Central Pattern Generators: Optimisation and Application

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Abstract. This chapter addresses optimisation of a class of biological neural networks, called Central Pattern Generators (CPGs), with a view to providing autonomous, reactive control to otherwise non-adaptive operators. CPGs are self-contained neural circuits which govern rhythmic motor activities such as locomotion, breathing and digestion. Neurons in this system interact to produce rhythmic oscillations without requiring sensory or central input. These phasic firing patterns can be adaptively adjusted, through neuromodulation, and in response to fluctuations in the environment. Thus, CPGs provide autonomous, self-modulatory control and are an ideal candidate to evolve and utilise for practical engineering solutions. An empirical study is described which generates CPG controllers with a wider range of operation than their counterparts. This work is precursory to producing controllers for marine energy devices with similar locomotive properties. Neural circuits are evolved using genetic algorithm techniques. The lamprey CPG, responsible for swimming movements, forms the basis of evolution, and is optimised to operate with a wider range of frequencies and speeds. Results demonstrate that simpler versions of the CPG network can be generated, whilst outperforming the swimming capabilities of the original network [34].

1 Introduction

Rhythmic motor behaviour plays a major role in any living organism, producing actions such as the regular gait of walking, or the slithering snake's body as it bends, alternating from side-to-side, or even the coordinated limb movement of an eight-legged spider. These rhythmic patterns are also evident in non-locomotive behaviours such as swallowing, respiration and digestion.

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The continuous, repetitive and voluntary nature of this class of movement distinguishes it from others, such as involuntary (and instant) reflexes (blinking, pupil dilation), stimulus-level responses (orgasm, sneezing) which are triggered once a threshold is reached and direct voluntary control (such as stretching, grasping).

The actuation of rhythmic movements relies on a central pattern generator or CPG, which is a specialised circuit, characterised by its generation of oscillatory or alternating motor patterns. It produces these regular patterns of output endogenously (i.e. without rhythmic sensory or central input). With *in vivo* preparations, this pattern of activity performs what is termed *fictive* locomotion, where the motorneurons fire in such a way that if they were still attached to their muscles, movements would occur.

This chapter describes the underlying structure, behaviour and performance of CPG architectures in biology. It provides several examples of these neural circuits and the functions they drive. Artificial representations of CPGs and their areas of application are then covered. A specific model is presented in more detail with an empirical study of the lamprey's spinal CPG. This is followed by a discussion on how this network is regenerated using evolutionary techniques, to increase the range in which the simulated lamprey swims. Based on the theory of natural evolution, a genetic algorithm is used to evolve alternative CPG configurations. Measures of fitness which steer the evolutionary process are constructed to reduce connectivity and produce efficient swimmers which can operate with a larger range of frequencies and speeds. This forms an initial step in our overall aim to develop bio-inspired reactive controllers for a very challenging engineering task in the area of marine energy where a wider range of operation is essential. Network evolution to drive reactive control of wave energy converters is discussed in the final part of this chapter.

2 Central Pattern Generators and Neuromodulation

A CPG is a self-contained network where populations of neurons interact to produce phasic (periodic on and off cycles) temporal and spatial activity. CPGs produce these rhythmic motor patterns, even in isolation from motor and sensory feedback. This characteristic was recognised as early as 1911 by Graham-Brown, where basic stepping was produced in the absence of descending or afferent inputs to the isolated spinal cord of a cat [18]. This important concept and discovery of the CPG has shaped and driven research on the neuronal substrates of invertebrate and vertebrate motor systems, including observations on humans with spinal cord injuries [8].

CPGs vary in anatomy and physiology, but in general, two conditions classify this rhythmic generator: 1) that two or more processes interact, passing activity between them through sequential increase or decrease of activity, 2) the system returns repeatedly to its starting condition through this interaction. A self-sustaining pattern of behaviour is thus produced. These enable precise timings of motor commands which actuate muscles or processes that operate in a synchronised manner (i.e. contracting or stretching, off or on). The following are examples of functions which operate with rhythmic patterns of activity and their underlying CPG networks.

2.1 Locomotion

In the analysis and artificial reproduction of locomotive control, CPG research plays a major role [1, 38]. The primary function of locomotor-CPG networks is to provide oscillatory motor commands with precise timings to coordinate efficient movement of related joints and muscles. The first modern evidence of such a neural network was produced by Wilson in 1961. He isolated the locust nervous system and demonstrated that it produces rhythmic output resembling the insect's flight patterns [47]. Since then, evidence has arisen for the presence of intra-spinal CPG networks which drive and coordinate locomotion in many animals. For instance, Sqalli-Houssaini et. al induce rhythmic locomotor-like activity by adding an excitatory amino acid receptor agonist (N-methyl-D,L-aspartate, NMA) to *in vitro* spinal cord preparations of neonatal rats. They demonstrate that even at birth, oscillatory patterns of activity are produced by these spinal neural networks with connections already established between peripheral sensory afferents and the CPG [45]. There is also evidence of this type of network in frog embryos [39]. What is interesting is that from a very early stage of development CPG networks are already functioning, interactive units of control.

Even though, the actual architecture of the CPG network is seldom observable *in vivo*, important aspects of their structure can be inferred by stimulation and observation of reactionary components. Many studies have been conducted with decerebrate cats (e.g. [18, 43]), all demonstrating the same principle rhythmic patterns of behaviour and control of different gaits, such as walking, trotting and galloping through altered levels of stimulation [43]. Studies have even found the presence of a human locomotive CPG, which is extremely robust and highly adaptable. The clearest evidence comes from Calancie et al. who witnessed step-like movements in a male subject who suffered a cervical spinal cord injury. Initially, he suffered total paralysis below the neck, but eventually regained some movement in his lower limbs. Still unable to support his own weight, when the subject lay down with extended hips, his lower extremities underwent step-like movements. *The movements (i) involved alternating flexion and extension of his hips, knees, and ankles; (ii) were smooth and rhythmic; (iii) were forceful enough that the subject soon became uncomfortable due to excessive muscle 'tightness' and an elevated body temperature; and (iv) could not be stopped by voluntary effort [8].*

A detailed example of a locomotor network is given in section 5 as it forms the basis of our wider research. This system is the spinal neural network of the lamprey, responsible for rhythmic swimming patterns by alternating motion from one side of its body to the other.

2.2 Respiration Pattern Generators

Breathing is a non-locomotive function governed by a CPG in many species. The amphibian brainstem/spinal cord preparation has been widely used to examine the mechanisms of respiratory rhythm generation (e.g. [46, 5]. It is a good example of a respiratory CPG, especially as there is evidence to suggest that the mechanisms

which regulate rhythmogenesis and respiratory motor output in amphibians, share many common features with mammals [15].

Larval amphibians accomplish gas exchange mainly through rhythmic ventilation of the gills, but as they develop into mature frogs, lung ventilation assumes a greater role in gas exchange [7]. This is a most interesting neural network as it performs a transitional function, from an aquatic to a terrestrial respiratory system, involving a shift from gill to lung ventilation [7, 46, 15]. Worthwhile comparisons can be made because both the tadpole and adult frog can be studied using identical experimental techniques at all stages of development.

A study by Broch, et al. isolated brainstem preparations of larval (tadpole) and adult bullfrogs. Respiratory motor output from each CPG, measured as neural activity from cranial nerve roots, was associated with *fictive* gill ventilation and lung ventilation in the tadpole and with only lung ventilation in the adult [5].

