

## Coupled van der Pol oscillators as a simplified model for generation of neural patterns for jellyfish locomotion

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### SUMMARY

In this paper, we present a simple system of coupled oscillators as a model of pattern generation for jellyfish locomotion. Coupled oscillator models have been successfully applied to model pattern generation in numerous biological systems including jellyfish locomotion, but the previous jellyfish models have required complicated oscillators or variation of coupling topology to produce gait variations. Here we show that a simple model consisting of identical van der Pol oscillators with fixed coupling topology suffices to produce dynamics corresponding to essential jellyfish gaits (co-ordinated bout swimming, hovering, and turning) solely by uniform adjustment of coupling strengths. Thus, a simple coupled oscillator model succeeds in producing a range of dynamic behaviour analogous to the essential neural dynamics for locomotion control of a simple animal. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: coupled oscillators; gait generation; phase-locking; synchronization; jellyfish; locomotion

### 1. INTRODUCTION

Simple animals are labelled ‘simple’ because they do not possess a complex feedback system, i.e. a brain, to control their function. Despite their lack of an actual brain, simple animals can display a rich variety of behaviour. Motivated by the dual goals of better understanding nature and supporting the development of biologically inspired robotic systems, we are led to consider the following question: How complicated (or perhaps more appropriately, how simple) can a mathematical model be while still capturing essential aspects of the behaviour of a simple animal? Such a question is admittedly too broad to be tackled in a single research paper, so we refine our focus to consider a single class of behaviour for a single simple animal. In particular, we consider neural pattern generation for locomotion of jellyfish.

Since 1876, with the classic work of Romanes [1], the locomotor system of medusae has challenged neurobiologists to understand the neural control of hydrozoan locomotion. Jellyfish

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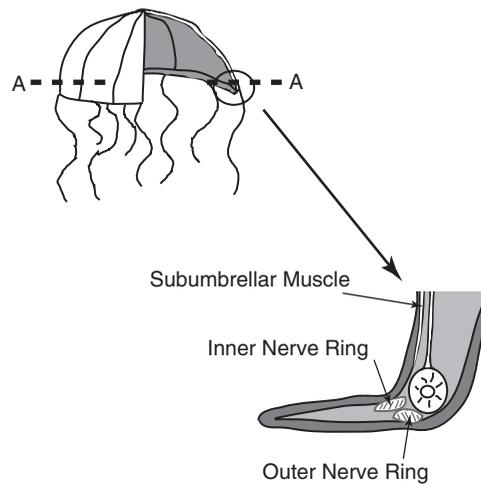


Figure 1. Schematic of hydrozoan nerve rings.

have been studied extensively because of their simple nervous systems, radial symmetry and well-defined locomotive behaviours.

Although there are variations between the different classes of cnidarians, the hydrozoa have a fairly uniform neuronal architecture consisting of an outer nerve ring and an inner nerve ring as shown in Figure 1. The inner nerve ring is responsible for incorporating the sensory input from the outer nerve ring and innervating the subumbrellar swimming muscles. Additionally, cells in the inner nerve ring generate endogenous rhythms and act as pacemakers. The outer nerve ring incorporates stimuli from the environment and transmits this information to the inner nerve ring via chemical synapses [2, 3].

Detailed electrophysiological experiments give insight to the coupling scheme within and between the inner nerve ring and the muscles. The concentric ring of swim motor neurons (SMN) are electrically coupled to each other via gap junctions and, in turn, activate the subumbrellar myoepithelium. The pacemaker cells overlay the SMN ring and are also electrically coupled to each other via gap junctions. Additionally, the pacemakers communicate with the SMN via chemical synapses and this communication can produce synchrony of the SMN output to the muscles [3]. Spencer and Satterlie [4] find that the co-ordinated output of the SMN yields action potentials with waveforms that exhibit the sharp rise followed by slow decay that is characteristic of relaxation oscillators.

Based on the presence of neural pacemakers, action potentials with a fast and slow time scale, and our desire for simplicity in modelling, we choose the van der Pol oscillator, (Equation (1)), as the fundamental building block for the model (presented in detail in the following section):

$$\ddot{x} + \varepsilon(x^2 - 1)\dot{x} + x = 0 \quad (1)$$

where dots represent differentiation with respect to time, and  $\varepsilon$  is the non-linearity parameter. The van der Pol equation is the simplest and best understood limit cycle (i.e. self-sustaining) oscillator that exhibits relaxation behaviour (alternating fast and slow time scales) for moderate values of non-linearity [5].

The van der Pol oscillator has been studied in great detail by both scientists and mathematicians. Its solution has been calculated to high order [6] and many researchers have studied synchronization criteria for systems of two or more coupled van der Pol oscillators [7, 8]. These systems of multiple coupled van der Pol oscillators have been used to model many complicated biological systems such as the neural synapses of swimming fish [9], the dynamic behaviour of the human heart [10] and the dynamic behaviour of certain sections of the digestive tract [11, 12].

While there is an extensive body of knowledge about the neuronal architecture of hydrozoan medusae, the precise rules of interaction at the cellular level are complex and vary between species, so we do not attempt to resolve such issues in this paper. Instead, we aim to construct the simplest possible analogous system of coupled van der Pol oscillators, and to analyse the dynamics of the model to see if the resulting dynamics is rich enough to capture the essential behaviours of jellyfish locomotion. Specifically, can a simple system of mutually coupled van der Pol oscillators mimic the neural patterns that generate gaits associated with the essential locomotive modes: co-ordinated bout swimming, hovering and turning?

In the remainder of the paper we specify the details of the model, present representative results of analysis and simulation based on the model, and discuss how the behaviours of the model relate to observed jellyfish locomotive patterns.

