensory feedback.

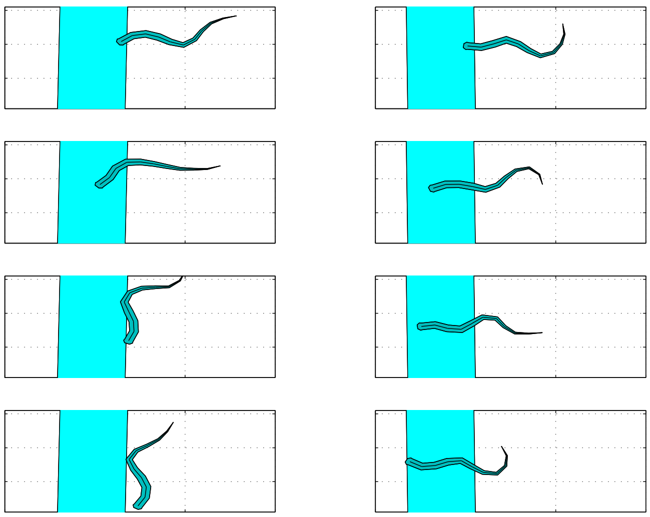

Figure 3 Effect of a speed barrier on swimming without (left) and with (right) evolved sensory feedback.

We carried out 5 evolutions with populations of 40 chromosomes using one of the fittest controller of the previous evolutionary stage. Without sensory feedback, the lamprey was not able to cross the speed barrier (Figure 3 *left*). The increase in local forces at the entrance to the barrier disturbs the undulation of the body and leads to extra bending of the most rostral part of the body which forces the lamprey to change its direction of swimming. The lamprey eventually swims perpendicularly to its initial direction. After 80 generations, all runs developed controllers with sensory feedback allowing them to cross the barrier (Figure 3 *right*). The feedback enables the crossing by sending excitatory signals to the motoneurons leading to a stiffer body and by acting as a burst terminator which tends to switch the neural activity from one side to the other when the latter is too much extended.

3.4 GA as a tool for neurobiological modeling

We believe that a GA can be a useful tool for neurobiologists to develop models, as it can be used to automatically generate instantiations of variables which are difficult to measure. As an illustration of this, we repeated the evolutions and restricted the space of possible solutions to controllers which preserve the segmental connectivity and the sign of neurons observed in the real lamprey. The evolutionary process generated thus a significant part (the synaptic weights and the interconnections) of the connectionist model that Ekeberg set up by hand.

We used the same evolutionary stages as for the artificial controllers. We firstly evolved segmental oscillators by evolving the synaptic weights of a network with a fixed configuration corresponding to the biological segmental connectivity. We found that Ekeberg's set of synaptic weights could be modified in order to optimize the frequency range. Frequency ranges much closer to those observed in real lampreys (between 0.25 and 10 Hz) could be obtained (the best solution covered a range between 0.9 and 11.0 Hz). The main observation is that the increase of the frequency range is obtained through an increase of the strength of some inhibitory connections (the contralateral CIN to LIN and ispilateral LIN to CIN connections).

In the second evolutionary stage, we evolved the couplings between segmental oscillators corresponding to those of Ekeberg's biological model. As these coupling are not perfectly known in the real lamprey, the idea was to study which kind of interconnections can produce phase lags between segments which are constant over the spinal cord and independent of the frequency of oscillation. There are opposing views on the origin of these phase lags in the real lamprey, in particular whether they are due to differences in the intrinsic frequencies of the oscillators or to the nature of the coupling, and, in the latter case, whether the dominant coupling is ascending or descending (see for instance (Matsushima and Grillner, 1992; Wadden et al., 1997)). We evolved interconnections with the same fitness function as for the artificial controllers and developed couplings which could produce the kind of phase lags observed in the real lamprey. The evolved solutions cover large ranges of lags and can reach slightly higher speeds than with Ekeberg's coupling. The evolved couplings in the five different runs we carried out (populations of 40 chromosomes) were all very similar and significantly different from the simplified coupling of Ekeberg's model. We find that the evolved CPGs seem to have no dominant coupling (for instance, no systematic asymmetry) and they present both rostral and caudal asymmetries of projection depending on the segmental connection. As for Ekeberg's coupling, the CPGs rely both on the nature of the couplings and on differences of intrinsic frequencies for creating travelling waves. The coupling is optimized for waves to travel from head to tail and the extra excitation of the most rostral segments determines the exact phase lag (giving more excitation to those segments amounts to increasing their intrinsic frequency).

