Using Evolutionary Methods to Parameterize Neural Models: a Study of the Lamprey Central Pattern Generator

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Abstract. The neural controller of anguilliform swimming in lampreys is particularly well studied because of its relative robustness and simplicity. In this chapter we look at connectionist models of the controller – in which populations of similar neurons are represented by abstract, differential-equation-based models – and describe the use of evolutionary computation techniques for investigating the space of appropriate architectures and parameters for such models. An introduction to this style of modeling is followed by a presentation of the lamprey central pattern generator model, devised by Ekeberg, and its development by Ijspeert using genetic algorithms. Some results on the robustness to body variation in the modelled controllers will be described, and the value of this approach to neural modeling work will be discussed.

1 Introduction

One of the many fascinating questions, to a roboticist, about animals is how they coordinate their movements. Consider a human walking: rhythmic motions of the legs, arms, and back (at least) must be generated and maintained in appropriate relationships; perturbations induced by the contact of the feet with uneven ground must be compensated for; and the whole process must not distract the person from monitoring the environment (have you noticed how very small children tend to fall over when something fascinates their attention?). Transitions between different gaits, such as standing, walking, running, and so on, must also be managed smoothly. In robotic terms, a complex mechanism with many degrees of freedom and complex, non-linear, elastic actuators, is being efficiently and effectively controlled. How is it done?

The answer appears to be that many animal nervous systems contain mechanisms that generate rhythmic sequences of activity given tonic (that is, non-oscillatory) input [2]. These mechanisms are found in both vertebrates and invertebrates, and are believed to be able to produce oscillatory patterns of activity in the absence of any sensory input. Such systems are called Central Pattern Generators.

Among vertebrates, one of the most studied CPGs is that of the lamprey, a primitive jaw-less fish, because of its robustness, accessibility and relative simplicity (compared to CPGs of mammals, for instance).

The lamprey swims in an eel-like (anguilliform) manner by propagating a travelling wave of muscular activity from head to tail. The wave is generated by activating the muscles of the body rhythmically so that muscles further toward the tail (more caudal) are activated later than those toward the head (more rostral) and by alternating activation between the left and right sides of the fish. The muscular activation causes the body to bend toward the active side, and the result is a wave of body displacement with amplitude increasing caudally. This mechanical wave drives the fish through the water.

The lamprey is able to change the frequency of the mechanical wave over a reasonable range (0.25–10 Hz [7]) to adapt to different swimming conditions, but the relative phases of the wave between different parts of the body are held constant over the range of frequencies, resulting in the wavelength of the mechanical wave being roughly equal to the body length.

More interesting, perhaps, is that in the lamprey the neural structures generating the rhythmic patterns of muscular activation can be successfully isolated. By careful dissection, the spinal cord of the fish can be removed without too much damage. If placed in a bath of excitatory neurotransmitter, the cord produces a travelling wave of neural oscillation with the properties necessary to generate the mechanical wave for swimming – activity alternates between left and right, can vary in frequency and maintain constant phase relationships between the 100 spinal cord segments. This phenomenon is referred to as fictive swimming.

To generate the travelling wave, the first few rostral segments of the cord are subjected to more excitation (a greater concentration of neurotransmitter) than the remaining ones.[1] The global concentration of the excitatory bath determines the frequency of oscillation, while the relative excess of rostral segment excitation controls the phase lag between segments of the cord.

Finally, the spinal cord can be further sectioned and it is possible to elicit oscillations from sections as small as two segments.

The lamprey spinal cord is thus a clear example of a central pattern generator, producing complex rhythmic neural activity from a constant excitatory stimulus, and furthermore is also fairly easy to study. The types of neuron and their interconnections within a spinal cord segment are thus fairly well understood, and the properties of the inter-segmental connections are also known but to a lesser extent. This has allowed a number of detailed computational models of the neurophysiology to be devised and investigated

[1] This is not completely true: extra excitation is not necessary for wave propagation, but it helps. A uniform excitatory bath usually leads to a traveling wave, but whose wavelength varies quite a bit (can even be backwards).

which, though outside the scope of this chapter, underpin the much simpler approximate model developed by Ekeberg described in the next section.

2 Building Models of the Lamprey Spinal Cord

The spinal swimming circuit of the lamprey has been extensively modeled. Three types of models can be distinguished: chains of non-linear oscillators [13,11,14], leaky-integrator neural networks [1,17,3,10], and detailed biophysical models based on compartmental neuron models [5].

Work on chains of non-linear oscillators has focussed on investigating the potential mechanisms underlying the generation of traveling waves. It has, in particular, tried to explain which mechanisms can produce waves over a large range of frequencies while maintaining a more or less constant wavelength of one body length. This is indeed an intriguing question in lamprey swimming because it means that the phase lag between segments from head to tail can not be simply due to conduction delays of action potentials traveling along axons from head to tail. Neurons have indeed conduction speeds which are more or less constant, and traveling waves due to conduction delays would therefore have wavelengths which vary as much as the frequencies (i.e. to the 40-fold increase of frequency between 0.25Hz and 10.0Hz would correspond a 40-fold variation of the wavelength). More realistic explanations of wave propagation are differences in the intrinsic frequencies between oscillators and/or the inter-segmental coupling. The most likely mechanism is an asymmetry between the ascending and descending couplings along the chain of oscillators. As summarized in [14], chains in which the ascending coupling is dominant correspond best to most data gathered on the lamprey.

While the analytical analysis of chains of oscillators provides interesting insights into the generic properties of inter-segmental coupling, it gives little information on the actual neural mechanisms necessary for implementing the inter-segmental coupling (although see [17] for a step in that direction) nor the segmental oscillators. Leaky-integrator neural networks [1,17,3,10] were specifically developed to test whether the observed connectivity between neurons within a segment and between segments could produce the rhythms and phase lags measured in lamprey's spinal cord. Our work is inspired by Ekeberg's model which will described in more detail in the next section. Leaky-integrator neural networks are at an interesting level of complexity between abstract oscillators and detailed biophysical models. They, for instance, allow one to relate the model to actual connections observed in the real lamprey (or to be more accurate, general pathways between groups of functionally similar neurons), while using simple enough neuron models to allow tractable simulations of the complete spinal cord coupled to a mechanical simulation of the body, as in Ekeberg's model.

At the most detailed level, biophysical models have been developed (see, for instance, [5,7,15]) to investigate the cellular properties of pattern generation. Most of the studies have been limited to the segmental network. While these models have provided very valuable insights into the cellular mechanisms of rhythmogenesis (in particular of the mechanisms involved in burst termination), they are difficult to extend to the complete swimming circuitry because of the huge number of parameters which need to be instantiated. Many of these parameters are not readily measurable from intracellular recordings, and need therefore to be set (usually by hand) to fit the biological data. The growing number of parameters which need to be artificially instantiated means that the larger the network, the more unreliable the simulation becomes.

3 Ekeberg's Connectionist Model

Using the neurophysiological work of Grillner and colleagues on the lamprey spinal cord, Örjan Ekeberg devised a connectionist model of the lamprey central pattern generator [3]. Ekeberg's model is the basis of the work described in this chapter, and is presented in some detail in this section.[2]

3.1 The Central Pattern Generator Model

The model comprises four kinds of neural element interconnected to form a segmental oscillator. One hundred of these segments are coupled together to model the complete spinal cord, and the neural system is connected to a simplified mechanical model of the lamprey's body to demonstrate the model's ability to induce suitable propulsive body motion.