## 2. MODEL

The detailed neural anatomy of the hydrozoa has been studied extensively [2–4, 13, 14], and a highly schematic representation of the neural system is shown in Figure 2 (view A–A from Figure 1). (We base our schematic for jellyfish neural systems on the neural geometry of hydrozoan *Polyorchis penicillatus*, one of the best studied species.) The inner and outer nerve rings contain electrically coupled neurons. The inner nerve ring contains the SMN and the pacemaker cells.

A lumped modelling approach is used to describe the composite output (action potential) of the two nerve rings. The rings are conceptually divided into segments each containing one neural pacemaker, and a single van der Pol oscillator is used to represent the intrinsic periodic neural activity in each segment. Figure 3 shows an example of the schematic for a jellyfish with 8 pacemaker cells.

The major remaining issue to be decided in specifying the model is determination of topology of the segment coupling. Dye diffusion experiments [2] indicate that dye injected into one pacemaker spreads throughout the entire ring within a single pacemaker period. (There is some delay in the chemical diffusion coupling that is proportional to the separation distance. However, the delay time is roughly 3 orders of magnitude smaller than the pacemaker period, so the delay is neglected here. For detailed studies of limit cycle oscillators with coupling delay, see Reference [15].) From this result we infer that each pacemaker is coupled to all other pacemakers, not just their neighbours.

We now have a basic model consisting of a collection of van der Pol oscillators with coupling between each of the oscillators. Continuing with our theme of simplicity, we take the coupling to be symmetric, uniform, diffusional (i.e. depending on the difference between the displacements and velocities of the pair of oscillators), and linear.

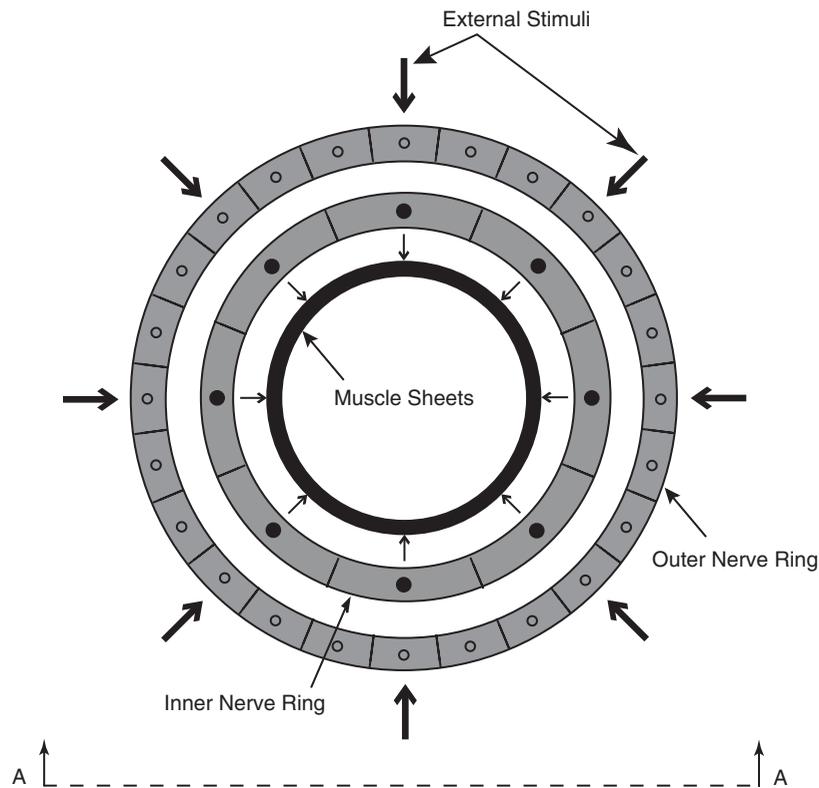


Figure 2. Schematic of hydrozoan neural system (View A–A from Figure 1). Solid black dots represent pacemaker cells and the arrows between the inner nerve ring and the muscle sheets indicate action potentials [3].

Rand and Holmes [7] first proposed a system of two coupled van der Pol oscillators with linear diffusive coupling

$$\begin{aligned}\ddot{x}_1 + \varepsilon(x_1^2 - 1)\dot{x}_1 + x_1 &= A(x_2 - x_1) + B(\dot{x}_2 - \dot{x}_1) \\ \ddot{x}_2 + \varepsilon(x_2^2 - 1)\dot{x}_2 + x_2 &= A(x_1 - x_2) + B(\dot{x}_1 - \dot{x}_2)\end{aligned}\quad (2)$$

where  $x_1$  and  $x_2$  are the dependent variables modelling the state of the oscillators, and  $A$  and  $B$  are coupling parameters that measure the strength of the interaction. The signs of the coupling parameters also serve to distinguish excitatory and inhibitory effects.

Our model for jellyfish neural activity is an expanded version of Equation (2) with additional dependent variables (one for each of the pacemaker segments) and additional linear diffusional coupling terms (so that the equation governing the evolution of each variable contains a coupling term associated with the state of each of the other segments). Again with the goal of simplicity, we assume uniformity; i.e. that each pacemaker has the same intrinsic frequency  $\omega$  and that the coupling parameters for the interaction between any pair of segments have the same value. After grouping terms by dependent variable on the right-hand sides, the mathematical