Finally, we also evolved sensory feedback to Ekeberg's controller which enabled the simulated lamprey to cross a speed barrier. Interestingly, the evolved connections correspond very closely to those observed in the real lamprey, with all connections from excitatory and inhibitory stretch sensitive cells established in the real lamprey (Viana Di Prisco et al., 1990) being also present with the same sign in the evolved controllers. Crossing a speed barrier may therefore be a good example of the situation for which sensory feedback has been developed through natural evolution for the real lamprey.

4. Evolving a locomotion controller for a salamander-like animat

We present next how swimming controllers can be extended to control the walking of a salamander-like animat. Keeping the idea of staged evolution in which increasingly complex control systems are incrementally built using elements of the previous stage, this can be seen as a fourth evolutionary stage following the evolution of the swimming controllers. As little is known about the neuronal circuits underlying the locomotion of salamanders (the locomotion of salamanders has only been investigated using kinematic and electromyographic studies, see for instance (Delvolvé et al., 1997)), this evolutionary stage can not be compared with neurobiological data. We evolve walking controllers for a simulated salamander based on two interconnected oscillatory networks which are copies of the segmental oscillators of the swimming controller. Two experiments are realised, with walking controllers extended from the biological controller of the lamprey (Ekeberg's model) in the first one, and from one of the best evolved artificial swimming controllers in the second one. The aim is to develop controllers which, when receiving simple excitatory signals, can switch from swimming to walking and control locomotion at different speeds.

4.1 Mechanical simulation

We have developed a mechanical simulation of a salamander-like animat by extending the simulation of the lamprey. To the ten rigid links representing the spinal cord of the lamprey, are added four rigid links corresponding to the limbs (Figure 4). All links are connected through one degree of freedom joints. Muscles, modeled as a combination of springs and dampers, are connected in parallel to each joint and can be contracted through an increase of their spring constant by the corresponding motoneuron. There are a total of 26 muscles, 18 muscles for the 9 joints of the spinal cord and one extensor and one flexor muscle for each limb.

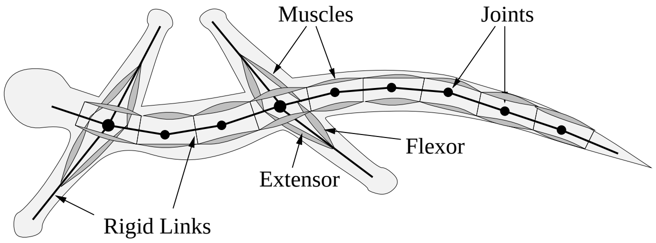

Figure 4 Mechanical configuration of the salamander-like animat.

The accelerations of the links are due to three forces: the torques due to the muscles, inner forces linked with the mechanical constraints and the forces due to the environment. The forces due to the mechanical constraints ensure that the segments stay connected at all times. 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. 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 walking. As only the accelerations in the horizontal plane are calculated, we represent the contact of a limb with the ground as an extra mechanical constraint. We assume that the contact in itself is determined by the signals sent to the horizontal extensor and flexor muscle of the limb. The limb is assumed to be in contact with the ground when the signal of the flexor is larger than that of the extensor, and in the air otherwise. The motoneurons for the flexor and extensor therefore not only determine the torque of the limb, but also its stand and swing phase. Once a foot is on the ground, a mechanical constraint is added which ensures that the foot does not move until it is lifted (i.e. the foot is temporarily 'pinned' to the ground). For more details see Appendix A.

4.2 Evolution of walking controllers

Similarly to the evolved swimming controllers, walking controllers are developed by evolving the connections and synaptic weights between neurons modeled by equations 1-4.

We evolve walking controllers under the following assumptions:

1. the walking controllers consist of two interconnected segmental oscillators which are copies of those of the swimming CPG,
2. the segments send signals to the muscles of the limbs and of the trunk, with the anterior and posterior segment projecting to the anterior and posterior muscles respectively,
3. the walking and the swimming controller receive excitation from the brain stem through different pathways.

Our aim is to evolve controllers which can switch between swimming and walking depending on which part of the controller is excited (Figure 5), and which can produce a speed of locomotion proportional to the level of excitation.