With controlled conditions, typical neural activity is recorded from tadpole and adult preparations (shown in fig.1 (reproduced from [5]). Bursts of activity are clearly distinguishable between the two generations. Tadpole preparations demonstrate *fictive* gill bursts of low amplitude and high frequency while the bullfrog

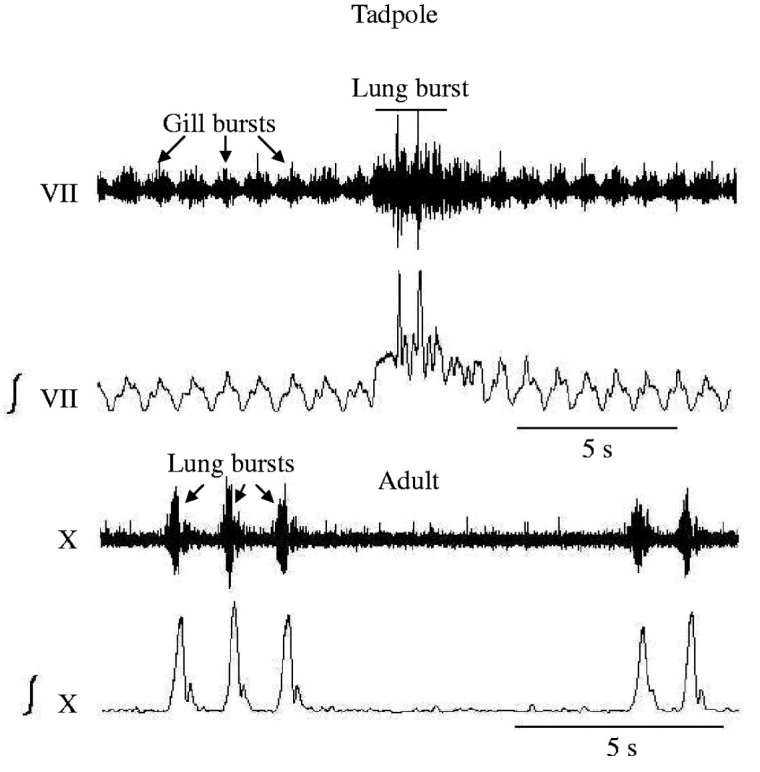


Fig. 1 Representative recordings from [5] of tadpole and bullfrog (*Rana catesbeiana*) respiratory brainstem preparations. Raw and integrated ($\int$) gill bursts and a lung burst are shown in the first two neural recordings and lung bursts of activity in the lower two.

tests present single (episodic) neural bursts of activity (high amplitude, low frequency) indicative of lung-related activity (see [46, 37]). Their results suggest that both mechanisms are dependent upon conventional chloride-mediated synaptic inhibition and that there may be a developmental change in the fundamental process driving lung ventilation in amphibians [5].

2.3 Heartbeat CPGs

Network-based rhythmicity is shown clearly by the leech heartbeat CPG. Two tubes pump blood through the leech's circulatory system, each alternatively constricting and relaxing. The CPG consists of eight pairs of interneurons. Of these, five pairs regulate the timing and rhythm of the heartbeat; they can reset and entrain the system, while the remaining pairs of interneurons coordinate motorneuron activity.

In fig. 2b, each heart neuron (HN) is indexed according to the extent along which its soma lies on the side of the leech's body. For instance, HN(L,2) is the neuron on the left hand side at segment two along the body of the leech. Notice that burst activity of neurons HN(R,4) and HN(L,4) (fig. 2b) fire out of phase with each other.

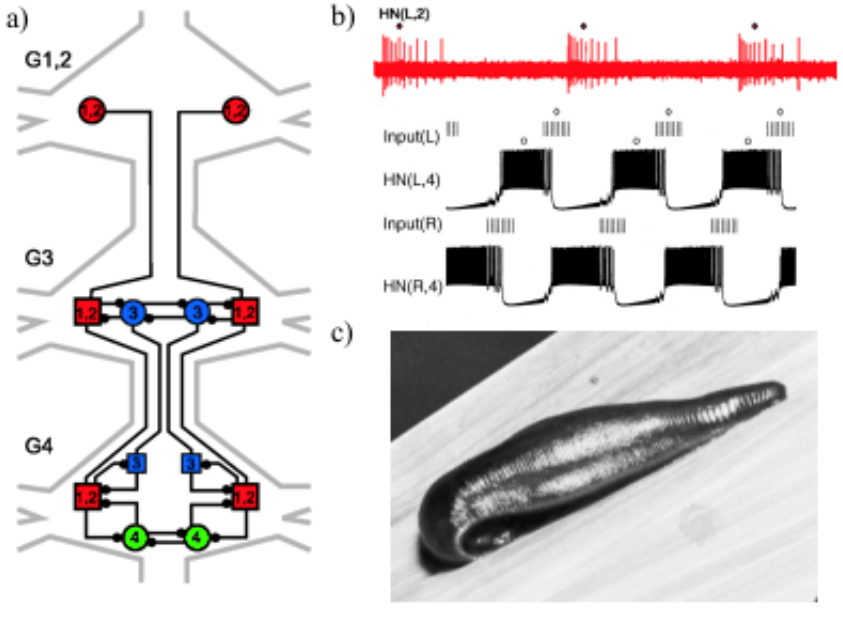


Fig. 2 a) The CPG network modulating heartbeat regulation in the leech (reproduced from [27]). Open circles represent cell bodies, open squares are sites of spike initiation and small filled circles represent inhibitory synapses. b) Neural recordings from some interneurons (HN(L,2) from [27] and HN(L,4), HN(R,4) from [21] c) the intact medicinal leech, *hirudo medicinalis*.

This is the kind of behaviour that produces antiphase patterns between two bilateral functions (inhaling or exhaling). Bursts of activity of each heart neuron also demonstrate the typical active and inactive cycles, which govern rhythmic muscle movement.

2.4 Swallowing Pattern Generators

A final example is the CPG responsible for swallowing patterns of activity. Swallowing involves the coordinated contraction of more than 25 pairs of muscles in the larynx, oesophagus and oropharynx. This complex interaction depends on a CPG located in the medulla oblongata, which involves several brain stem motor nuclei and two main groups of interneurons: a dorsal swallowing group (DSG) and a ventral swallowing group (VSG). Neurons in the DSG generate the swallowing pattern, while those in the VSG distribute commands to the various motorneuronal pools [26]. The swallowing CPG is an interesting one because of its flexibility. Some of its neurons can belong to several CPGs (e.g. the swallowing and respiratory control networks) and thus perform multifunctional roles [10].

2.5 Neuromodulation

Organisms must adapt their behaviour to meet the needs of their internal and external environments. As well as governing centrally-generated base rhythms, CPGs can be modulated to produce several different physical actions depending on the immediate needs of the animal. This family of different motor outputs results from internal and external innervation. Internally, neurotransmitters act on the CPG system to produce appropriate changes in its activity. Evidence suggests that related, but distinct functions can be performed dependant upon the level and type of neurotransmitter released. For example, in a type of sea slug called the *Tritonia diomedea* (fig. 3), a CPG modulates escape swimming, reflexive withdrawal and crawling whereby one function is unaffected by neuromodulation of another. Reflexive withdrawal is actuated in response to weak sensory input, escape swimming with strong sensory input [35] and crawling occurs after escape swimming has ceased. Dorsal swim interneurons (DSIs) within the pattern generator release serotonin to convert to swim mode, while the application of serotonergic antagonists prevents the swim pattern.

The ability to rapidly convert from one mode to another is a fascinating mechanism of CPG networks. Feedback from the environment cause chemical reactions which in turn enable the neural system to respond and change its mode or rate of behaviour. This type of self-regulatory control has gained much interest in the Artificial Intelligence community, particular in the area of robotics where autonomy is crucial for developing responsive systems.