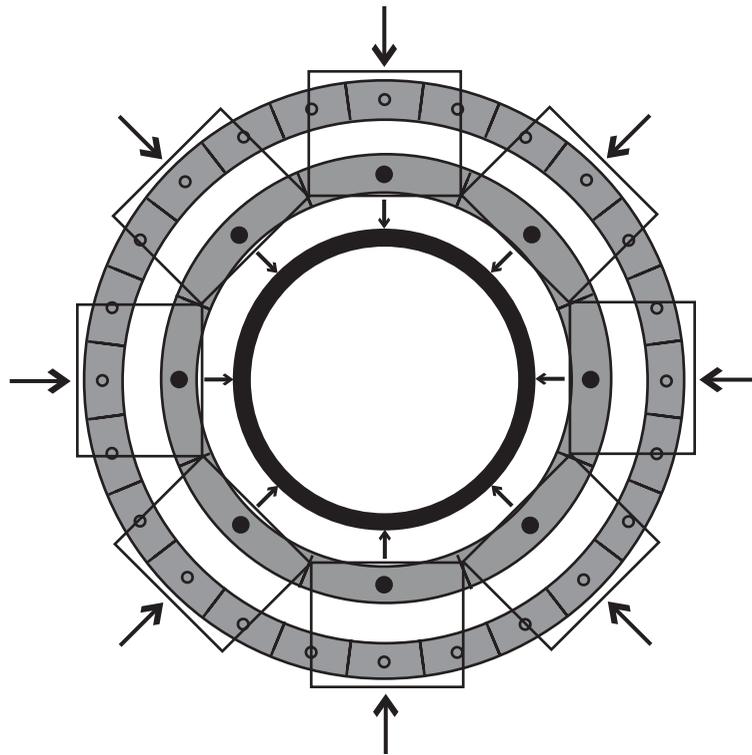


Figure 3. Schematic of segmented modelling scheme.

model for  $n$  oscillators takes the form

$$\begin{aligned}
 \ddot{x}_1 + \varepsilon(x_1^2 - 1)\omega\dot{x}_1 + \omega^2x_1 &= A(-(n - 1)x_1 + x_2 + \dots + x_n) + B(-(n - 1)\dot{x}_1 + \dot{x}_2 + \dots + \dot{x}_n) \\
 \ddot{x}_2 + \varepsilon(x_2^2 - 1)\omega\dot{x}_2 + \omega^2x_2 &= A(x_1 - (n - 1)x_2 + \dots + x_n) + B(\dot{x}_1 - (n - 1)\dot{x}_2 + \dots + \dot{x}_n) \\
 &\vdots \\
 \ddot{x}_n + \varepsilon(x_n^2 - 1)\omega\dot{x}_n + \omega^2x_n &= A(x_1 + x_2 + \dots - (n - 1)x_n) + B(\dot{x}_1 + \dot{x}_2 + \dots - (n - 1)\dot{x}_n)
 \end{aligned} \tag{3}$$

This particular coupling scheme is aptly labelled a network, as each oscillator is coupled to every other oscillator. The behaviour of this coupling scheme has been studied in depth [16, 17]. The results of these studies have described the synchronization of the coupled van der Pol system analytically and numerically in terms of the non-linearity parameter  $\varepsilon$  and the coupling parameters  $A$  and  $B$ . To perform the numerical solution, the mathematical model was built as a system of coupled differential equations using the Simulink toolbox within the Matlab computational software. The equations were solved numerically using the Adams method with a time step of 1 ms (0.001 s) and a tolerance of  $10^{-6}$ .

### 3. RESULTS

Here we consider the implications of the phase-locked dynamics of systems of coupled van der Pol oscillators in the context of modelling neural pattern generation for jellyfish locomotion. In particular, we choose the value of the non-linearity parameter ( $\varepsilon = 5.0$ ) to produce a limit cycle that closely resembles the observed waveform of jellyfish action potentials, and we focus on numbers of oscillators corresponding to the number of pacemakers in various species of jellyfish. Note that jellyfish frequently exhibit tetrameric symmetry, so we will present results for  $n = 4, 8$ , and 16. However, we also present results for  $n = 15$  to demonstrate that our results do not depend on the presence of such symmetry. (In fact, particular jellyfish species can exhibit a significant variation in  $n$ , the number of pacemakers. For *Cladonema californicum*, *Gonionemus vertens*, *Muggiaea atlantica*, and *Phialidium hemisphericum*, and *Probosciodactyla flavicirrata*,  $2 \leq n \leq 15$  [2]. For *Aequorea aequorea*,  $5 \leq n \leq 8$  [2]. For *Polyorchis penicillatus*,  $6 \leq n \leq 15$  [2].)

We present results to illustrate the phase-locked solutions of the coupled system that aim to model locomotive gaits. Figure 4(II) shows an example of a phase-locked solution for a system of 4 oscillators. Each of the 4 oscillators exhibits a waveform that is very similar to the limit cycle of an isolated oscillator but, by comparing the vertical lines that mark the zero crossings, it is apparent that not all of the oscillators share the same phase. Without loss of generality, we choose  $x_1$  as the reference oscillator and define its phase angle as  $\phi_1 = 0^\circ$ . In this case, we see that  $x_3$  is in phase with  $x_1$  so that  $\phi_3 = 0^\circ$  also. We can also see that  $x_2$  and  $x_4$  are in-phase with each other, but their zero crossings occur after those of  $x_1$  and  $x_3$  by a fraction of a cycle corresponding to a phase lag of  $\phi_2 = \phi_4 \approx 45^\circ$ . Figure 4(I) uses corresponding shading to illustrate common phase relationships for oscillators in the network arrayed in a radial fashion corresponding to the physical location of segments around the bell of the jellyfish. For a more concise presentation of the essential phase information, Figure 4(III) shows the equivalent of a bar graph of the phase lag for each oscillator in the network. We will use such phase plots exclusively to present the remaining results concerning phase-locked behaviours.