The Ekeberg's neural model [3] is derived by a process of abstraction from detailed models of the various neural types found in the lamprey [5,16], replacing populations of spiking neural models with simpler equations tuned to replicate the input-output dynamics of the spiking models. Each model neuron stands for a population of physical neurons of that type.

The model comprises three ordinary differential equations per neuron.

$$\tau_D \dot{\xi_+} + \xi_+ = \sum_{j \in W_+} u_j w_j \tag{1a}$$

$$\tau_D \dot{\xi_-} + \xi_- = \sum_{j \in W_-} u_j w_j \tag{1b}$$

$$\tau_A \dot{\zeta} + \zeta = u \tag{1c}$$

[2] We actually simplify Ekeberg's model somewhat in this presentation, omitting the stretch-sensitive edge cells found in the lamprey's spinal cord and discussed and modelled by Ekeberg (*op. cit.*). They were found by Ekeberg to have little effect on swimming performance in stationary water, but to become significant in the presence of water currents.

A pair of leaky integrator processes, one for excitatory dendritic inputs (1a) and one for inhibitory inputs (1b), model dendritic summation and delay, summing neural outputs, u_j, over the sets of excitatory (W_+) and inhibitory (W_-) input connections. For some of the neurons, frequency adaptation effects occur which gradually reduce neural output activity for constant input and these are model-led by the third leaky integrator process (1c).

A squashing function (2) maps the outputs of these processes to a measure u of the neuron's activity (in $[0, 1]$).

$$u = \begin{cases} 1 - e^{\Gamma(\Theta - \xi_+)} - \xi_- - \mu\zeta & u > 0 \\ 0 & \text{otherwise} \end{cases} \tag{2}$$

Here, Γ is a gain, Θ is a neural activation threshold, and μ controls the level of frequency adaptation. Excitatory input above the activation threshold is squashed using a saturating function (the exponential in (2)), the inhibitory input and the frequency adaptation term are subtracted, and the result indicates the activity of the model neuron. Negative outputs are clipped to zero, indicating that the neuron is off.

Ekeberg's segmental oscillator uses four kinds of neuron, described using the equations above, arranged in two groups (left and right) as shown in Fig. 1: motoneurons (MN), which drive the muscles of the fish; excitatory interneurons (EIN), lateral inhibitory neurons (LIN) which make connections to neurons on the same (ipsilateral) side of the network, and contralateral inhibitory neurons which connect to the opposite (contralateral) side of the network. The parameters of each type of neuron [3] are reproduced in Table 1 – they are chosen to match the model dynamics to the properties of the detailed neural models simulated by Ekeberg, Wallén, and colleagues [5,16].

Table 1. Parameters of the four neural types used by Ekeberg [3]

Type	Θ	Γ	τ_D	μ	τ_A
EIN	−0.2	1.8	30 [ms]	0.3	400 [ms]
CCIN	0.5	1.0	20 [ms]	0.3	200 [ms]
LIN	8.0	0.5	50 [ms]	0.0	—
MN	0.1	0.3	20 [ms]	0.0	—

The synaptic connections shown in Fig.1 match synapses found experimentally in the lamprey spinal cord in type and target, but the connection strengths cannot be determined easily from experiment and were derived by trying to match the behaviour observed in the lamprey spinal preparation during fictive swimming [16].

The synaptic connectivities used by Ekeberg [3] are shown in Table 2. Positive weights represent excitatory connections, negative weights imply inhibitory synapses. (The numbers in square brackets after each weight are

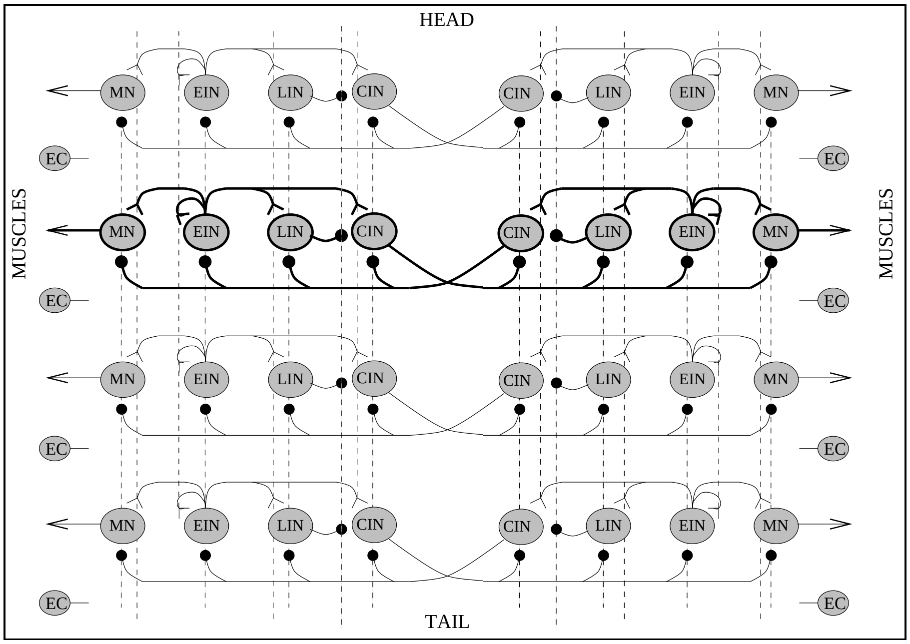

Fig. 1. The structure of Ekeberg's segmental oscillator. The network comprises identical left and right sub-networks. Open circles represent excitatory synapses, filled circles inhibitory synapses. The CCIN neuron makes inhibitory synapses with all contralateral neurons, indicated by the bold circle round each half of the network

discussed below.) In addition to intra-segmental connections, the segmental oscillator receives a tonic input from brainstem neurons as indicated in the table.

The complete lamprey spinal cord comprises 100 interconnected segments, each of which is an individual segmental oscillator. Ekeberg therefore replicates the segmental oscillator network 100 times to make the complete model. Little is known about the details of inter-segmental connections, so Ekeberg assumes that neurons in a given segment connect to targets in local neighbours analogous to their intra-segmental target. Thus the LIN_L neuron in segment 25, say, connects to the CCIN_L neuron in segment 25 but also to that neuron in segments 20–24 and 26–30. The connection strength listed in Table 2 is shared among the 11 connections, that is, each connection has effective weight $\frac{1}{11}$ in this case. At the ends of the spinal cord, the connection ranges given are truncated where they indicate connections to non-existent segments.