3 Artificial Central Pattern Generators

Although CPGs are generally discussed in relation to biological entities, they can also be replicated artificially for robotic applications [36, 1, 38]. The only requirement is that they produce continuous rhythms of behaviour after an initial stimulus. Examples of artificial neural networks (ANNs) based on CPGs include biophysical models, connectionist models and systems of coupled oscillators. Biophysical models are detailed depictions incorporating chemical properties of individual neurons in the system such as ion pumps and channels (e.g. [20]). They tend to closely resemble actual biological networks. Connectionist models comprise networks of simplified neuron units (e.g. [12]). These networks demonstrate the typical activity of the system using less realistic models of neurons. A detailed example is provided in section 5 where Ekeberg's connectionist network of the lamprey CPG is detailed. These representations demonstrate that complicated neuronal mechanisms are not necessary to produce oscillatory patterns and that modelling connectivity itself is sufficient. Finally, at the most abstract level, coupled oscillator networks

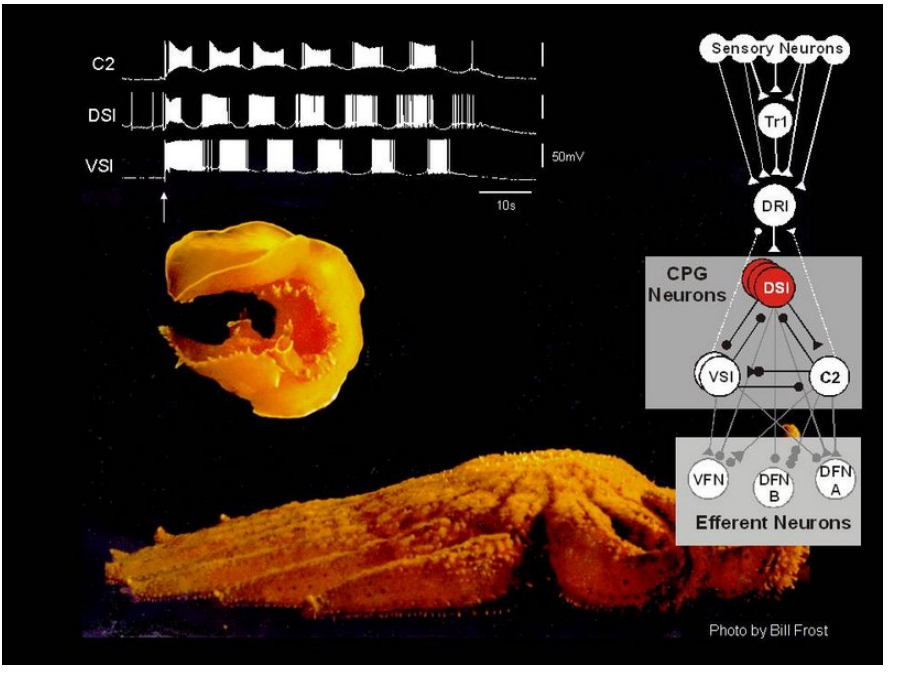


Fig. 3 The sea slug *Tritonia Diomedea* escaping from a sea star, *Pycnopodia*. The top of the diagram shows simultaneous intracellular electrophysiological recordings taken from an isolated brain from the three central pattern generator neurons: C2, DSI and VSI. A body wall nerve was stimulated at the arrow, producing oscillatory discharges with activity alternating between DSI and VSI neuron groups. These result in dorsal and ventral body flexions indicative of escape type swimming. The right hand side displays the CPG circuit from sensory neurons to efferent output. Image reproduced from [28].

model only the behaviour and dynamics of neural populations. They focus on properties of the entire network rather than just individual neurons or sets of neurons to produce phase relations. For example, see [25] where coupled nonlinear oscillators are used to construct a salamander-type robot with a CPG for its body coupled with limb CPGs to enable swimming in water and a trotting gait on land.

Typically, ANNs, inspired by biology and its architecture, form the basis for autonomous control in numerous applications [4, 42, 29]. Such technology is developed to provide a degree of intelligent control to an otherwise non-adaptive operator. For example, sensory robots can navigate and explore inhospitable areas such as the oceans [2] and space [14, 44]. Although they behave in a complex manner, they are designed according to simple control principles from biological exemplars such as stick insects and lobsters.

Unlike conventional approaches, these biomimetic systems are not reliant upon error-prone and expensive reprogramming or fine-tuning by the operator. As a result, the engineered solutions are often more efficient, productive and independent, whilst less labour and time intensive.

Optimum performance of neural circuitry can be generated with evolutionary techniques such as genetic algorithms. However, despite their ability to find superior solutions, evolutionary techniques are not frequently deployed to increase the performance of CPGs (with the exception of [24, 32, 33]). Instead, mainly in the robotics domain, they are used to computationally calculate parameters of neural controllers for locomotion such as biped walking [41], hexapod limb coordination [3] and *anguiliform* swimming [23] where manual, intelligent configuration is virtually impossible. The motivation to design better artificial intelligence (AI) systems for real-world engineering problems underpins the work of this research, and ultimately uses genetic algorithms to generate task-specific, optimised CPG controllers for wave energy devices. As with most AI solutions, inspiration is provided by models of real biological networks and these form the basis of evolution.

4 Optimisation with Evolutionary Algorithms

Evolutionary algorithms (EAs) are search and optimisation techniques for finding optimal solutions to a given problem. They include methods such as:

1. Particle Swarm Optimisation (PSO) [30] which is based on the flocking behaviour of birds (or swarming behaviour of bees).
2. Ant Colony Optimisation (ACO) [11] based on how ants leave pheromone trails along the shortest route to food. These trails diffuse with time to enable newer, shorter routes to dominate.
3. Estimation of Distribution Algorithms (EDAs) [31] which determine fit solutions according to probabilities of where good solutions lie in the solution space.
4. Genetic Algorithms (GAs), based on survival of the fittest mechanisms in nature where good parent solutions are paired to produce child solutions which are tweaked and then evaluated.

Each technique may differ but their overall aim is to find optimal solutions. Of these methods, the genetic algorithm is the most commonly used.

Inspired by Darwin's theory of natural selection and genetics, a Genetic Algorithm (GA) [16, 17, 13] computationally encodes candidate solutions as chromosomes, within which genes represent evolvable elements. The search is directed towards better solutions by the careful construction of an evaluation function. Individuals that score well are more likely to survive and be chosen for the basis of subsequent generations.

Evolution typically starts with a randomly generated population of individuals, covering the entire solution space (although sometimes solutions can be "seeded"). It cycles through several generations, evaluating the fitness of each individual in the population. Three operations are applied each generation, which are selection, variation and elimination. *Selection* involves choosing pairs of parent chromosomes, based on their fitness ranking. Generally, fitter individuals have a greater chance of being selected depending on the level of elitism adopted. *Varying* some of the genes of some chosen parents is the next stage in the GA process. This results in new child candidate solutions which are evaluated in the subsequent generation. It is considered that children will possess good quality genes from their parents and with some tweaking, may result in better fitness. The level of genetic modification and number of cells to vary can be stipulated with probability ratios. Finally, *elimination* involves rejecting the worst solutions, being replaced by higher ranked new candidates to maintain a consistent overall population size.

If well constructed, this evolutionary approach is resistant to problems of local minima that beset other algorithms. Ideally, a good combination of exploration and honing is required. At the appropriate level of search, the GA should converge to find optimal solutions. Furthermore, it is a common and efficient choice for optimisation and exploring the space spanned by a model. For these reasons, this tool is used to re-evolve alternative, wider functioning and more efficient swimming CPGs based on an invertebrate called the lamprey.