Four common phase-locked behaviours (model gaits) for a system of four oscillators are shown in Figure 5. In Gait I, a stable phase-locked solution obtained with coupling parameter values  $A = 2.0$  and  $B = 0.1$ , all oscillators beat in-phase; and such a solution is conventionally referred to as the ‘in-phase mode’. In Gait II (with  $A = 2.0$  and  $B = -0.1$ ), the phase lag

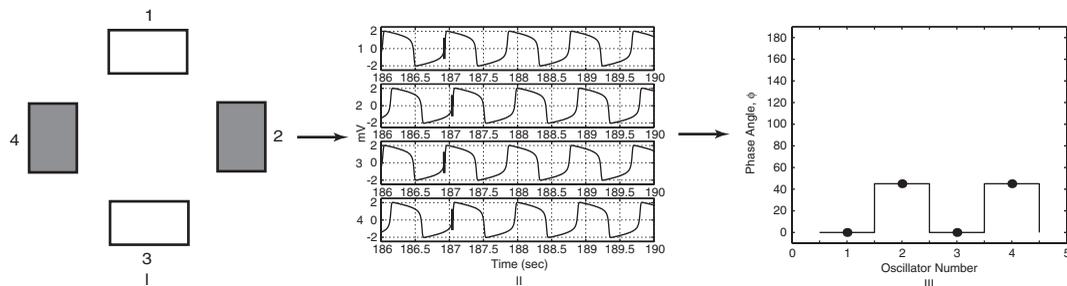


Figure 4. Phase-locked behaviour of a system of 4 oscillators.

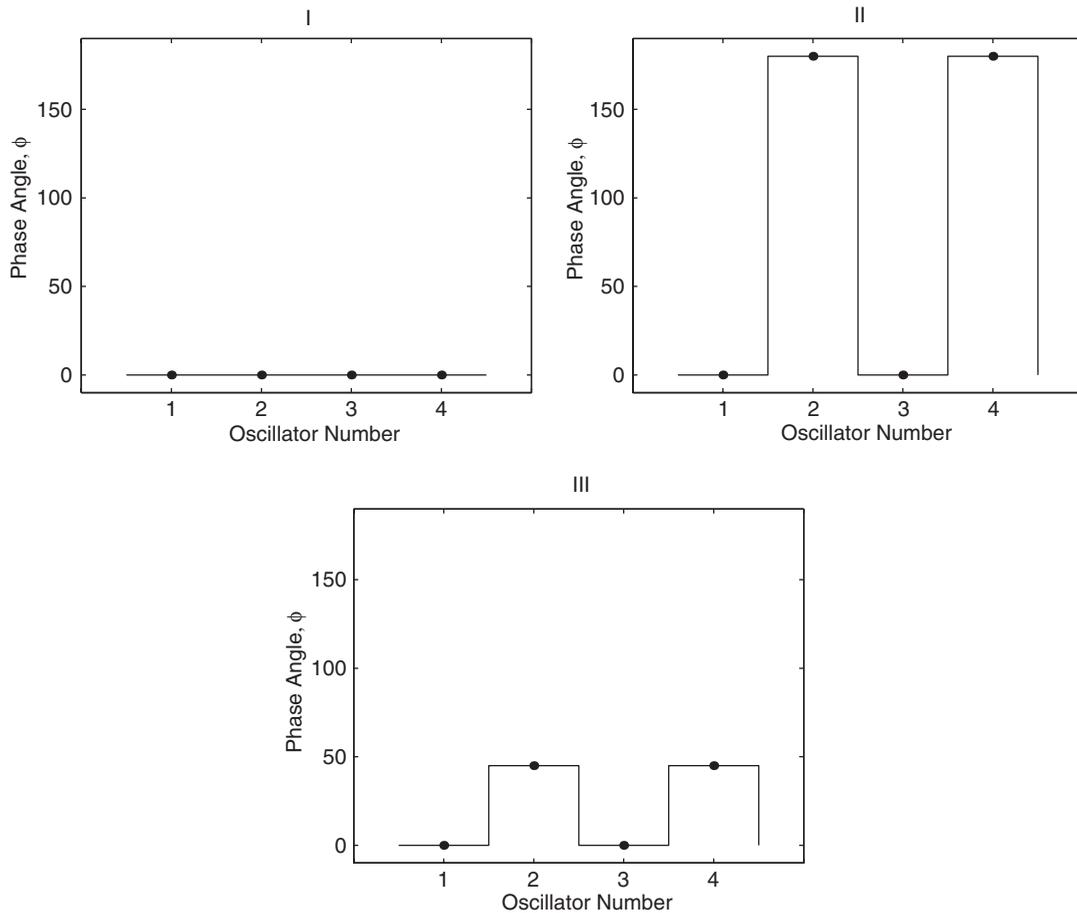


Figure 5. Gaits of 4 oscillators. Gait I In-Phase,  $\varepsilon = 5.0$ ,  $A = 2.0$ ,  $B = 0.1$ . Gait II Every other Anti-Phase,  $\varepsilon = 5.0$ ,  $A = 2.0$ ,  $B = -0.1$ . Gait III Shifted,  $\varepsilon = 5.0$ ,  $A = 2.0$ ,  $B = 0$ .

alternates between  $\phi = 0^\circ$  and  $180^\circ$ . Neighbouring oscillators exhibit a  $1/2$  cycle phase lag, and this stable phase-locked motion is referred to as the ‘anti-phase mode’. In Gate III (with  $A = 2.0$  and  $B = 0$ ), the phase relationship once again alternates, but the phase lag between neighbouring oscillators is other than  $0^\circ$  or  $180^\circ$ . This stable phase-locked solution is referred to as a ‘shifted mode’. It is important to emphasize that each of these solutions represents a stable phase-locked ‘gait’ and that all that is required to change gaits is to uniformly change the value of a coupling parameter.

Stable phase-locked solutions corresponding to gaits for a network of 8 oscillators are shown in Figure 6. Once again, we see the in-phase mode (with  $A = 1.5$  and  $B = 0.1$ ), the anti-phase mode (with  $A = 1.5$  and  $B = -0.1$ ), and a shifted mode (with  $A = 1.5$  and  $B = 0$ ).