Each connection then, in addition to a strength, has an extent in the rostral and the caudal directions. These extents need not be the same and are listed in the Table. Notice the asymmetry of extensions in the connections from the CCIN neurons – the caudal bias in these extensions facilitates

Table 2. Synaptic connectivities in Ekeberg's [3] segmental oscillator. Only connections from the left side are tabulated; connections from the right are analogous. Positive weights denote excitatory synapses, negative weights denote inhibitory synapses. Brainstem connections are indicated by BS. The extension of connections to neighbouring segments (see text) are indicated by the $[r, c]$ annotations (r gives rostral extent, c gives caudal extent)

Connection	Weight	$[r, c]$	Connection	Weight	$[r, c]$
$\mathrm{EIN}_L \rightarrow \mathrm{EIN}_L$	0.4	$[2, 2]$	$\mathrm{CCIN}_L \rightarrow \mathrm{EIN}_R$	−2.0	$[1, 10]$
$\mathrm{EIN}_L \rightarrow \mathrm{CCIN}_L$	3.0	$[2, 2]$	$\mathrm{CCIN}_L \rightarrow \mathrm{CCIN}_R$	−2.0	$[1, 10]$
$\mathrm{EIN}_L \rightarrow \mathrm{LIN}_L$	13.0	$[5, 5]$	$\mathrm{CCIN}_L \rightarrow \mathrm{LIN}_R$	−1.0	$[1, 10]$
$\mathrm{EIN}_L \rightarrow \mathrm{MN}_L$	1.0	$[5, 5]$	$\mathrm{CCIN}_L \rightarrow \mathrm{MN}_R$	−2.0	$[5, 5]$
$\mathrm{LIN}_L \rightarrow \mathrm{CCIN}_L$	−1.0	$[5, 5]$	BS $\rightarrow$ EIN	2.0	—
			BS $\rightarrow$ CCIN	7.0	—
			BS $\rightarrow$ LIN	5.0	—
			BS $\rightarrow$ MN	5.0	—

the production of the travelling wave needed for swimming. The extensions presented here, taken from [3], are consistent with the known extents of the corresponding projections in the lamprey.

3.2 Behaviour of Ekeberg's Model

Ekeberg's segmental oscillator network, pictured in Fig. 1, produces alternating left-right patterns of activation when provided with constant excitation from the brainstem input. The frequency of the oscillations depends on the strength of the excitatory input, increasing with increasing excitation up to a point where the network saturates (all neural outputs on one side go to 1, and the other side outputs 0).

The oscillations are the result of the mutual inhibition of the CCIN neurons. Suppose that CCIN_L is active: it keeps the four right-hand-side neurons turned off, and is maintained in active state by the ipsilateral EIN. The LIN has a longer time constant and higher threshold than the CCIN so it is initially off. After a delay, which depends in part on the tonic brainstem activation, sufficient input turns the LIN neuron on and its output inhibits the ipsilateral CCIN. This releases the contralateral neurons, and the contralateral EIN begins to turn them on. As the contralateral CCIN activity increases it further inhibits the formerly active CCIN, and its ipsilateral partners, and activity switches to the opposite side of the network. A typical plot of the neural activation of the eight units in the segmental network is shown in Fig. 2.

We simulated Ekeberg's complete pattern generator network over the full range of excitation parameters for which it produces oscillations (i.e. does not saturate) [9]. It is able to produce a travelling wave of neural activity

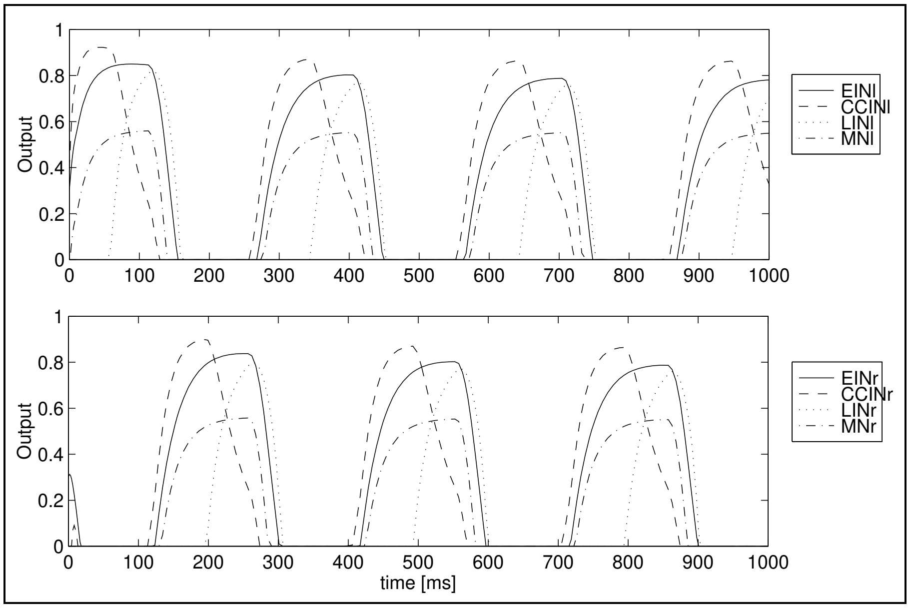

Fig. 2. Neural activation plotted against time for Ekeberg's segmental oscillator network with brainstem excitation 0.4 [arbitrary units]. Note the alternating lateral activity and the LIN-initiated switching from side to side

over a range of frequencies from 1.6–5.5 Hz, depending on global brainstem excitation, with inter-segmental phase lag controllable between 0.0–2.4% of a period as the extra rostral excitation varies. The frequency and phase lag are nearly independent. The inter-segmental phase lag is roughly constant over the spinal cord except in the ten most rostral and most caudal segments where it decreases toward zero. These results are consistent with those reported by Ekeberg [3].

3.3 The Lamprey's Body

Ekeberg also models the physical substrate on which the central pattern generator acts – the lamprey's body. The model is formulated in two dimensions[3] and comprises ten rigid-body links connected by hinge joints actuated by model muscles. Each link is an elliptic cylinder with its major axis vertical, the width of the links decreasing toward the tail of the body. Link masses are determined by assuming that the fish body is neutrally buoyant (that is, its density matches that of water). The forces exerted on the body by the surrounding water are assumed to be inertial (the effects of turbulence

[3] Ekeberg has also produced a three-dimensional body model [4] but we do not discuss it here.

and vorticity are neglected) and additive so that the effects of transverse and longitudinal motion through the water combine linearly.

The body model is implemented as a set of Newtonian equations of motion expressed in global Cartesian coordinates. Each link experiences inertial and water forces caused by its own motion, joint torques generated by spring-and-damper muscles attached across each joint, and constraint-preserving inner forces that maintain the links in the correct geometrical relationship. The equations of motion are integrated carefully, to ensure that the stiffness of the equations due to the inner forces does not cause numerical problems, using a standard numerical method. For details, consult [3].

Each joint is driven by a pair of muscles, whose spring constants are determined linearly by the input from their motoneurons. This allows the central pattern generator to control both the static torque applied to each joint – proportional to the difference between the motoneuron outputs for the left and right sides of the neural network – and the stiffness of the joint (its resistance to deflection) which is determined by the average of the left and right motoneuron outputs. The damper component of the muscle model is implemented in the standard way, by including a torque proportional to the deflection velocity of each joint which acts against the joint motion.

Ekeberg chooses realistic size, mass and inertial parameters for the lamprey body model, and uniform parameters for the muscle model. Details of the parameters can be found in [3] (but note that the mass and inertial parameters presented there appear to be miscalculated and a corrected set can be found in [8]).

3.4 Connecting the Central Pattern Generator to the Body

Ekeberg's paper [3] is not completely clear about the way the central pattern generator should be connected to the body model. Because the neural model has 100 segments, while the body has only 10, there are two obvious possibilities: each joint could be driven by a single segment of the full network, such segments being spaced equally among the 100 segmental oscillators [9]; or each joint could be driven using the average MN output of groups of segments spaced evenly along the full model [12]. In practice, these alternatives produce no qualitative difference in swimming performance, though they do give a quantitative difference with the second alternative producing rather slower swimming.