5 Modelling the Lamprey's CPG Network, Musculature and Environment

The lamprey (shown in fig. 4a) is an eel-like fish which propels itself by propagating an undulatory wave from its head to its tail. A CPG network (schematically modelled in fig. 4b), along its spine, governs this swimming module by causing rhythmic activity of motorneurons. These actuate muscles which cause motion to alternate between the two sides of the fish's body.

This vertebrate's CPG has been mapped thoroughly after careful analysis and innervation of reactionary components [19] and modelled artificially [12]. This has been possible because the intact spinal cord can survive *in vitro* for several days after being removed, because it is a relatively simple network, with few neurons, and it can be stimulated to produce the *fictive* swimming (without tonic input) motion indicative of a CPG.

a)

b)

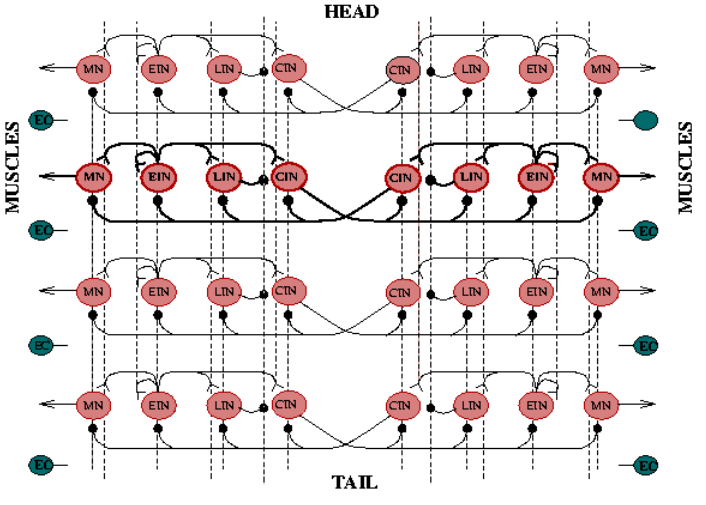


Fig. 4 a) the lamprey, a vertebrate belonging to the family *Petromyzontiformes*; b) the connectionist model of the lamprey's spinal CPG. Excitatory connections are shown as closed circles and inhibitory input as open forks.

Several copies of an oscillatory neural circuit (one is highlighted amongst the four shown in fig. 4b) are interconnected along the fish's spine. On each side of a single network there are four types of neuron governing rhythmic patterns as follows:

1. On the dominantly active side, the excitatory interneuron (EIN) group excites neurons on its side (ipsilaterally). Meanwhile, contralateral inhibitory interneurons (CINs) inhibit all cells on the opposite side (contralaterally). This results in the ipsilateral motorneuron (MN) activating the muscles.
2. After a short delay, a burst terminating mechanism causes control to switch sides. Burst termination is caused by the lateral inhibitory interneurons (LINs) becoming active later in the cycle, which suppresses the active CIN, relinquishing control from one side and building it up on the other.

This ensures that only one side is active at a time, with periodic transfer of control between sides. This behaviour continues while the segment receives base excitation from the brainstem.

Tonic (i.e. non-oscillating) signals (global excitation) from the brainstem (or from neurotransmitters when *in vitro*) regulate the frequency of oscillation. This principle of control is reported in [43], where different levels of stimulation on a decerebrate cat's brainstem results in walking, trotting or galloping. In the lamprey, oscillation frequency and speed of swimming can be adjusted by adding neurotransmitter agonists such as amino acids [9] or L-Dopa [40]. A further tonic input, referred to as extra excitation, is applied to the CPG's headmost segments to invoke a phase lag along the length of the lamprey's body and this causes forward motion. This is achieved *in vitro* by applying a greater concentration of neurotransmitter to the rostral section of the network. For clarity, these tonic inputs are not shown in fig. 4b.

Finally, edge cells (ECs) seen in the schematic (fig. 4b), are external sensors, which inhibit contrateral activity and excite ipsilateral activity. They provide feedback to the circuit from external forces, and invoke adjustments in activity, which maintain straight line swimming.

The lamprey's CPG network, described here, can be reduced to a simplified connectionist model. Neurons are non-spiking and belong to a population of similarly functioning nerve cells. The CPG receives delayed excitatory and inhibitory input and its output is calculated from first order differential equations:

$$\dot{\xi}_+ = \frac{1}{\tau_D}\Big(\sum_{i\varepsilon\Psi_+} u_i w_i - \xi_+\Big), \tag{1}$$

$$\dot{\xi}_- = \frac{1}{\tau_D}\Big(\sum_{i\varepsilon\Psi_-} u_i w_i - \xi_-\Big), \tag{2}$$

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

$$u = max(0, 1 - \exp\{(\Theta - \xi_+)\Gamma\} - \xi_- - \mu\vartheta) \tag{4}$$

In this set of equations, output u represents the mean firing frequency of each neuron population. A time delay (τ_D) is applied to summed excitatory (ξ_+) and inhibitory (ξ_-) inputs, Ψ_+ and Ψ_- represent groups of presynaptic inputs (excitatory and inhibitory respectively) and w_i is the weight associated with each input (eqns. 1-2). The term u_i denotes inputs received from neurons within the single network and from neurons of connected segments, whereas u refers to output of a single neuron. A transfer function (eqn. 4) provides saturation for high levels of excitatory input. A leak is included as delayed negative feedback (eqn. 3) and is subject to a time delay (τ_A). The parameters threshold (Θ), gain (Γ) and adaptation rate (μ) in eqn. 4 are tuned to match observed characteristics in some real neurons (see [12]).

Assymmetric initialisation of these equations leads to out-of-phase bursts of activity and involves setting $\xi_+(0)$=1, $\xi_-(0)$=0 for all left neurons and $\xi_+(0)$=0, $\xi_-(0)$=0 for all right neurons. This enables calculation of the initial output value(s) (u) which are used in subsequent differentiations. Weights, neural parameters and

time delay values of the biological model are shown in table 2, section 6.3, originating from [12].

Individual CPG networks are coupled to their neighbours via interneural connections towards the head (rostrally) and tail (caudally). These are depicted as vertical dotted lines in fig. 4b. Interconnections are important as they coordinate longitudinal movement by generating a time delay between successive CPG units. Phase lags are 1% of the period of oscillation and so a single wavelength can be maintained along the length of the body independent of swimming velocity.

Details of intersegmental connectivity in the real lamprey remain unknown, thus, in the original model Ekeberg [12] applied symmetrical connections in both directions. He achieves this by dividing each synaptic weight value by the number of CPG units it is linked to. Since neurons at each end of the complete CPG have fewer afferent connections, their synaptic weights are calibrated accordingly.

A complete simulated CPG interacts with a model of its body in water to demonstrate the expected *anguiliform* swimming behaviour [12, 24, 34]. The mechanical body comprises ten rigid links, each 30mm long, and corresponding to ten neural segments. Their movement is constrained, forcing them to stay connected, by joints with one degree of freedom. Width (generally 30mm) and mass of the lamprey decrease at the caudal end (i.e. the tail narrows). As in Ijspeert's model [24], mass and inertia of each link is calculated by assuming that the density of the lamprey is constant and equal to the surrounding water. Muscles connecting each link are modelled as a combination of springs and dampers. The forces acting upon each link are:

1. *Water forces* apply both horizontal and vertical pressure to the body. These depend on the speed of the body relative to the water and in the model they can be reasonably approximated by considering the water as stationary and applying a 3D water force vector on each link.
2. *Inner forces* exert pressure from neighbouring units. These joint constraints ensure links remain connected together at all times.
3. Muscle *torque forces* prevent links from bending in both directions at once. A linear relationship can be considered to exist between motorneuron activity, these forces and resulting muscular spring constants. Torque forces function as feedback from the neural CPG to the mechanical model. This feedback loop is completed with stretch sensitive edge cells providing information about the local curvature of muscles (assumed to be equal to the length of the body) to the CPG.