As we increase the size of the oscillator network from 4 to 8, no new stable phase-locked gates are observed. Does this conclusion hold as we consider larger networks? To address this

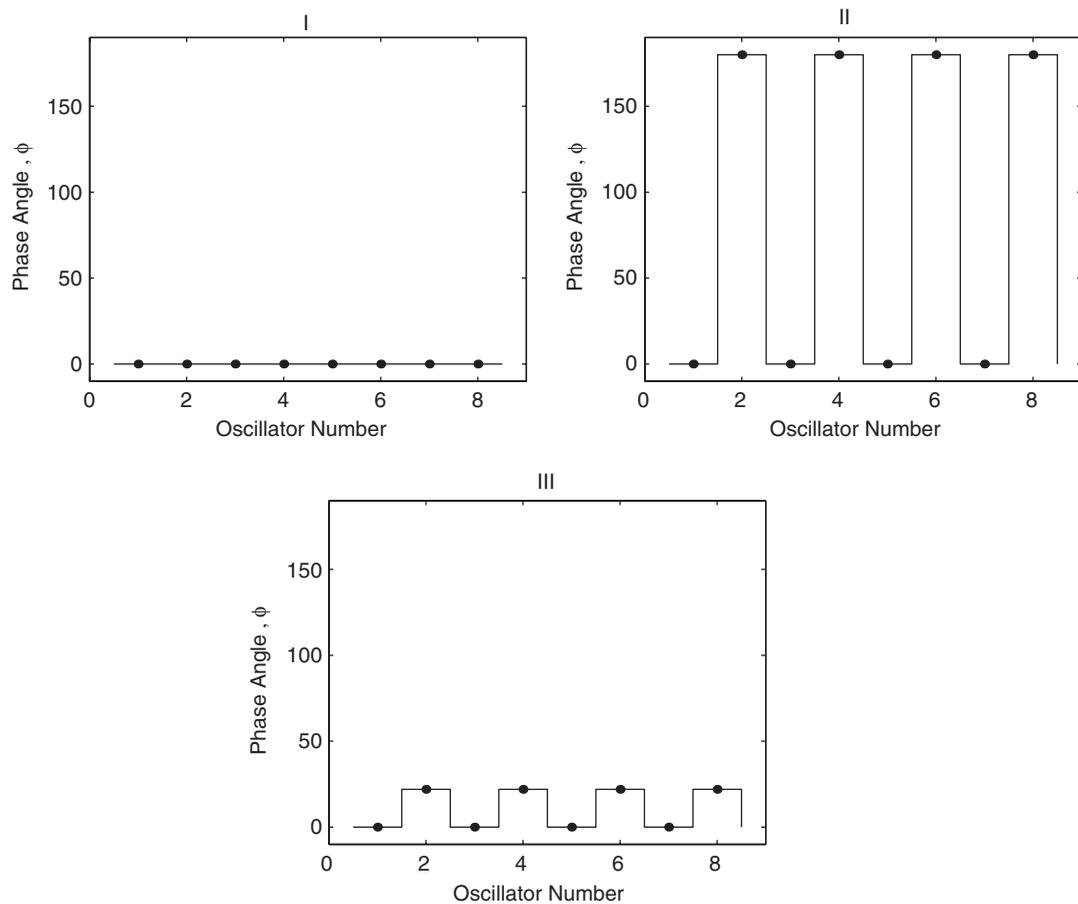


Figure 6. Gaits of 8 oscillators. Gait I In-Phase,  $\varepsilon = 5.0$ ,  $A = 1.5$ ,  $B = 0.1$ . Gait II Every other Anti-Phase,  $\varepsilon = 5.0$ ,  $A = 1.5$ ,  $B = -0.1$ . Gait III Shifted,  $\varepsilon = 5.0$ ,  $A = 1.5$ ,  $B = 0$ .

question, Figure 7 shows the stable phase-locked gaits for a network of 16 oscillators. While Gait I (with  $A = 2.5$  and  $B = 0.1$ ) corresponds to the in-phase mode and Gait II (with  $A = 2.5$  and  $B = -0.2$ ) corresponds to the anti-phase mode, Gaits III (with  $A = 3.0$  and  $B = -9.5$ ) and IV (with  $A = 3.0$  and  $B = -8.5$ ) introduce new behaviour. The phase is not strictly alternating, and these solutions can be interpreted as asymmetric gaits in which alternating subsets of the network are in-phase or anti-phase. In particular, for Gait III oscillators 5–7 and 8–10 constitute regions of local in-phase synchronization while the remaining oscillators beat anti-phase.

To determine if the existence of the observed gaits depends on tetrameric symmetry, we present stable phase-locked solutions for a network of 15 oscillators in Figure 8. The observed gaits are quite similar to those observed for a network of 16 oscillators. Gait I ( $A = 1.0$  and  $B = 0.1$ ) is the in-phase mode. Gait II ( $A = 1.0$  and  $B = -2.0$ ) is as close as possible to an anti-phase mode for an odd number of oscillators. (Oscillators 1 and 15 are the single inevitable