3.5 Behaviour of the Complete – Neural and Mechanical – Model

When the central pattern generator is coupled to the mechanical model and provided with suitable excitation, a propulsive mechanical wave can be produced. The amplitude of the body movements increase toward the tail, a characteristic of this kind of swimming produced by the mechanical properties of the body and its interaction with the water [3]. Ekeberg reports speeds of up to 0.73 ms^{-1} with oscillations at 4 Hz. A full simulation over the whole excitation parameter range, using corrected mechanical parameters as noted above, gives a top speed for straight-line swimming 0.5 ms^{-1} for a 5.5 Hz wave with 1.2% inter-segmental phase lag [9].

The complete model lamprey can also execute turns, if a short burst of asymmetric brainstem input is provided. The model lamprey turns toward the side with higher excitation since the higher excitation increases the muscle activation on that side and so bends the body more that way. A constant asymmetry in the brainstem excitation results in swimming in a circle [3].

3.6 Some Unanswered Questions

To summarise, Ekeberg's model demonstrates behaviour like the real lamprey swimming controller generated by a connectionist network whose topology is modelled on that observed in the fish, using neurons whose characteristics are matched to those found in the fish, and with connection strengths hand-tuned to match lamprey-like behaviour. These leaves a number of interesting questions open.

For instance, given that the model does not generate the full range of frequencies produced by the lamprey, is it possible to do better? Can a better set of parameters than Ekeberg's hand-tuned ones be found and, if so, how? Are other segmental oscillator arrangements possible and, if so, how does their performance compare with that of Ekeberg's biologically-derived model? What variation is possible in the inter-segmental connection arrangement while preserving the properties of the central pattern generator? How critically do the properties of the pattern generator network depend on the characteristics of the neurons used? Perhaps most interesting of all, how might one grow such a pattern generator – i.e. can we model the process of development as well as the final adult state of the system?

Answers to all but the last two of these questions are given in the remainder of this chapter.

4 Evolving Central Pattern Generators

To answer questions like those just raised, we need a method of varying the parameters of the connectionist model subject to constraints (for instance, changing the connection strengths while maintaining the topology) while monitoring the behaviour of the system. The problem is exacerbated by the complexity of the complete central pattern generator and body simulation, and by the fact that the exact desired behaviour of each part of the system is unknown. Fortunately, characteristics of likely-successful behaviour can be identified for each component, for instance the output of the segmental oscillator should alternate between the left and right side.

The tool we chose to make this investigation was the genetic algorithm, described in detail below, as this technique allows a search of a large parameter space while not requiring exact templates of desired behaviour for evaluation of performance. Note that we are not attempting to recapitulate the (natural) evolution of the lamprey's pattern generator here – that would be impossible given the current state of knowledge – but rather we employ an evolutionary algorithm as a search and optimisation tool.

4.1 A Technological Digression

A genetic algorithm (GA) is a stochastic population-based search technique which can be used to search very large search spaces. It is (loosely) derived from the operation of Darwinian evolution and works as follows. (For a much fuller treatment. consult [6].)

Solutions to the problem of interest are represented, typically as a vector of binary values or of structures, in a way that allows solutions to be derived systematically from the representation and allows the representation to be manipulated using genetic operators such as crossover and mutation (see below). The GA begins with a population of these representations, usually generated randomly though sometimes seeded with potential good solutions.

Each individual, referred to as a chromosome (by analogy with natural heritable material), in the population is evaluated as a solution to the problem of interest and is awarded a (usually) numerical fitness. A new population is then constructed by *selecting* parent chromosomes from the current population, applying *genetic operators* to those individuals to produce children – new chromosomes derived from the selected parents – which are evaluated as solutions and assigned a fitness, and finally by mixing members of the current population with children according to a *replacement* scheme. The new population is then used for a further cycle of the algorithm, each cycle being referred to as a *generation*.

There are many choices available to the user of a GA. The most fundamental is the choice of representation of the problem in the chromosome. That choice determines the genetic operators to use. In general, GAs use crossover, in which a pair of individuals are combined to produce one or two children by mixing together blocks of data from each individual parent, and mutation, in which elements of an individual are randomly perturbed to produce a representation of a new solution.

In the work described here, the chromosome representation is a vector of real numbers between zero and one representing either individual synaptic strengths (in section 4.2) or synaptic extensions (in section 4.3). The $[0, 1]$ range of each chromosome element is linearly mapped to give the appropriate parameter – weight or extent – during the decoding of the chromosome.

Further details of the exact encodings used are given in the following two sections.

The crossover operator, applied with a certain probability, takes a pair of chromosomes and cuts them at two uniform-randomly chosen places. The first part of one chromosome is then combined with the second part of the other and the tail part of the first to form a new solution. The complementary combination is also produced. (If crossover is not applied, the parents pass through unchanged.) Next, a mutation operator which, with a certain probability, adds a small uniform-random number to an element of the chromosome is applied independently to each element of each of the two children. Finally, a pruning operator may be applied, also probabilistically, setting an element of the chromosome to the value giving a zero connection strength. The pair of children thus produced are then evaluated.

Replacement is elitist – that is, the new evaluated children are sorted together with the current population and the worst individuals are dropped from the population. Selection of parents is based on rank, with the best individual having P chances of being chosen (where P is the population size), the worst having 1 chance of being chosen, and intermediate quality individuals having a chance depending on their position in the ranking.

To complete the description of the GA, we need a definition of the evaluation procedure. This procedure takes a chromosome and computes a *fitness* – in our case, as in most, a numerical measure of the quality of the individual as a solution to the problem. The fitness of a set of connection strengths is computed by placing those values into the segmental oscillator network or complete pattern generator and evaluating its behaviour. Good fitness accrues to a segmental network that can sustain oscillation over a wide range of frequencies in response to varied brainstem input, or to a complete pattern generator that is able to produce effective swimming. The detail of the fitness assessment is given in the sections below.

4.2 Evolving a Segmental Oscillator

We evolved neural circuits for swimming using a staged evolution approach. In a first stage, small networks representing segmental oscillators are evolved. These networks are evolved to be able to oscillate independently of each other, as observed in small sections of the lamprey's spinal cord. Inter-segmental connections are then evolved in a second stage to develop complete, 100-segment, swimming circuits. We here give a summary of these evolutions, a more detailed description can be found in [9].

Fitness function for the segmental oscillator The fitness function for the segmental oscillators was designed to reward some key characteristics observed in the segmental oscillators of the real lamprey. These are:

(a) 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.
(b) A frequency of oscillation which can be varied and which increases monotonically with the level of external excitation.
(c) A minimal set of connections.

Mathematically, the fitness function was a product of several factors corresponding to these desired characteristics, with each factor being comprised between 0.05 and 1.0 (1.0 being the best score). The range of frequencies of oscillation was, for instance, rewarded by carrying out a set of simulations with different levels of external excitation, and by measuring the minimum and maximum frequencies which could be obtained with a monotonic frequency-excitation relation. The ratio between maximum and minimum frequencies was then given a value between 0.05 and 1.0 by linear interpolation between a *bad* and a *good* boundary. The good boundary can be seen as the desired target of the evolution. By determining the total fitness using a product of these different factors, rather than a sum, we ensured that solutions which perform evenly in all aspects receive the highest fitness value.