The entire lamprey swimming model was first defined in [12], and refined in [32, 33, 34] to more realistically fit physical data. It characterises the biological lamprey's swimming network with some accuracy [12], provides a tool for further exploration of network connectivity and activity (e.g. [34]) and offers potential for developing systems for more complex control. Achieving this type of unmanaged, responsive control in unpredictable conditions is a major challenge in engineering. Such problems can be resolved through CPG architecture coupled with the power and speed of evolutionary computing. The flexibility of the CPG network parameters and swimming capabilities are explored further with the aim to develop a solution in the area of marine energy (discussed in section 7). An initial goal towards this

solution is to develop CPGs capable of swimming in wider operative ranges. To achieve this, both the neural CPG and mechanical model of the network interacting in water are modelled (as described in section 5) and then further enhanced with genetic algorithms.

6 SuperLamprey Controllers: Optimised to Increase Swim Ranges

In order to remodel the circuitry for a new and complex control task, the flexibility of the lamprey CPG requires further exploration. Detailed analyses of candidate biological neural systems are essential and must explore whether nature's evolved configurations are unique, whether simpler versions perform effectively, and whether their operation range can be optimised for similar mechanical engineering tasks.

Two GA processes are implemented to enhance the capabilities of the simulated lamprey CPG: the first evolves synaptic weights and neural parameters of an independent neural module and the second generates interconnections between the best solutions (of the first phase) to produce complete multi-segment controllers. The goal of the first GA is to generate a single rhythmic oscillator [32] which operates over a wider range and is less complex, the latter property is important for eventual silicon reproduction. The second GA takes improved CPG units and determines longitudinal connections between neighbouring segments, with optimum performance signified by their capacity to control swimming at different speeds, oscillation frequencies and phase lags between segments.

The decision to implement the evolutionary process in two stages is for the following reasons: (1) computational efficiency - invoking the GA in one process would result in the assessment of far fewer candidates yet over a much longer period, wasting valuable resources, (2) to avoid lengthy testing of linked controllers which have already failed to oscillate in isolation, (3) reducing the problem into subgoals is a widely used and accepted method of developing plausible solutions, (4) each network component (single-segment oscillators) must function, even in isolation [12, 32, 33] and our approach guarantees this. The condition of isolated segments operating independently is also imperative for our engineering solution if continued operation is to be maintained even when part of the system fails.

A random initial population is generated for each experiment of an evolutionary process. They loop through the standard operations of selection, variation and rejection, each generation. Selection involves a fixed number of parents being chosen according to rankbased probability. An elitist procedure is adopted, selecting the fittest individuals of each generation to create offspring. Two-point crossover, mutation and pruning (for isolated CPGs) are applied to vary candidates. Finally, the worst solutions (denoted by their fitness ranking) are rejected, being replaced by higher ranked new solutions. Parameters of both GA procedures are outlined in table 1.

Probability rates and ranges in table 1 describe the degree to which chromosomes are altered. For example, crossover (where substrings of paired parent chromosomes

Table 1 Genetic evolution parameters for generating single rhythmic controller solutions and complete, multilinked swim modules

	Unitary CPG (GA1)	Multilinked CPG (GA2)
population size:	100	60
number of children:	30	18
crossover probability:	0.5	0.5
mutation probability:	0.4	0.4
mutation range	0.2	0.2
pruning probability	0.1	-
pruning range	1.0	-
number of generations	500	50

are swapped) occurs with 50% chance. Pruning is a non-standard GA procedure, where every connection is considered independently for removal (setting it to 0) with a probability of 10%. This is to explore solutions with fewer connections. Of course, their calculated fitness determines the success of this arbitrary removal of connections on a solution-by-solution basis. In addition to this arbitrary pruning through the lifetime of the GA, weak connections of the final population which do not affect neural activity are eliminated through a final prune. This is applied by setting any weight below 0.1 to 0, provided that doing so does not diminish this individual's fitness value. If the pruned candidate is inferior, the original value is reinstated. This procedure is repeated with decrements of 0.02 until all ineffectual or weak connections are eliminated.

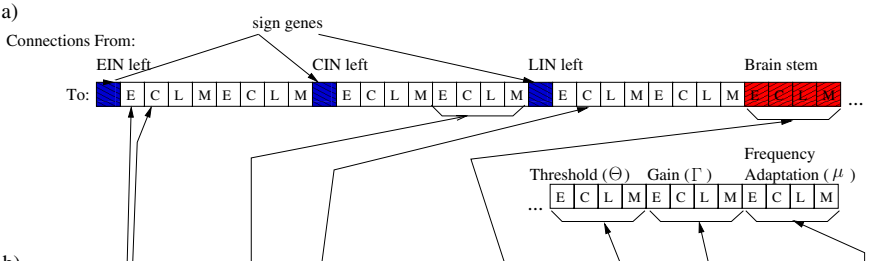
The properties in table 1 are held consistent with [24], to ensure confounds are not introduced and because they generate satisfactory results within a reasonable process time. The following sections outline the distinct characteristics of each GA, including their genetic composition and fitness criteria.

6.1 GA1 - Evolving Independent CPG Oscillators

The primary GA optimises independent lamprey CPGs, seeking solutions with improved performance ranges and low-level system complexity. Ekeberg's artificial network [12] featured hand-tuned network values, developed through measurement, trial and error. Ijspeert [24] used a genetic algorithm to evolve synaptic inputs. In my work [34], these are generated together with neuron-specific parameters (threshold, gain and adaptation rate) that describe the dynamics of the model neurons, exploring their diversity, while testing the true flexibility of the modelled CPG. However, the functional form and circuit structure of Ekeberg's original model is maintained to ensure consistency with the underlying biology.

A real value GA is used, comprising decimal numbers rather than traditional binary digits. Individual solutions are encoded as fixed length strings of 43 genes. Each gene corresponds directly to one evolvable parameter of the neural configuration as shown in fig. 5.

a)



b) Table of synaptic weight values

from: / to:	EINl	CINl	LINl	EINr	CINr	LINr	Brain Stem	Θ	Γ	μ
EINl	0.4				−2.0		2.0	−0.2	1.8	0.3
CINl	3.0		−1.0		−2.0		7.0	0.5	1.0	0.3
LINl	13.0				−1.0		5.0	8.0	0.5	0.0
MNl	1.0				−2.0		5.0	0.1	0.3	0.0
EINr		−2.0		0.4			2.0	−0.2	1.8	0.3
CINr		−2.0		3.0		−1.0	7.0	0.5	1.0	0.3
LINr		−1.0		13.0			5.0	8.0	0.5	0.0
MNr		−2.0		1.0			5.0	0.1	0.3	0.0

Fig. 5 a) An example chromosome solution for the GA evolving a single oscillating network. b) Table showing values corresponding to each evolved gene in the chromosome.