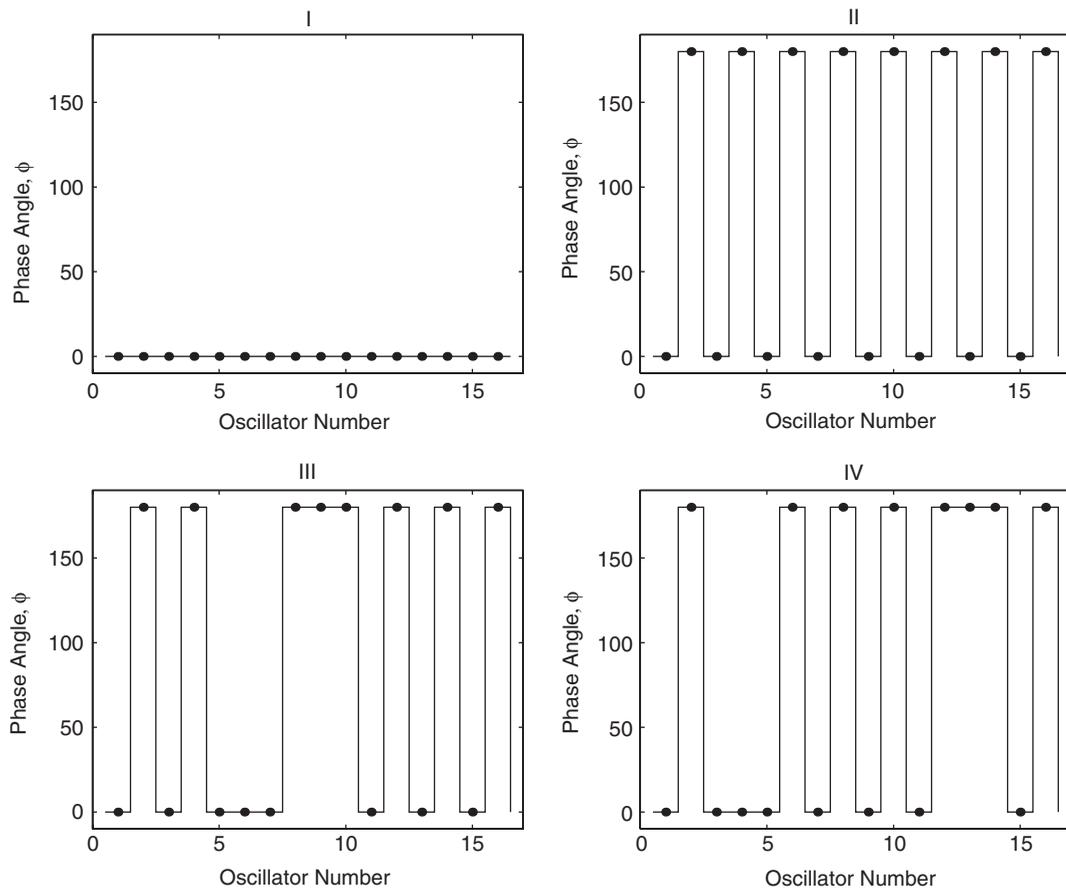


Figure 7. Gaits of 16 oscillators. Gait I In-Phase,  $\varepsilon = 5.0$ ,  $A = 2.5$ ,  $B = 0.1$ . Gait II Every other Anti-Phase,  $\varepsilon = 5.0$ ,  $A = 2.5$ ,  $B = -0.2$ . Gait III Shifted,  $\varepsilon = 5.0$ ,  $A = 3.0$ ,  $B = -9.5$ . Gait IV Shifted,  $\varepsilon = 5.0$ ,  $A = 3.0$ ,  $B = -8.5$ .

pair of in-phase neighbours.) Gait III ( $A = 0.5$  and  $B = -2.0$ ) and Gait IV ( $A = 0.7$  and  $B = -2.1$ ) again correspond to asymmetric gaits with localized subsets of oscillators that are in-phase or anti-phase. The new feature is that the asymmetric gaits also have an oscillator with a phase shift other than  $0^\circ$  or  $180^\circ$ .

While it would be beyond the scope of this paper to attempt to present a comprehensive summary of the dynamics of networks of coupled van der Pol oscillators (e.g. unsynchronized behaviour can also occur), the results that we have presented clearly illustrate the existence of 3 classes of stable phase-locked gaits: (1) the in-phase mode, (2) the anti-phase mode, and (3) asymmetric modes with localized regions of in-phase and anti-phase synchronization. Moreover, all 3 classes of gaits can be achieved without requiring asymmetry, non-uniformity or topological transformation of the network; all that is required is tuning of the coupling parameters.