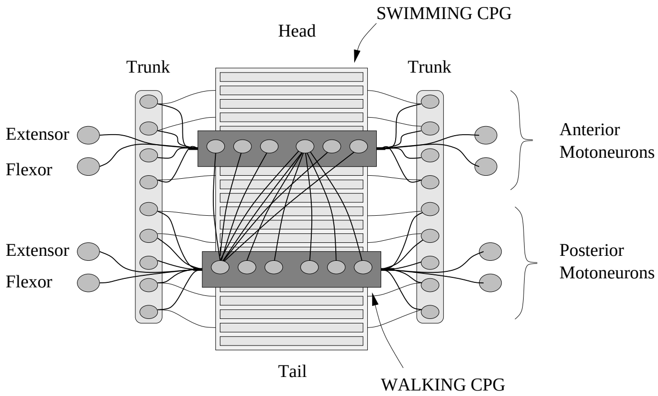

Figure 5 Neural configuration of the locomotion controller for the salamander-like animat. The controller is composed of two parts, the swimming and the walking CPG. All neurons receive an input from the brain stem (connections not shown), and swimming or walking patterns are generated depending on which CPG is excited.

Encoding A 'chromosome' encodes the synaptic weights of: the projections from the neurons of the 2 segments to the motoneurons, the connections from the brain stem to the motoneurons, and the connections between the 2 segments (see Figure 5). The connections within a segment and those from the brain stem to the segments are fixed and correspond to those of the swimming controller. We assume a left/right symmetry. The chromosome is made of 39 genes $\in [0, 1]$, with each gene encoding a synaptic weight and corresponding (via a linear transformation) to a real value between -5 and 0 if the pre-synaptic neuron is inhibitory or between 0 and 15 otherwise.

Genetic Algorithm The algorithm used is a variation of the standard GA (see for instance (Goldberg, 1989)) with the usual binary encoding being replaced by a real

number encoding. The algorithm starts with a randomly generated initial population. At each generation, a fixed number of children are generated using two operators, *crossover*, and *mutation*. The *crossover* operator chooses couples of parents, with a rank-based probability, for breeding and creates couples of children either by two-point crossover (probability *Prob_Xover*) or by simply copying the two parents. The *mutation* operator mutates each gene of the children with a probability *Prob_mut* and the mutation consists of adding or subtracting a small random number within a mutation range:
$new\_value = old\_value + Mut\_Range \cdot rand$
where $rand$ is a random number $\in [-0.5, 0.5]$. The children are then evaluated, and the size of the population is kept constant by rejecting, at each generation, the worst solutions of the increased population (old population plus children). The evolutions are carried out with populations of 40 chromosomes and 12 children at each generation. The crossover probability is 0.5, the mutation probability is 0.4 and the mutation range is 0.2.

Evaluation Solutions are rewarded for their capacity:

1. to perform fast walking in a straight line,
2. to cover a large range of different speeds when the excitation of the CPG is varied, with the speed increasing with the excitation, and
3. to use four limbs.

The last point was added to prevent premature convergence to solutions using only 2 limbs. Initial tests (without the third point) showed that this often happened (especially with these small populations), because using 4 limbs handicaps progression unless the limbs are perfectly coordinated (in which case higher speeds can be reached).

The mathematical definition of the fitness function is the following:
$Fitness = fit\_max\_speed \cdot fit\_speed\_range \cdot fit\_limbs$
$\in [(0.05)^6, 1]$, where

- *fit_max_speed* varies linearly between (and is limited to) 0.05 and 1 when the maximum speed of the salamander varies between 0.0 and 0.5 m/s respectively.
- *fit_speed_range* varies linearly between (and is limited to) 0.05 and 1 when the speed range (difference between the highest and the lowest speed) varies between 0.0 and 1.0 m/s respectively. The speed range is measured by making a set of simulations at different levels of excitation, and only ranges in which the speed increases monotonically with the excitation level are rewarded.
- *fit_limbs* is made of four factors, one for each limb, which vary linearly between (and are limited to) 0.05 and 1 when the time on the ground of each limb varies between 0 and 25% of the simulation duration, respectively.

The simulations are carried out for a fixed duration (1000ms) with asymmetric initial conditions for the neural activity (left interneurons of the anterior segment excited) and with an initial straight body with the limbs perpendicular to the body.

Results We carried out two sets of 5 runs (populations of 40 chromosomes), runs 1-5 are evolutions of walking controllers based on the biological controller of the lamprey (Ekeberg's model), and runs 6-10 are based on one of the fittest evolved artificial swimming controllers.