Fig. 5 visually depicts the structure of each solution chromosome with corresponding gene values relating to weights within the CPG (shown in the table of fig. 5b). Each chromosome is a vector of values representing: synaptic connections from EIN (E), CIN (C), LIN (L), Brain Stem Input, Threshold, Gain and Adaptation (as labelled above the chromosome) to E, C, L, MN (labelled within the chromosome). The symmetric nature of the network means that only half of the values require coding into the chromosome. Note that the values in this particular example correspond to Ekeberg's original model. Finally, the sign (excitatory or inhibitory) of each neuron group is contained in three chromosome units. These determine whether the connection is excitatory or inhibitory. Motorneurons only connect to muscles and so their outputs are not evolved. The single CPG unit GA guides solutions according to a fitness function (detailed in [34]), designed to select candidates which favour effective oscillatory behaviour. The following are the objectives incorporated into this evaluation together with justification for their inclusion:

1. Frequency is controllable by simple tonic excitation from the brainstem. It should increase monotonically with input levels. This is to enable variable control of oscillation frequency which in turn varies extensor or flexor phases of muscles.
2. Oscillations must be regular and have only one peak of activity each period. An imperative feature of CPGs is regular activity to ensure cyclic phases of on and off states so that the muscle contracts once it has reached the extent of its stretching phase. This makes this a necessary condition of new solutions.
3. Motorneuron activity must alternate between left and right sides of the CPG. Out-of-phase activity is crucial for rhythmic swimming in the lamprey. This ensures

only one side of each particular section of its body is active at any time. Again, this is a necessary condition for CPG function.
4. Oscillators operating over a wider frequency range are highly favoured. In order to demonstrate improved control, it was considered important to have controllers which performed outside the limits of the biological model. This is also a goal for our intended application in wave energy, where a wider operation bandwidth will be required.
5. The biological frequency range must be included within the operating range of the new solution. Although not essential for marine energy solutions, this was an important aspect to enable a basis for comparison between the biological model and newly evolved CPGs. The evolved solution should perform with wider control ranges than Ekeberg's original solution.
6. Low connectivity is desirable. For converting any CPG solution into silicon, simplicity in network configuration is of major importance. This would make the system more robust, easier to implement and cheaper to manufacture and maintain. Low connectivity is encouraged via a pruning operator (described in section 6).

6.2 GA2 - Evolving Linked Oscillators

As described in section 5, the lamprey comprises several interconnected oscillatory segments. For the whole body to coordinate movements, oscillators need to be linked to their immediate neighbours. Therefore, the function of this GA is to evolve the extent of interlinking connections to coordinate efficient swimming. Still retaining the basic architecture of Ekeberg's model, intersegmental connections between 100 copies of a fixed segmental network are generated. The best segmental oscillators of the previous evolutionary stage (section 6.1 and in [32]) are used and five discrete evolutionary experiments invoked.

Candidate solutions are coded into integer-valued chromosomes, with genes depicting the extent of connections in rostral and caudal directions. Each chromosome comprises 51 genes. Owing to Left-Right symmetry, A CPG's 96 rostral/caudal interconnects are coded as 48 of these. Each has a value between 1 and 12 to incorporate biological prototype values. The other three genes denote whether the inputs are excitatory or inhibitory. These sign genes are preassigned according to the value this connection held in the unitary oscillator and therefore not evolved.

The fitness function (detailed in [34]) rewards solutions based on their ability to control swimming with wide operation bandwidths. These include large ranges of speed, oscillation frequency and phase lags between segments. Stated as objective criteria, multilinked controllers should:

1. be able to alter the oscillation frequency monotonically (with global excitation) and wavelength of undulation (with extra excitation) independently,
2. generate stable oscillations within each CPG unit, with coordinated phase differences to enable travelling undulations of the body, and
3. be able to change the speed of swimming by altering the CPG's oscillation frequency or the wavelength of undulations [33].

These are implemented to ensure efficient, smooth and linear control and to remain within the scope of the biological mechanism for swim control. Also, in line with the biological CPG, emphasis is placed on controllers which invoke swimming with a wavelength corresponding to the length of the fish's body (i.e. phase lag of 1% per segment). Resulting CPG controllers from both evolutionary processes are described in the following section.

6.3 Results of Single- and Multi-Segment GA Phases

Neural weights and parameters of an independent CPG module are evolved as a first-phase genetic algorithm (GA). A second GA takes the best of these solutions and evolves interconnects between neighbouring segments.

Fifty percent (20 experiments) of the first process generate improved oscillators than in [12, 24]. At the second GA stage, five of the best are chosen and four of these demonstrate wider swim ranges when interconnected as complete swim modules. The decision to terminate processes at 500 and 50 generations, for each GA phase respectively, is because most of the populations are stable by this point. Simulation times for the second evolutionary algorithm are significantly greater and so extra process time for little gain seemed unnecessary.

Most evolved solutions in our study demonstrate improved control. The statistics and neural configuration of the best of these is compared (table 2) with the original CPG prototype [12] (where all values were hand-tuned) and the best fixed parameter controller of [24] (where neuron-specific parameters threshold, gain and adaptation rate were hand-tuned values of [12]).

An interpretation of the results presented in table 2 is as follows:

Fitness - evolved CPG oscillators (of the first GA process) produce fitness values of 0.15 to 0.8. Of these, 90% outperform Ekeberg's prototype (fitness 0.11) and 30% out-evolve the fixed parameter (FP) networks (best of [24] is 0.31). Therefore, generating both neural weights and neuron specific parameters proves crucial to the development of high-performance networks.

Linking these via interconnections (the purpose of the second GA) also demonstrates improved swimming performance, with the controller of our study receiving a fitness value of 0.51 compared to 0.2 (biological model) and 0.16 (FP).

In one case, an improved CPG unit failed when it was interlinked to form a multisegment controller. This was due to poor independent control of oscillation frequency and phase lag. This demonstrates the importance of the second phase GA; and more generally that a good oscillator does not necessarily mean it will operate well when cross-coupled.

It is worth noting that Ijspeert's best segmental oscillator (shown in table 2) did not perform as well as the biological prototype when coupled to its neighbours, also confirmed by his results [24] and that another controller superceded it. However, this controller is still not as effective as the best lamprey CPG evolved in our experiments.

Table 2 Comparison of statistics and CPG configurations of the biological [12], fixed parameter [24] and evolved controller [34]. In column order, for each test, the table shows the CPG and level of intra-CPG connectivity (Conn), resulting objective values (GA1 and GA2), operative ranges of frequency, speed and phase lag, synaptic weights with the extent of cross-coupling in square brackets, brainstem input (BS), and finally, evolved neural parameters of threshold (θ), gain (Γ) and adaptation rate (μ). Due to the symmetrical nature of these controllers only half the inputs need to be shown. The complete weight set is derived by substituting l (left) with r(right) and vice versa.

CPG and Conn[a]	**FitV**[b] **GA1, GA2**	**Frq**[c] **Range (Hz) Spd**[d] **Range (m/s) Lag Range (%)**	**Synaptic Intra-CPG weights and Inter-CPG connection extent [rostral, caudal]**							**Neural Parameters**		
			From: To:	EINl	CINl	LINl	EINr	CINr	LINr	BS	θ	Γ	μ
bio	0.11, 0.2	1.74 - 5.56 0.01 - 0.45	EINl	0.4 [2,2]	-	-	-	-2.0 [1,10]	-	2.0	-0.2	1.8	0.3
26		0 - 1.165	CINl	3.0 [2,2]	-	-1.0 [5,5]	-	-2.0 [1,10]	-	7.0	0.5	1.0	0.3
			LINl	13.0 [5,5]	-	-	-	-1.0 [1,10]	-	5.0	8.0	0.5	0
			MNl	1.0 [5,5]	-	-	-	-2.0 [5,5]	-	5.0	0.1	0.3	0
FP	0.31, 0.16	1.2 - 8.0 0.06 - 0.41	EINl	-0.8 [12,4]	-3.8 [12,10]	-	-0.9 [5,10]	-0.7 [1,10]	-	0.8	-0.2	1.8	0.3
22		0.73 - 1.37	CINl	-	-	-	-3.5 [2,2]	-3.7 [9,9]	-	13.0	0.5	1.0	0.3
			LINl	-	-	-	-	-	-	-	8.0	0.5	0
			MNl	-0.4 [9,2]	-3.2 [8,1]	- -	-	-	- -	3.8	0.1	0.3	0
Evo	0.8, 0.51	0.99 - 12.67 -0.01 - 0.6	EINl	-	-4.6 [3,4]	-	-	-	-	3.06	-1	0.7	0
16		0 - 1.59	CINl	5.53 [1,8]	-	-	-	-2.9 [10,1]	-	-1.18	-1	0.48	0
			LINl	-	-	-	-	-	-	-5.0	-1	0.7	0
			MNl	-	-4.3 [8,6]	- -	-	-	- -	10.8	-1	0.27	0

[a] Conn = Connection Density, [b] FitV = Fitness Value, [c] Frq = Frequency, [d] Spd = Speed.