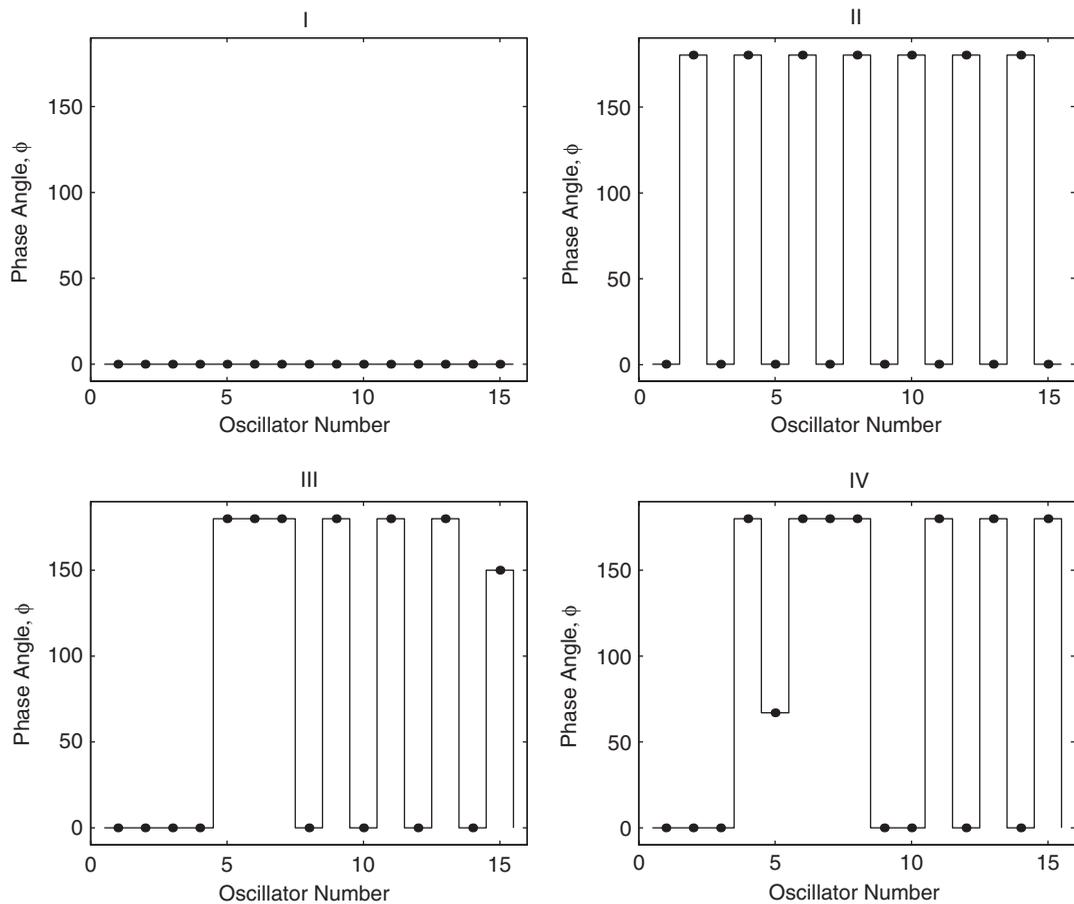


Figure 8. Gaits of 15 oscillators. Gait I In-Phase,  $\varepsilon = 5.0$ ,  $A = 1.0$ ,  $B = 0.1$ . Gait II Every other Anti-Phase (Except 1 and 15),  $\varepsilon = 5.0$ ,  $A = 1.0$ ,  $B = -2.0$ . Gait III Shifted,  $\varepsilon = 5.0$ ,  $A = 0.5$ ,  $B = -2.0$ . Gait IV Shifted,  $\varepsilon = 5.0$ ,  $A = 0.7$ ,  $B = -2.1$ .

#### 4. DISCUSSION

Let us now consider how the stable modes of the coupled oscillator networks can relate to pattern generation needs of jellyfish. Observations of undisturbed jellyfish indicate 3 essential behavioural modes related to locomotion: (1) co-ordinated bout swimming, (2) hovering, and (3) turning. (The ‘undisturbed’ qualifier is included because jellyfish also exhibit a fast swimming flight mode to escape perceived threats. This fast swimming mode is thought to be initiated directly from the outer nerve ring whose detailed behaviour is not considered in the simple model presented in this paper.)

Co-ordinated bout swimming refers to periods during which the muscle sheet around the bell of the jellyfish is periodically and uniformly contracted to expel water and generate thrust. The thrust is typically directed upward since, in most cases, the opening of the bell faces down. The

word 'bout' implies that jellyfish are not always engaged in this co-ordinated swimming behaviour. They can also stop swimming and enter the mode we refer to as 'hovering'. In this state, the neural system of the jellyfish continues to function and continued motion of the bell is observed, but significant thrust is not produced and the jellyfish can essentially ride the prevailing current. Since the local current can be strong (and not precisely horizontal), the orientation of the jellyfish can be displaced from the vertical so the jellyfish needs to have a turning mode in order to re-establish its desired vertical orientation. (It is well-established that jellyfish possess sensory organs called statocysts that enable them to sense orientation [18].)

The main point of this paper is to establish that the simple model consisting of a complex of coupled van der Pol oscillators suffices to produce neural gaits that are plausibly related to the basic modes of jellyfish locomotion. If we interpret the stable phase-locked modes exhibited by the model as analogs to the action potentials that produce contraction of the local portion of the muscle sheet surrounding the bell, we can speculate about how to translate neural gaits into modes of locomotion.

The obvious (and accepted) connection involves in-phase synchrony of the neural pacemakers and the periodic uniform contraction of the bell associated with co-ordinated bout swimming. What we can add to the accepted state of understanding is the fact that the stability of the in-phase mode of the oscillator network provides not only a mechanism for maintaining co-ordination during bout swimming, but also a mechanism for ending the bout (by changing to coupling parameter values for which the in-phase mode becomes unstable). Note that the boundaries of the region in the parameter space ( $A, B, \epsilon$ ) for which the in-phase gait is stable have been determined analytically by deriving the linear variational equation governing the growth of small perturbations and computing the associated Hill's determinant [16, 17].

We propose that the stable anti-phase mode provides an analog for hovering mode. In localized regions around the bell, one segment is telling the nearby muscle to contract while the neighbouring segment is relaxing after a contraction. Thus, the stable anti-phase mode provides a mechanism for the neural system to remain active while producing insignificant net change in bell volume and negligible thrust.

We also propose that the asymmetric gaits provide a mechanism to drive asymmetric contraction of the bell to produce directional thrust and achieve turning capability. (Note that other turning mechanisms have been proposed, but they are not of primary interest to the current discussion because they require distinct input from the outer nerve ring associated with flight response.)

An additional parallel between the behaviour of the model and actual jellyfish involves the frequency of bell contractions during swimming. The muscle that contracts during swimming consists of myoepithelial cells that are arranged as a sheet of cells and thus basically constrained to two dimensions. As jellyfish grow, their muscles do not 'bulk' or grow additional fibres in parallel, as is the case for most skeletal muscle. Nonetheless, the work required to expel the water in the bell increases as the jellyfish grows and the volume of water in the bell increases. In order to increase the work produced, the muscles contract longer, not harder, and that timing is determined by the duration of the action potential. Spencer and Satterlie show that the duration of the action potential is directly proportional to the bell diameter of the jellyfish [4]. This property of the action potential is related to the growth of the jellyfish and does not change once the jellyfish is full grown. The van der Pol oscillator behaves in a similar fashion. Increasing the

non-linearity parameter ‘stretches’ the response by increasing the time between sudden jumps. For large values of  $\varepsilon$ , the period of the van der Pol limit cycle is linearly proportional to the non-linearity [19,20] and the effect of increasing the bell size can be simulated by increasing the effective non-linearity.

