

Abstract

The small (1 mm) nematode *Caenorhabditis elegans* has become widely used as a model organism; in particular the *C. elegans* connectome has been completely mapped, and *C. elegans* locomotion has been widely studied (c.f. <http://www.wormbook.org>). We describe a minimal reaction-diffusion model for the *C. elegans*. This may be considered a simple model for Xu et al.’s ”descending pathway” description of the *C. elegans* central pattern generator (CPG) [1]. Olivares *et al* [2] present a likely more realistic model which relies on small networks of neurons, and presents a distributed model of the CPG. In particular, we use simulation methods to show that a small network of FitzHugh-Nagumo neurons (one of the simplest neuronal models) can generate key features of *C. elegans* undulation, and thus locomotion. Finally, we recreate the required oscillations and coupling with a network of coupled Keener [3] analog neurons.

The FitzHugh-Nagumo model

The FitzHugh-Nagumo equations have the form:

$$\begin{aligned}\frac{dv}{dt} &= f(v) - w + I_{ext} + D \cdot (v_{\text{driving}} - v) \\ \frac{dw}{dt} &= \epsilon(v - \gamma w + \beta) \\ f(v) &= v - \frac{v^3}{3}\end{aligned}$$

where v is the membrane potential, w is a slow inhibitor variable, and ϵ , γ and β are constants. It turns out that $f(v)$ can be any cubic-like function which sufficiently approximates $v - v^3/3$. A method for diffusive inter-neuron coupling has been introduced in green. D is the diffusion coefficient, and can be positive (excitatory synapses, gap junctions) or negative (inhibitory junctions). The quantity scaled by D is simply the voltage difference between the driving neuron and the driven one.

The central pattern generator

A central pattern generator is a small neural circuit which generates and regulates the movement of complex organisms. This structure is present in different forms in many animals, and it regulates many types of periodic motion. *C. elegans* is a small nematode with a well-known neuronal layout. Its central pattern generator can be sufficiently approximated by a simple neuronal network, arranged as such:The central pattern generator has two principal components.

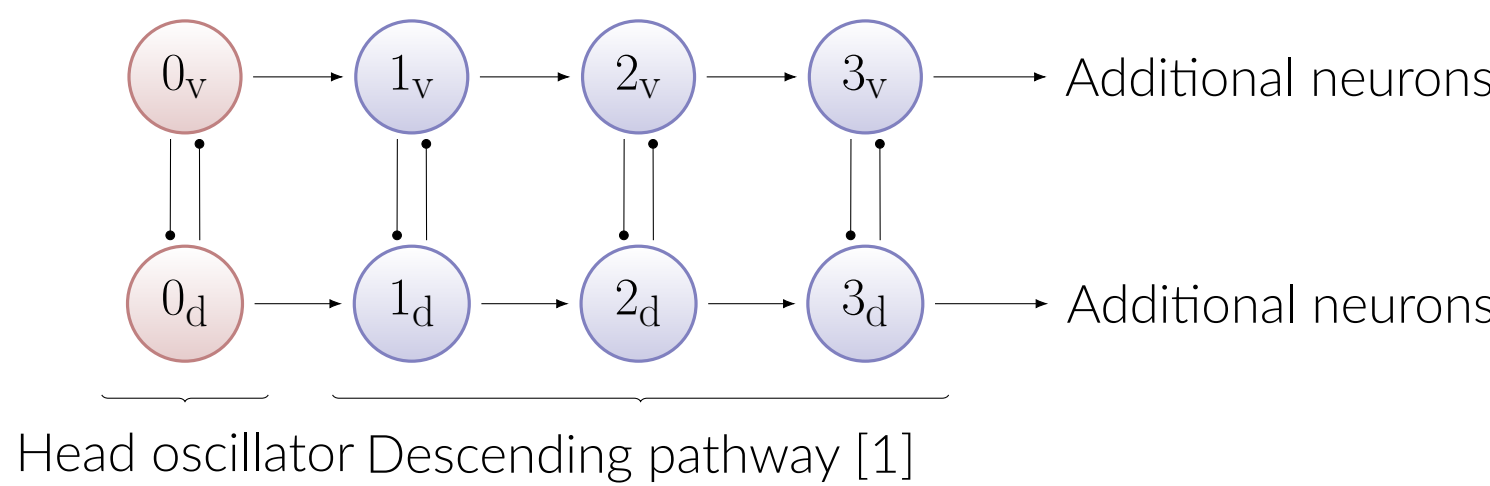


Figure 1. The central pattern generator, simplified.

wherein $0 \rightarrow 1$ represents unidirectional diffusion coupling, and $0 \leftrightarrow 1$ represents bidirectional diffusion coupling. The head oscillator drives the descending pathway to create sinusoidal oscillations.