Connection density - sparse connectivity is far more efficient computationally and thus a very important consideration for silicon reproduction. This is especially the case when there are several copies of that same unit (as with multilinked controllers). Compared to the former models, the least densely connected CPG unit is produced in our results (with 16 vs. 22 and 26 intra-connections).

Frequency range - the range of frequencies covered by the best evolved controller is 0.99 - 12.67 Hz. This is substantially greater than the frequencies covered

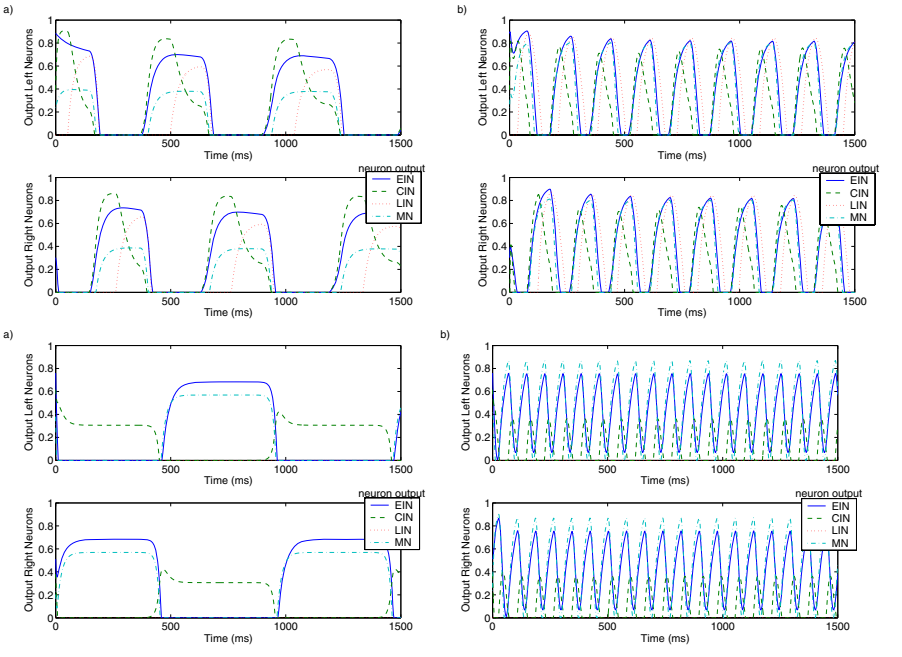


Fig. 6 Neuron behaviour of Ekeberg's biological network [12] (top four graphs) compared to our evolved controller [32] (bottom four graphs): part a) is the lowest oscillation level and part b) the highest frequency, for each CPG network. Network operation is simulated for a fixed duration of 3000ms (for clarity, oscillations for only 1500ms are shown in the charts), with asymmetric initial conditions (all left neurons excited).

by the biological and FP networks (1.74 - 5.56 Hz and 1.2 - 8 Hz respectively). This demonstrates over 100% of a performance increase over prior work where key variables remained static. Frequency is modulated by varying the tonic input, termed global excitation (as it is applied to the whole network). Lowest and highest frequencies are displayed in fig. 6b comparing the biological CPG and our best evolved solution.

The sets of graphs in fig. 6 demonstrate activity of Ekeberg's CPG (top fig. 6 a and b) with our evolved network (bottom fig. 6 a and b). It is evident from them that the evolved network operates with a broader frequency bandwidth than Ekeberg's model. Each set of graphs displays activity of the left neurons (top of each set) and the right neurons (bottom of each set). In all cases, the left-neurons operate antiphase to right-neurons; therefore only one side is active at any time as per stipulated conditions for *fictive* swimming. Other characteristics developed into the fitness evaluator include regular, oscillatory activity (see objective 2 in section 6.1), which is also demonstrated by each solution.

Speed range - The multilinked controller, when interacting with the environment swims within a greater range of speeds than the other networks; numerically,

-0.01 - 0.6 m/s (compared with 0.01 - 0.45 m/s (biological) and 0.06 - 0.41 m/s (FP)). The negative speed recording (-0.01) is due to the kind of wriggling the lamprey performs and not considered an adverse effect.

Lag range - The phase lag between interconnected units ranges from 0 - 1.59% (compared to 0 - 1.165% (biological) and 0.73 - 1.37% (FP)). This is recorded at the midrange of oscillation frequency and by monotonically altering the extra excitation tonic input.

Synaptic weights and interconnections - The magnitude of possible configurations due to connection permutations and synapse strengths can produce very diverse solutions. This is exemplified by the notable differences in type, quantity, sign and weights of active neurons in each solution shown in table 2. It can also be seen graphically by the chart activity shown in fig. 6 where different neurons interact to produce the eventual motorneuron burst patterns. Unlike the biological prototype, oscillatory activity of the best evolved solution occurs by opposing CIN neurons inhibiting each other, while the active EIN excites the CIN ipsilaterally. The non-dormant CIN also suppresses the EIN and MN neurons on its side, thus MN (and EIN) activity is asynchronous with the CIN on each side.

Although the neuron-naming scheme has been kept for comparison purposes, it is worth noting that each neural population loses its functional meaning and even the sign it had in the biological model. This is even true of prior evolved controller networks (i.e. [24]). The only feature they retain are the original dendritic time delays of τ_D = 30ms, 20ms, 50ms and 20ms for the neuron types EIN, CIN, LIN and MN respectively and τ_A = 400ms and 200ms for EIN and CIN. These accord the original solution in [12].

Neural parameters - As with synaptic weights and interconnections, a distinct pattern does not emerge for neuron-specific parameters (threshold, gain and adaptation rate) when solutions are compared. The evolved network parameters seem to bear no commonalities with the fixed parameter CPGs. Furthermore, the best evolved solution is simpler through the elimination of frequency adaptation ($\mu = 0$), removing the need for the leak (eqn. 3, section 5) without affecting preferred swimming capabilities. Note that this parameter's behaviour should not be confused with the role of tonic input changes or edge cell feedback, which perform frequency modulation of the interlinked swim system. Rather, parameter μ relates to an individual neuron group generating time-changing rather than constant output. Since the system does not seem to need this feature to meet its objectives, there is no reason to force its existence. This variation between CPGs demonstrates diversity in the solution set and suggests that there is a spectrum of continuous models as opposed to a distinct number of species.

6.4 Discussion

This study demonstrates that Ekeberg's CPG model [12] of the lamprey spinal controller is not a unique solution and that many simpler versions with wider operative

ranges can be generated. Evolved networks operate with a wider frequency, phase lag and speed range with independency of control. Improvements of over 100% are achieved. Our methodology builds upon previous work [24], but improves *anguiliform* swimming performance substantially by relaxing some constraints and exploring variables (threshold, gain and adaptation rate) previously fixed in value. Therefore, the true flexibility of the CPG network is assessed.