After 40 generations, all runs converged to controllers able to produce a walking gait with the speed of motion dependent on the level of excitation. The fitness and the maximum speed of the fittest solutions of each run are given in Table 1. All evolved controllers use all four limbs for locomotion, except the controller of run 4 which uses only the hindlimbs (which explains its low fitness value). There seem to be no significant differences in the type of walking developed by the two sets of runs, except that the runs based on the biological controller reach on average slightly higher speeds.

Table 1 Fitness and maximum speed of the evolved walking controllers

Run	1	2	3	4	5	6	7	8	9	10
Fit	0.38	0.71	0.37	0.00	0.62	0.27	0.15	0.14	0.48	0.60
Spd m/s	0.42	0.73	0.42	0.37	0.62	0.36	0.25	0.24	0.48	0.58

While all solutions move their left and right limbs strictly out of phase, the phase relation between fore- and hindlimbs varies among the nine controllers using four limbs. Five controllers have developed a strictly out of phase relation between fore- and hindlimbs (runs 1,2,3,5 and 9), two have a relation which is almost out of phase with one oscillator leading slightly the other (runs 7 and 8) and two have have fore- and hindlimbs which are in phase which means that they have the limbs on the same side being lifted simultaneously (runs 6 and 10).[3] All five solutions which, similarly to the salamander, move their fore- and hindlimbs out of phase have developed connections to the anterior trunk motoneurons such that one side of the anterior part of the trunk contracts simultaneously with the flexor on the same side leading to an increased reach of the extended and lifted limb of the other side.

Figure 6 (up) shows the simulation of walking controlled by the evolved solution of run9. The walking mode is obtained when the walking CPG receives excitation from the brain stem. Increasing the level of excitation leads to an increase of the frequency of the oscillators and

[3] These solutions may not be stable in a three-dimensional simulation (risk of rolling).

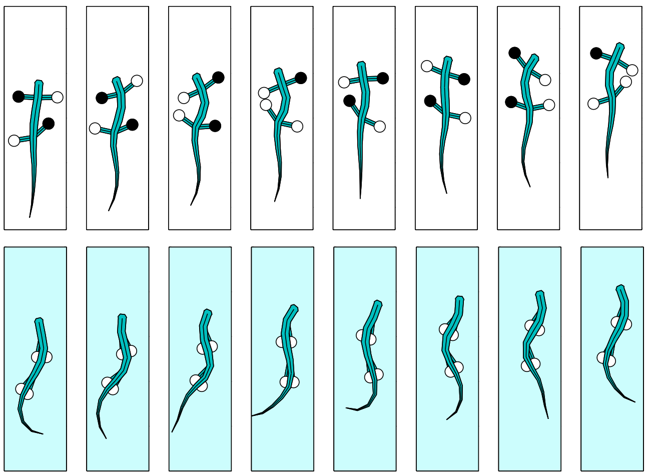

Figure 6 Walking (*Up*) and swimming (*Bottom*) salamander (fittest of run 9). A filled circle indicates that the limb is on the ground.

therefore to an increase of the speed of locomotion. Although it is not rewarded in the fitness function, for some solutions a limited turning can be induced when asymmetrical excitation is applied. When the swimming CPG is excited and excitation is given to the flexor muscles of the limbs (in order to stick the limbs to the trunk), swimming can still be produced (Figure 6, bottom). However, because of the extra forces due to the limbs (inertia and forces due to the water), the speed of swimming obtained is approximately 35% lower than that of the lamprey.

5. Discussion

Inspired by the CPG of the lamprey, we have developed connectionist models for the control of undulatory swimming and of salamander-like walking. The evolution of swimming controllers for the lamprey alternative to Ekeberg's biological has demonstrated that there exists a variety of possible solutions which can control swimming with the same efficiency. The solutions differ from the biological model in terms of which neurons are interconnected, of the excitatory or inhibitory influence of the interneurons and even of the number of neurons involved in the rhythmogenesis. Similarly to Ekeberg's model, the evolved solutions can modulate the frequency and the wavelength of the undulation, hence the speed of swimming, by varying the global level of excitation of the CPG and the extra excitation given to the most rostral segments. Turning can also be induced when asymmetrical excitation is given.

Walking CPGs have been successfully developed using oscillators of the swimming controllers. Most evolved CPGs produce a walking gait (or trot to be more accurate) similar to that of salamanders with the fore- and hindlimbs out of phase and contractions of the upper part of the trunk which increase the reach of the limbs. The speed of the walking increases with the excitation level. As only small changes of directions can be induced with asymmetrical excitation, further evolutions should include a factor in the fitness function rewarding the capacity to turn.