Genetic encoding for the segmental oscillator We carried out two types of evolutions of segmental oscillators. In one set of evolutions, we developed oscillators which have the same connectivity as observed in the lamprey and used by Ekeberg in his model, while in the second set, we evolved oscillators without restrictions on the connectivity. The first set of evolutions can be seen as an example of how to use the GA to automatically instantiate parameters in a network of known connectivity (i.e. to use the GA to do the work Ekeberg did by hand), while the second set of evolutions is more exploratory and investigates whether alternative connectivities can lead to efficient swimming controllers.

In both cases, we used a simple one-to-one encoding of parameters of the neural network into the real number genes (between 0.0 and 1.0) of the corresponding chromosome. In order to reduce the search space, the number and type of neurons were fixed, and corresponded to those of Ekeberg's model. For the evolutions of controllers subject to the biological connectivity, a chromosome was composed of 13 genes encoding the 26 synaptic weights of the biological segmental oscillator (a left-right symmetry is assumed). For the evolutions of controllers with open connectivity, a chromosome was composed of 31 genes, of which 3 genes encoded whether the three types of interneurons are inhibitory or excitatory, and 28 genes encoded the synaptic weights of the network. In this case, the synaptic weights of all possible connections between the interneurons were encoded (i.e. not only those observed in the biological system).

Evolved segmental oscillator For each type of encoding, we carried out ten evolutions starting with random populations of 100 chromosomes. Evolutions were stopped after 500 generations, which was enough for interesting solutions to be created. Note that while it is relatively easy to design by hand a small oscillatory network, the difficulty here is to develop stable oscillators whose frequency can be varied by external excitation, and this over a large range.

While a detailed analysis of the results is beyond the scope of this chapter, several interesting observations can be made. For the evolutions with the biological connectivity, the main outcome of the evolutions is that the GA successfully found sets of synaptic weights which produce patterns of oscillations like those observed in the real lamprey. Interestingly, the evolved solutions are closer to biological data than Ekeberg's hand-coded network: the best oscillator covers a frequency range from 0.9 to 11.0 Hz which is almost twice the range of Ekeberg's model (1.6 to 5.5 Hz), and which is close to the frequencies observed in the real lamprey (from 0.25 to 10.0Hz). This therefore illustrates that a GA can not only be used to do automatically part of the modelling which is usually done by hand, but also to optimize the model for some specific characteristics.

The evolutions with open connectivity led to a variety of different oscillator architectures all capable of producing frequencies over a large range. One of the evolutions converged to an architecture very similar to the biological one, which therefore appears to correspond to a local maxima in the search space. A variety of other solutions were however found illustrating that the biological solution is not unique. Several evolutions converged to an almost identical configuration using only 4 interneurons for rhythmogenesis. Figs. 3 and 4 show the connectivity and patterns of oscillations of one of these oscillators.

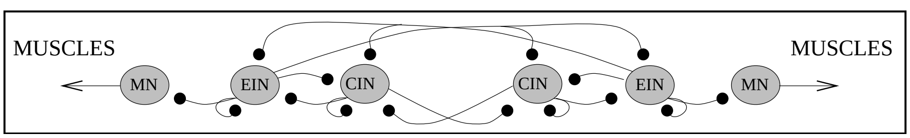

Fig. 3. Synaptic connectivity of an evolved segmental oscillator network

4.3 Evolving Complete Pattern Generators

For this stage, the task is to develop complete CPGs by evolving the coupling between 100 segmental oscillators. Oscillators are therefore chosen and copied 100 times. Coupling between oscillators is obtained by extending connections between neurons within one segment to corresponding neuron in neighbouring segments (a process called *synaptic spreading* [17]). We carried out evolutions based on Ekeberg's segmental oscillator, and on the best evolved oscillators with open connectivity.

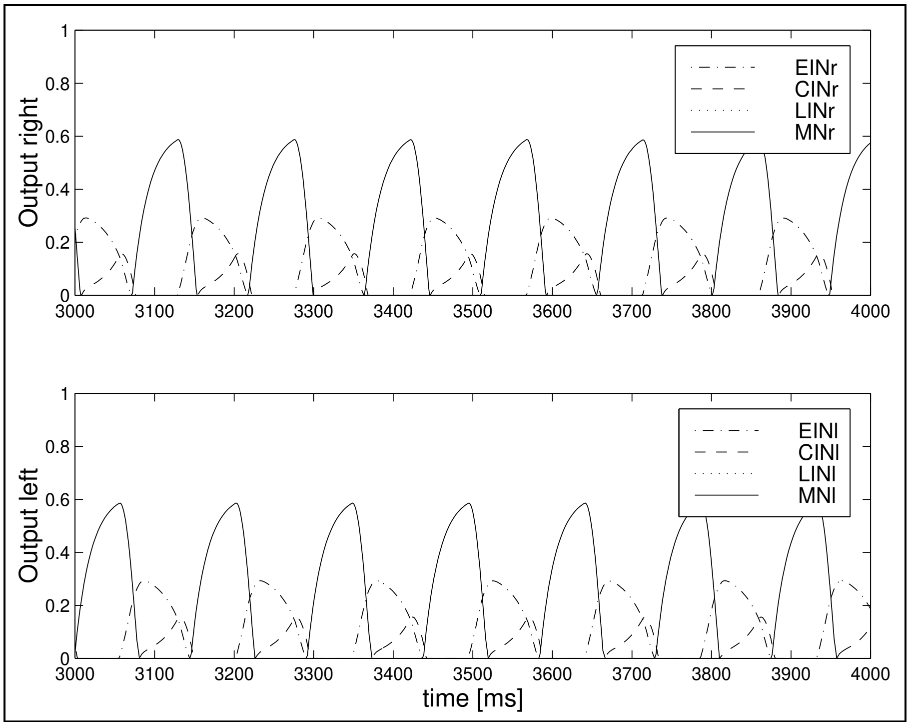

Fig. 4. An exmaple of the neural activation plotted against time for the evolved segmental oscillator network

Fitness function for the complete CPGs Multi-segmental controllers are evaluated for their capacity to control swimming in the mechanical simulation. The required features for the controllers are:

(a) generation of stable oscillations in the 100 segments with coordinated phase differences for the creation of traveling undulations of the body,
(b) ability to change the speed of swimming by changing either the frequency of oscillation or the wavelength of the undulation,
(c) 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.

The chromosomes are therefore tested over a large range of commands settings (variations of global and extra excitation) in order to determine the range of speeds which can be produced. Point c above was introduced first of all to reproduce the striking ability of the lamprey to swim over a whole range of frequencies while keeping the wavelength constant, but also to develop controllers with well defined control properties.

Genetic encoding for the complete CPGs A chromosome encodes the extent of the inter-segmental projection to neighbouring segments for each segmental connection. As these projection can be different for rostral (upward) and caudal (downward) directions, the number of genes is twice the number of segmental connections. A left-right symmetry is again assumed, as well as a symmetry along the segments of the spinal cord. The extents are integers which are rounded from the real number genes between 0 (no projection to neighbor segments) and a maximal extent of 12. The connection weights of the segmental networks are fixed except for a rescaling depending on the extension of the interconnection: the weight of a connection to a neuron is divided by the number of segments it receives input from.

Evolved complete CPGs We carried out two sets of evolutions using different segmental oscillators as template oscillators. In a first set of five evolutions, all template oscillators corresponded to Ekeberg's oscillator, while in a second set of ten evolutions, all used different oscillators, each of them corresponding to the best oscillators of the ten evolutions with open connectivity of the previous stage.

All evolutions converged to complete controllers which can produce stable swimming patterns over large speed ranges. Note that coupling oscillators in a stable manner is far from trivial, as coupling these types of non-linear oscillators often leads to unstable activity even when they have the same intrinsic frequency (as is the case here).