In terms of system connectivity, evolved networks are vastly simpler than the biological prototype [12] and fixed parameter solutions [24]. They have reduced parameter sets, which also simplify the original equation set. This is desirable if an integrated VLSI controller is to be developed, especially where this network is one of many functional units of a complete, dynamic system. Furthermore these improvements do not come at the expense of performance.

Since these controllers are developed with specific goals in mind they do not necessarily incorporate all the functionality of the biological prototype. For example, constraints of the natural lamprey may include attributes for mating, searching for food and / or escape swimming. However, since these actions are not essential in a wave power device, it is not worthwhile building them into the new control unit just to keep them in line with the biological model. Instead, targeting specific and necessary behaviours (i.e. rhythmic patterns and adaptation) within the architecture and basic routines of the lamprey CPG, produces streamlined, better solutions.

Additionally, there is absolutely no reason why a natural evolved solution should be optimal even in its own multifunctional capabilities, since evolution does not work that way. Natural lamprey parameter choices could be a result of historical contingency, that is, they are what the genome could build given what it had available at that time. The important point is that it is not possible to know why the biological lamprey neurons use the parameters they do, but if the lamprey could freely optimise for performance, perhaps it would choose different ones. This form of behaviour is intriguing in the context of real biological systems. It is potentially of enormous importance when seeking bio-inspired advances in engineering applications, where the fitness function is different and the rules imposed by the biological substrate are absent.

A large motivator of this work is to develop high performance mechanical controllers based upon, but not limited by or linked slavishly to the underlying biology. Our work therefore out-evolves the natural organism's operation range rather than out-evolving nature. Improving the range of operation is fundamental to developing bio-inspired solutions for alternative control tasks.

In summary, our experiments show that, by relaxing some of the constraints associated with a biological exemplar, controllers (and potentially other computational structures) can be evolved that can capture the strengths of biological computation in a simpler, or perhaps more effective manner. This is intrinsically interesting, as a contribution to understanding the naturally-evolved performance of real organisms. It is also an enormously encouraging first step towards re-evolving other CPG controllers, and potentially other biological processors, for different tasks, using non-biological computing substrates.

7 Towards Controlling Wave Energy Devices and Improving Power Capture Efficiency – A Bio-inspired Solution

Marine energy devices operate with similar rhythmic routines, locomotion and in the same environment as the lamprey. Adding reactive control to these machines can result in autonomy, improved efficiency and increased productivity in the marine energy sector.

The depletion of natural energy resources and the need to reduce carbon dioxide emissions has generated a huge interest in renewable energy. Significant power is stored in the motion of the seas. However, harnessing this energy effectively remains a very difficult challenge. This is due to the highly unpredictable and dynamic nature of seas which are influenced by factors such as wind strength, wind direction, drag forces, as well as superposition and counteracting incoming waves, with different frequencies and velocities.

Wave energy converters (WECs), such as the one displayed in fig. 7, harness some of this energy but cannot adapt autonomously to irregular and changing sea conditions. Instead they rely on past wave data to make inaccurate predictions of future waves or use compromise operational settings until manually reset. As a result, they operate at sub-optimal efficiency. An active and adaptive approach would provide the currently lacking, but necessary, self-regulatory control, thus producing more power and under more robust conditions. Biology already invokes this kind of adaptive control (and does it very well) in the swim module of the lamprey and inspires application of a similar mechanism for marine energy devices.

The general underlying mechanism of WEC operation is to perform managed movements in the oceans, converting wave energy into usable electricity. Locomotion is usually oscillatory, and devices try to match the complex characteristics of wave frequencies or forces. Again, this bears similarity with the type of locomotion governed by lamprey CPG circuits.

In this chapter, the wave power solution has not been addressed directly as there are many contributory components that require attention. This chapter reports on issues that must be resolved with the bio-inspired model, which in turn will be used to advance wave technology. The work assesses the flexibility of the biological architecture intended for use with wave power devices to determine how much it can

Fig. 7 The Pelamis, a wave energy converter developed by Pelamis Wave Power Ltd. It resembles the lamprey (in fig. 4a), both visually and in locomotion.

be stretched to accommodate the wider range of operability required for the engineering solution. The following section discusses other aims in developing this bio-inspired solution for wave energy.

8 Working towards Wave Power

The aim is to develop adaptive controllers based on the lamprey's CPG architecture to boost the efficiency of wave power devices (both articulated devices and single-point absorbers) operating in irregular sea states. The intention is to increase the renewable power these devices extract from the sea in a reactive rather than static, currently inefficient manner. The lamprey CPG model is an ideal control architecture within which to work. Initially, the biological model was explored without the constraints imposed by the biological substrate. Redevelopment will focus on tuning it to power-extraction elements of WECs, replacing swimming efficiency with power efficiency in the fitness function.

The flexibility and operational boundaries (ranges) of the network were explored by evolving the CPGs interneuron control parameters. The majority of the conditions built into the fitness functions of these genetic programs are also requisite for wave energy control (WEC) solutions. Some promote efficient, streamlined and cost-effective outcomes, such as simplification of the network. Others may require tweaking such as ranges of operation to match requirements of wave conditions. Other factors will require complete implementation such as operations relating to the measurement and dissipation of power. Other developmental goals will include:

1. Complete remodelling of the mechanical body, its effect on surrounding water, and of the waves as they interact with the device.
2. Evolution of sensory input cells - edge cells will play a big role, with fluctuations in wave conditions being fed back to the neural controller in order to modulate or alter the system's behaviour. This will involve a further GA process and related fitness functions to evolve sensory feedback components.
3. Further reorganisation of the network - if the tonic inputs are to serve a more direct reactive role (with inputs feeding directly back to the network rather than modulating patterns of activity from a higher command node).
4. Alternative control strategies - although reactive control is the main aim, other control strategies will be investigated and compared (e.g. latched control [22]) to ascertain their efficiency and resource requirements.
5. A longer term goal, once the concept has been proven - individual implementation of each wave power device, related fitness functions and evolution according to device-specific criteria.

The evolution of improved lamprey CPGs has been a crucial step towards achieving these next stages of WEC application control.

9 Concluding Remarks

This chapter has discussed a class of neural networks called Central Pattern Generators (CPGs), responsible for rhythmic patterns of behaviour. CPGs comprise organised neuronal populations which function collectively to coordinate activity of several cells to produce oscillatory output. CPG modules do not require sensory input to generate rhythmic behaviour, but temporal and phasic signals from afferent sensory inputs can modulate its intrinsic activity.

It has been shown that CPGs control a broad range of functions in animals. Furthermore, they are widely variable and adaptable with age, environment and behaviour. Although anatomical details of CPG circuits are known in only a few cases, most originate from vertebrate spinal cords which are generally small autonomous networks which govern rhythmic patterns of behaviour. A model of the lamprey's (an eel-like fish) CPG is described in detail.

This neural circuit's ability to self-regulate behaviour to meet the needs of a changing environment, and the fact that the system produces the same *fictive* swimming when implemented artificially, make it an ideal candidate for providing similar artificial intelligence to other real tasks where automation would result in increased efficiency and productivity.

Evidence has been presented to demonstrate the flexibility of this network with genetically evolved, more superior controllers (in terms of their operation ranges). These will be further evolved and implemented with wave energy devices to boost the energy they extract from unpredictable and everchanging seas; a task that requires similar rhythmic locomotion and self-regulation that the lamprey's swim module displays. Thus this provides a bio-inspired solution to a challenging engineering task.

Finally, inspiration does not end here; there are many other CPG-driven tasks that could benefit from bio-inspired technology. These include heart-pacemakers, responsive, for example, to changes in the level of physical activity, robotic locomotion (much research is already evident in this area), and hearing-aid modulators (an area not previously considered).

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