We have developed walking controllers based on oscillators of swimming controllers which have specialised to control the limbs. It seems reasonable to think that a similar specialisation has occurred in vertebrates through natural evolution. It is well established that evolution from swimming gaits to legged gaits has seen morphological changes of the bones and the musculature of some segments of the trunk to become fins and then limbs. It is therefore quite probable that the oscillators for the limbs have followed a corresponding specialisation from the trunk segmental networks (see (Cohen, 1988) for a discussion). It is less clear, however, how the interconnections between the segments of the trunk have evolved to allow both travelling waves for swimming and standing waves for walking. As far as we know, the neural circuitry responsible for the control of locomotion in the salamander is not well understood yet, although (Delvolvé et al., 1997) presents an interesting hypothesis of how limb oscillators may influence a trunk CPG similar to that of the lamprey. Here we have assumed (without any biological evidence) that the walking CPG has direct connections to the muscles of the trunk (without influencing the interneurons of the swimming CPG), with the anterior segment projecting to the upper part of the trunk and the posterior segments projecting to lower part, i.e. the tail. The swimming or walking gaits are then obtained depending on whether the segments of the trunk (the swimming CPG) or the segments of the walking CPG receive excitation from the brainstem.

Note that our mechanical simulation is only a crude description of the body of the salamander, especially in the way the limbs are simulated and because only accelerations in the horizontal plane are calculated. Salamanders have three-jointed limbs which therefore need much more complex control than the rigid links of our 2-dimensional simulation. Our interest, however, was mainly to study the neural mechanisms for switching from travelling to standing waves, and we could imagine that extending the controller to a more realistic 3D model could be done by coordinating oscillators for the different muscles of a limb with the signals of the corresponding principal oscillator that we have evolved.

Controllers were evolved using a GA with a staged-evolution approach. Although these swimming and walking controllers have strong evolutionary links, the GA was used as a design tool and not as a simulation of natural evolution. The method of staged evolution has allowed us to incrementally build controllers with each stage using elements of the previous stages. Such a decomposition has the advantage of reducing the time needed to evolve a complete controller by structuring the evolution and avoiding evaluation of whole controllers whose segmental oscillators do not oscillate correctly even when isolated. It presents the risk, however, of developing sub-optimal controllers as the fittest solutions of one stage may not necessarily be the best starting elements of the next stage. Although the decomposition and the simple encoding scheme (for instance, fixed neuron models and fixed maximum number of neurons) have strictly limited the type of controllers that could be evolved, the multidimensional search space was still large enough to generate a variety of interesting CPGs.

The main advantage of using a GA for the design of neural controllers is its ease of implementation and use. There are, for instance, no mathematical restrictions on the fitness function. Unlike most error functions minimised by learning algorithms for dynamical neural networks (like variations of the backpropagation algorithm), the fitness function does not need to be differentiable or even continuous. There is also no need to produce a specific oscillation (limit cycle) that the network should learn. This has allowed us to define the desired oscillations indirectly, either by qualitative aspects (as in the first evolutionary stage) or by the performance of the mechanical simulation. Another interesting aspect of the GA is the parallel search of the parameter space it performs (each chromosome is in a different place in that space), reducing the risk of convergence to local maxima. This parallel search and the stochastic nature of GAs makes them particularly suitable for visiting the space of possible solutions and designing, potentially, a variety of solutions.

It is interesting to see that a GA could also be used by neurobiologists to develop biological models. As we demonstrated for the lamprey's swimming controller, a significant part of a connectionist model —the synaptic weights— can be generated by the GA when biological observations are used to constrain the encodings and to define the fitness functions. Although it is possible, in the case of the lamprey, to define satisfactory values by hand (as Ekeberg did), the GA proved useful for searching the different possibilities and to optimise the unknown values for specific criteria. In particular, we showed that Ekeberg's model could be improved to cover a larger range of frequencies, much closer to that observed in real lampreys. From a general point of view, note that, although the GA can be very useful for demonstrating that a model can produce a specific behaviour (by finding efficient sets of unknown variables), it is less useful for invalidating a hypothetical model as an inability to find successful variable instantiations may be due to failings of the model or to problems with the GA set up, or both.

6. Conclusion

This paper has described how a Genetic Algorithm can be used to develop connectionist Central Pattern Generators for the control of the swimming and the walking of a simulated salamander-like animat. Inspired by the swimming controller of the lamprey, we first generated, in three evolutionary stages, controllers which can produce the patterns of oscillation necessary for anguiliform swimming. Walking controllers were then developed based on two oscillators of the swimming controllers. Similarly to biological CPGs, the resulting controllers can produce complex patterns of oscillation when receiving simple excitatory signals. In particular, the evolved controllers can switch between swimming and walking gaits and produce locomotion at different speeds depending on the excitation.