Fig. 5 shows the swimming gait produced by one of the evolved controllers. This swimming gait is generated by coordinated oscillation of the 100 segments comprising the CPG. Each segment oscillates as shown in Fig. 6. More caudal segments' oscillations are delayed relative to their rostral neighbours, as illustrated in Fig. 7.

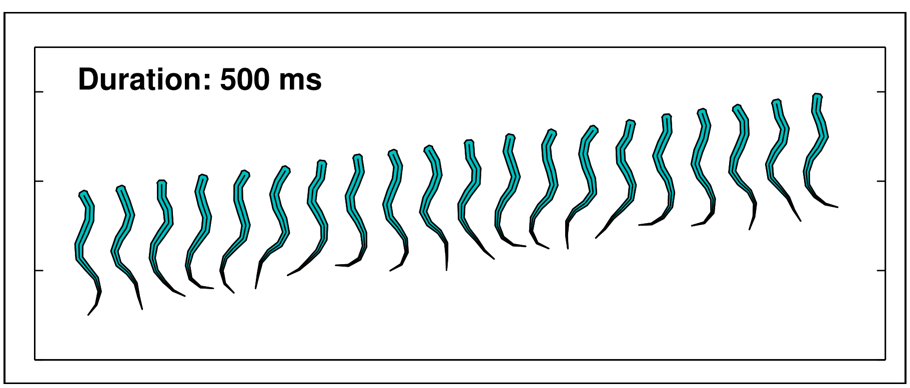

Fig. 5. Swimming gait produced by an evolved controller network oscillating at 4.8 Hz with intersegmental phase lag 1.1%, achieving a speed of 0.45 m/s

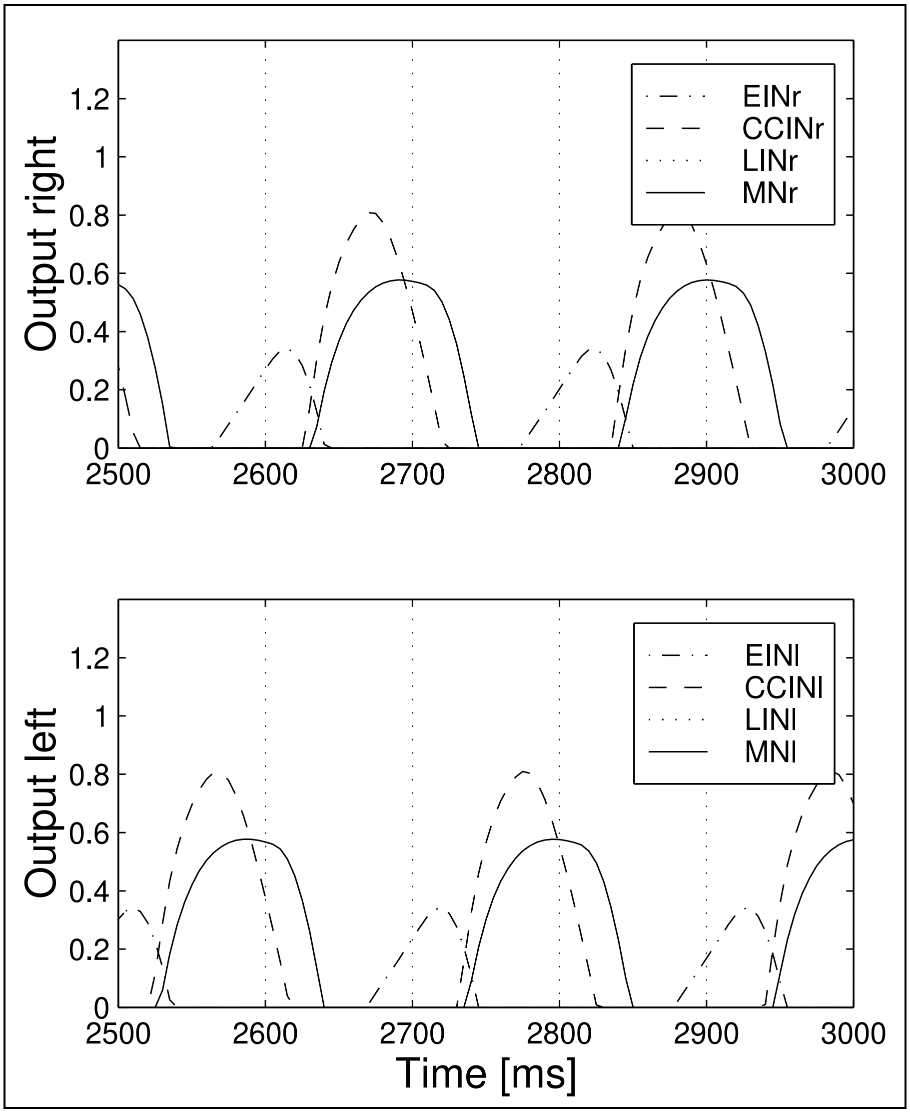

Fig. 6. Segmental oscillation producing the swimming gait of Fig. 5

In the case of the evolutions based on the biological segmental connectivity, these evolutions allowed us to investigate which types of inter-segmental couplings can produce the swimming patterns observed in the lamprey. As mentioned in Section 3.1, Ekeberg choose a simplified inter-segmental coupling compared to the most recent findings on the real animal. Interestingly, all evolutions with the biological segmental connectivity converged to quite similar types of inter-segmental couplings, which differed significantly from