## 5. CONCLUSION

In this paper we have presented a network of coupled van der Pol oscillators to be considered as a simple model for the neural pattern generation governing typical locomotion in jellyfish. The model is derived by choosing the simplest possible (and best understood) continuous relaxation oscillator to model the jellyfish neural pacemaker and connecting each pacemaker with the simple, uniform, symmetric, linear diffusive coupling. The dynamics exhibited by this simplest oscillator network includes 3 classes of stable phase-locked modes: in-phase, anti-phase and asymmetric. Given the accepted understanding that neural oscillators trigger local contraction and relaxation of nearby muscle fibres, we propose that these stable phase-locked motions provide plausible analogs for the essential modes of ‘non-flight’ jellyfish locomotion: co-ordinated bout swimming, hovering and turning.

While asymmetric modes were absent from networks with very few oscillators ( $n = 4$  and  $8$ ), it still seems fairly remarkable that a system consisting of a few handfuls of the simplest non-linear oscillators with very simple coupling can produce behaviours arguably analogous to the variety of gaits needed for locomotion in a simple animal. Moreover, the model provides a simple mechanism for changing gaits (i.e. uniformly changing the effective strength of the coupling) that does not require any asymmetry, non-uniformity, or ‘rewiring’ of the system. Clearly future experimentation to achieve a more detailed understanding of how jellyfish function is a desirable goal, but until such detailed understanding is achieved, it remains interesting to determine the level to which simple models can capture the essential behaviours of seemingly complex systems. Given the current state of the art, animals as ‘simple’ as jellyfish still qualify as complex systems with rich and interesting behaviour, and appropriately simplified models can help us to determine how to advance our level of understanding.

## ACKNOWLEDGEMENT

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## REFERENCES

1. Romanes GJ. Physiology of the fresh-water medusa. *Nature*, London 1880; **22**(24 June):179–181.
2. Satterlie RA, Spencer AN. Neuronal control of locomotion in hydrozoan medusae. *Journal of Comparative Physiology A* 1983; **150**:195–206.
3. Spencer AN, Arkett SA. Radial symmetry and the organization of central neurones in a hydrozoan jellyfish. *Journal of Experimental Biology* 1984; **110**:69–90.
4. Spencer AN, Satterlie RA. The action potential and contraction in subumbrellar swimming muscle of *Polyorchis penicillatus* (hydromedusae). *Journal of Comparative Physiology A* 1981; **144**:401–407.
5. Minorsky N. *Nonlinear Oscillations*. Van Nostrand: Princeton, NJ, 1962.

6. Andersen CM, Geer JF. Power series expansions for the frequency and period of the limit cycle of the van der Pol equation. *SIAM Journal on Applied Mathematics* 1982; **42**:678–693.
7. Rand RH, Holmes PJ. Bifurcation of periodic motions in two weakly coupled van der Pol oscillators. *International Journal of Non-Linear Mechanics* 1980; **15**:387–399.
8. Storti DW, Rand RH. Dynamics of two strongly coupled van der Pol oscillators. *International Journal of Non-Linear Mechanics* 1982; **17**(3):143–152.
9. Cohen AH, Holmes PJ, Rand RH. The nature of the coupling between segmental oscillators of the lamprey spinal generator for locomotion: a mathematical model. *Journal of Mathematical Biology* 1982; **13**:345–369.
10. Di Bernardo D, Signorini MG, Cerutti S. A model of two nonlinear coupled oscillators for the study of heartbeat dynamics. *International Journal of Bifurcation and Chaos* 1998; **8**(10):1975–1985.
11. Linkens DA. Analytical solution of large numbers of mutually coupled nearly sinusoidal oscillators. *IEEE Transactions on Circuits and Systems* 1974; **CAS-21**(2):294–300.
12. Linkens DA. The stability of entrainment conditions for *RLC* coupled van der Pol oscillators used as a model for intestinal electrical rhythms. *Bulletin of Mathematical Biology* 1977; **39**:359–372.
13. Passano LM. Pacemakers and activity patterns in medusae: homage to Romanes. *American Zoologist* 1965; **5**:465–481.
14. Spencer AN. The parameters and properties of a group of electrically coupled neurones in the central nervous systems of a hydrozoan jellyfish. *Journal of Experimental Biology* 1981; **93**:33–50.
15. Wirkus S, Rand R. The dynamics of two coupled van der Pol oscillators with delay coupling. *Nonlinear Dynamics* 2002; **30**:205–221.
16. Storti DW, Reinhall PG. Phase-locked mode stability for coupled van der Pol oscillators. *Transactions of the ASME Journal of Vibration and Acoustics* 2000; **122**(3):318–323.
17. Low LA, Reinhall PG, Storti DW. A numerical investigation of phase-locked and chaotic behaviour of coupled van der pol oscillators. *Journal of Vibration and Acoustics* 2003; **125**(2):162–169.
18. Vancouver Aquarium Marine Science Centre. Aquafacts: Jellyfish. <http://www.vanaqua.org/education/aquafacts/jellyfish.html>
19. Dorodnicyn AA. Asymptotic solution of the van der Pol equation. *American Mathematical Society Translation Series 1*, 1962; **4**:1–23.
20. Kevorkian J, Cole JD. *Perturbation Methods in Applied Mathematics*. Springer: New York, 1981.