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A Mechanical simulation of the salamander

Newton's law of motion The acceleration of each link i (trunk and limb) depends on the torques due to the muscles T, the inner forces due to the constraints F_{in} and the forces due to the environment F_{env}:
$m_i\ddot{x}_i = F_{env,i,x} + \sum F_{in,i,x}$
$m_i\ddot{y}_i = F_{env,i,y} + \sum F_{in,i,y}$
$I_i\ddot{\varphi}_i = \sum T_i - \sum F_{in,i,x}\frac{l_i}{2}\sin\varphi_i + \sum F_{in,i,y}\frac{l_i}{2}\cos\varphi_i$
where x_i and y_i are the position of the middle of the link and φ_i is its angle.

Geometry The trunk of the salamander is 300 mm long (10 links of 30 mm). Each link has an elliptical cross section with height of 30 mm and width of 20 mm for the four first links and then decreasing towards 0 at the tail. The limbs are modeled as cylinders of 50 mm long and 10 mm width which are attached to the first and the fourth joints of the trunk. The masses and moments of inertia of the links are calculated by assuming the density of the salamander to be constant and equal to that of water (Table A).

Torques due to the muscles The torque acting at a particular joint is determined by the motoneuron activities (M_1 and M_2) of the corresponding parallel muscles:
$T = \alpha(M_1 - M_2) + \beta(M_1 + M_2 + \gamma)\Delta\varphi + \delta\Delta\dot{\varphi}$
where $\Delta\varphi$ is the difference bewteen the actual angle of the joint and the default angle (when $M_1 = M_2 = 0.0$). The parameters of the spinal cord muscles are: $\alpha = 9.4$ [N mm], $\beta = 0.94$ [N mm], $\gamma = 10$ and $\delta = 94$ [N mm ms]; and those of the limb muscles: $\alpha = 30.0$ [N mm], $\beta = 3.0$ [N mm], $\gamma = 10$ and $\delta = 300$ [N mm ms].

Table 2 Parameters for the mechanical simulation.

link	w_i [mm]	m_i [g]	I_i [g mm^2]	$\lambda_\perp$ [Ns^2/m^2]	$\lambda_\parallel$ [Ns^2/m^2]
1	20.0	14.1	1414	0.45	0.3
2	20.0	14.1	1414	0.45	0.2
3	20.0	14.1	1414	0.45	0.1
4	20.0	14.1	1414	0.45	0.0
5	17.2	12.2	1137	0.45	0.0
6	15.0	10.6	944	0.45	0.0
7	11.7	8.3	691	0.45	0.0
8	8.3	5.9	465	0.45	0.0
9	5.0	3.5	271	0.45	0.0
10	1.7	1.2	90	0.45	0.0
Limbs	1.0	4.0	850	0.25	0.1

The parameters of link 1-10 correspond to those of the lamprey simulation. Note that we have corrected some of Ekeberg's parameters which did not correspond to the assumptions made in the text (see (Ijspeert et al., 1998)).

Forces due to the environment In water, it is assumed that the forces due to the water are mainly inertial (high Reynolds number). It is also assumed that the water is stationary and that the parallel and perpendicular components of that force on each segment can be calculated separately. The components of the force can therefore be calculated as: $F_{env\parallel} = \lambda_\parallel v_\parallel^2$ and $F_{env\perp} = \lambda_\perp v_\perp^2$, where $v_\parallel$ and $v_\perp$ are the components of the speed of the link relative to the water and $\lambda_\parallel$ and $\lambda_\perp$ are coefficients which depend on the density of the fluid, the area perpendicular to the movement and the drag coefficient C dependent on the shape of the link (here $C_\perp = 1$ and $C_\parallel = 0$ for all links except those close to the head. See Table A).

On the ground, the links of the trunk are subjected to a friction force opposite to their motion and proportional to their weight (gm): $F_{env} = \mu gm$. In the simulations presented here, μ has been fixed to 0.8.

Inner forces due to the mechanical constraints Inner forces arise from the constraints on the movements by the joints which force the rigid links to stay connected. On the ground, new constraints are added as soon as a limb is assumed to be on the ground (flexor activity greater than extensor activity). The end position of the limb (the foot) is then fixed and inner forces are created to keep that position constant until the foot is lifted.

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