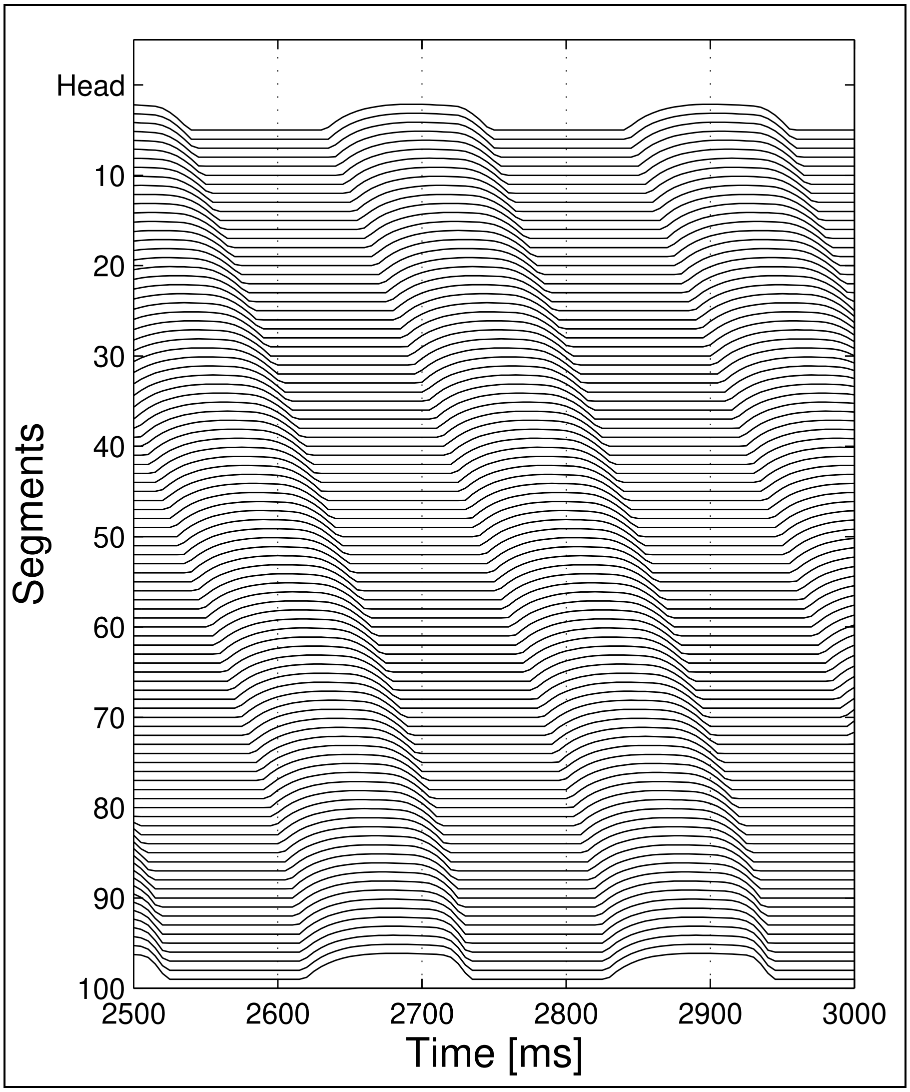

Fig. 7. Motor neuron output of the full CPG when producing the swimming gait of Fig. 5. Notice the progressive phase lag from head to tail, a travelling wave of neural excitation which induces a mechanical analogue in the body.

the one chosen by Ekeberg. We found that the evolved CPGs do not have a 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 traveling 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).

5 Back to the Body

The foregoing sections have demonstrated that it is possible to construct a variety of central pattern generator circuits that exhibit parameterisable behaviour. Changing the global brainstem excitation given to the pattern generator changes the frequency of oscillation while changing the extra excitation given to the first few rostral segments allows control of the inter-segmental phase lag. These two parameters make possible a range of steady swimming gaits when coupled to the body mechanical simulation.

However, a number of questions remain unanswered at this point. In this section we address two of them; the reader can undoubtedly think of others — there is plenty of possibility for further work!

First, consider that the brainstem signals used to test-drive the evolved pattern generators are constant and stable. Excitation conditions are set up at the start of, and endure throughout, each test. What will happen to the pattern generator if these control signals vary during a test? What if they vary with similar frequency to the pattern generator output? This kind of variation may be expected in a real fish swimming toward a moving target, for example, and section 5.1 below explores this situation.

Second, the pattern generators we have been discussing are 'optimised' by the genetic algorithm for the standard mechanical body simulation. However, bodies of both fish and robots are considerably more variable. Will the pattern generator work in other bodies? This question is interesting to roboticists and is addressed briefly in section 5.2.

5.1 Usability of the locomotor circuit

An important issue in locomotion control is the issue of pattern modulation. The rhythmic pattern generated in the spinal cord needs to be constantly modulated to allow the animal to adapt the speed and direction of locomotion to its needs in the environment. In short, the locomotor circuit must be "usable" by higher control centers.

Similarly to Ekeberg's model, the speed and direction of swimming of our evolved controllers can be modulated by varying the amount of excitation

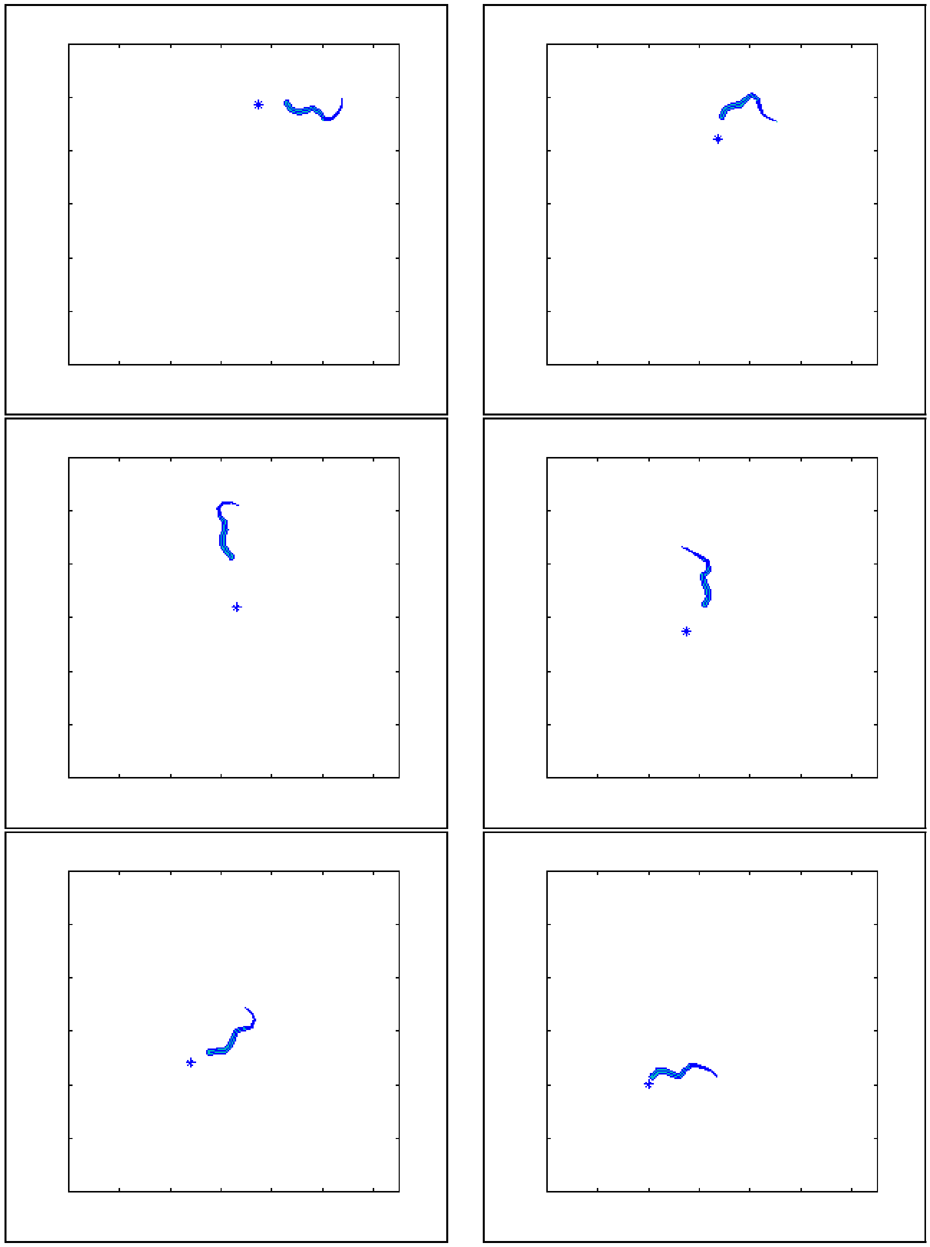

Fig. 8. Tracking a Randomly Moving Target: six frames from a tracking sequence showing the simulated lamprey chasing a target, drawn as an asterisk $*$.

applied to the network. Asymmetrical excitation between left and right sides of the spinal cord yields asymmetrical amplitudes of motoneuron signals. Short asymmetries can be used to change direction, while long asymmetries lead to swimming in a circle.

In a unpublished study, we showed that the swimming patterns are very robust against continuously changing input commands, and that the evolved CPGs can readily be used to track a randomly moving target in a two-dimensional space. The bearing of the target relative to the axis of the head was used to determine the left and right input signals (the higher the angle on one side, the more that side received excitation). Fig. 8 shows a sequence of six frames from an extended run in which the simulated lamprey tracks the randomly moving target, indicated by an asterisk $*$ in the figures.

From a control point of view, these varying input commands can be seen as perturbation to the system with a periodic (due to the head movement) and a stochastic (due to the random motion of the target) component. The evolved circuits were sufficiently robust to produce stable swimming gaits despite the perturbation.

5.2 Variations in Body Parameters

One interesting application of the ideas described herein is to robot control: the pattern generators constructed using the techniques presented above might be used to control a robotic body similar to the simulated body of the mechanical model. However, the real robotic body is unlikely to match the simulated body exactly (and, perhaps more seriously, the real physics is certain not to match the simulated physics, since various hydrodynamic forces are neglected in the mechanical simulation on the grounds that they are negligible in practice — which assumption may prove unfounded). It is thus interesting to inquire how tolerant the evolved controllers are of variation in the parameters of the simulated mechanical body.

Work by Or and Hallam [12] is a first step toward answering this question. In this study four pattern generators – three neural network and one comprising sine-wave generators with appropriate frequency and phase parameter settings – were tested using a set of scaled versions of the standard mechanical simulation. The physical parameters of the body were adjusted to be consistent with a scaling of the body length of between $0.7\times$ and $1.5\times$: the size parameters scale linearly with length, water forces as the square of length, volumes as the cube (so also the body mass, if neutral buoyancy is assumed), moments of inertia as the fifth power of length. Muscle forces are assumed to scale like body mass.

The four pattern generators used in the study were: Ekeberg's controller and two evolved controllers from [9], one using Ekeberg's intra-segmental connections and weights, the other using an evolved segmental network. The amplitude of the outputs of the sine-wave pattern generator was set to 0.8,

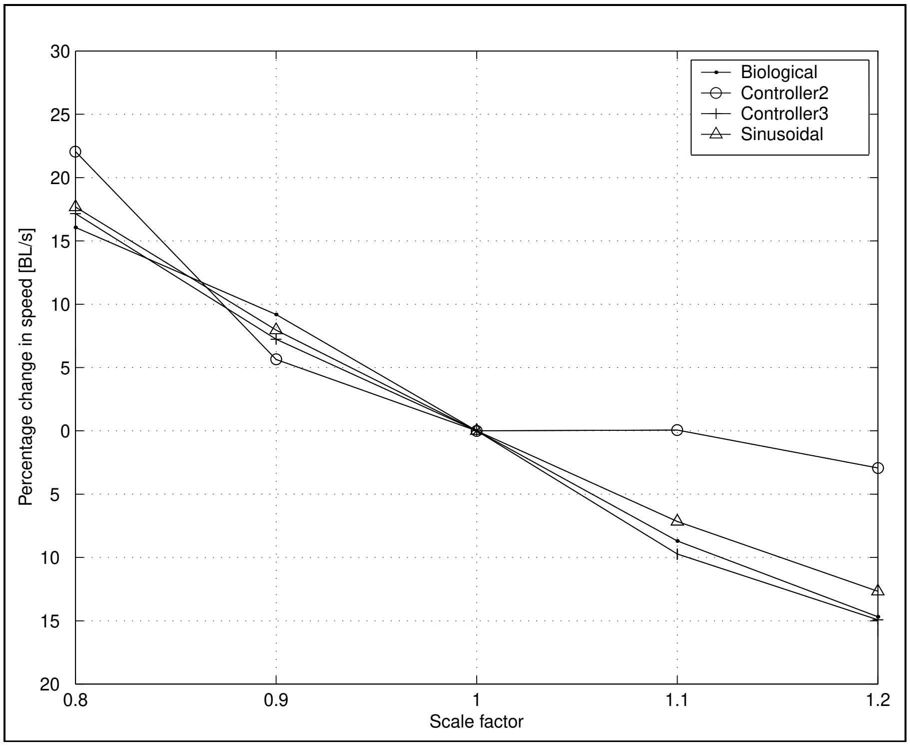

Fig. 9. Variation in maximum swimming speed, in body-lengths per second, with variation in body scale, plotted as a percentage change with respect to speed at nominal scale. The 'Biological' controller is Ekeberg's model, while Controller 2 and 3 are evolved by Ijspeert and colleagues. Controller 2 uses Ekeberg's intra-segmental organisation while Controller 3 uses an evolved intra-segmental circuit; both use evolved inter-segmental connectivity

somewhat larger than the average amplitude produced by the three network-based pattern generators.

In each test the maximum swimming speed of the body was recorded, by searching the space of reasonable pattern generator parameters to find the best set. Since the pattern generator can generate any swimming speed between zero and this maximum, measuring the range gives a straightforward indication of the performance of a controller.

Fig. 9 shows the performance of the four controllers over the range of scale from 0.8 to 1.2, i.e. a ±20% variation in body length. Forward speed is expressed in body-lengths per second rather than, say, metres per second, to normalise swimming speed for different sizes of fish, allowing a more natural comparison.)

The graph plots the percentage change in maximum speed relative to the top speed at nominal scale. All four pattern generators perform roughly similarly, with the maximum swimming speed decreasing relative to body length as the scale increases. Controller 2 has a much flatter profile for scales greater than nominal, showing that it is able to increase maximum swimming speed more closely to match the increasing body length. The variation in speed is not much greater than the variation in body size and all the controllers are able to generate effective swimming gaits in bodies across a range of scales from 0.8 to 1.2 (and beyond, see [12]).

6 Conclusion

The connectionist modelling approach we have followed, and illustrated, in this chapter is widely used, in part because if offers an attractive compromise between the more abstract mathematical treatments and the more detailed models of neurons and their circuitry. The former class of model capture the important features of a system but have to be relatively simple in order to be mathematically tractable. The latter class tend to bury the modeller in detail.

The main difficulty with constructing such models of neural systems is the choice of parameters. Ideally, the parameters selected shown correspond to those used in the neural system, but this can be difficult to determine. Patterns of synaptic connectivity and the associated strengths necessary for the connectionist models can be particularly hard to elucidate. In this context, the evolutionary algorithm technology displayed hear comes into its own. Parameter sets can be chosen and ‘optimised’ with respect to rather abstract descriptions of the desired behaviour of the system. For instance, “swim in a controllable manner in response to modelled tonic brainstem signals” summarises the criteria we have employed to explore the space of suitable parameters in Ekeberg’s model.

The results presented here demonstrate that Ekeberg’s original model is quite robust with respect to parameter variation – other similar segmental circuits and complete pattern generators, with equivalent or better performance according to criteria such as range of controllable oscillation or speed of swimming, are relatively easy to construct using the genetic algorithm.

As we have suggested in the foregoing sections, there are many further properties of the connectionist model of the lamprey’s central pattern generator to explore. Current work focusses on the use of the genetic algorithm to construct controllers robust to variations in body parameters – with a long-term aim of incorporating such controllers in real models of lamprey bodies – and on controllers that generate energy-efficient swimming behaviours, on the exploration of swimming and walking controllers for salamander bodies, and on developmental issues (how is it possible to grow a pattern generator of this type, while having it work at all stages of development?).

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