Simulation and experimental data

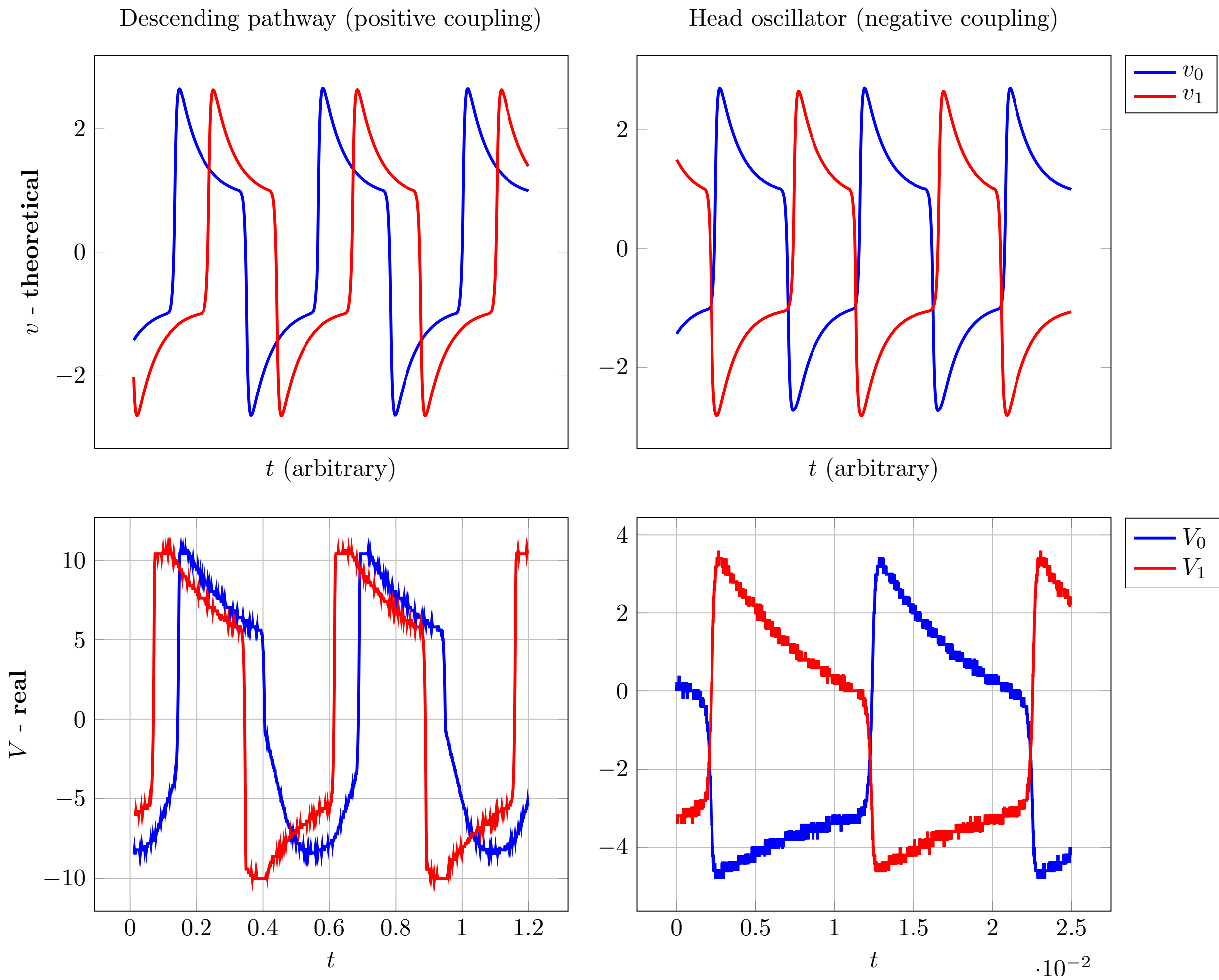
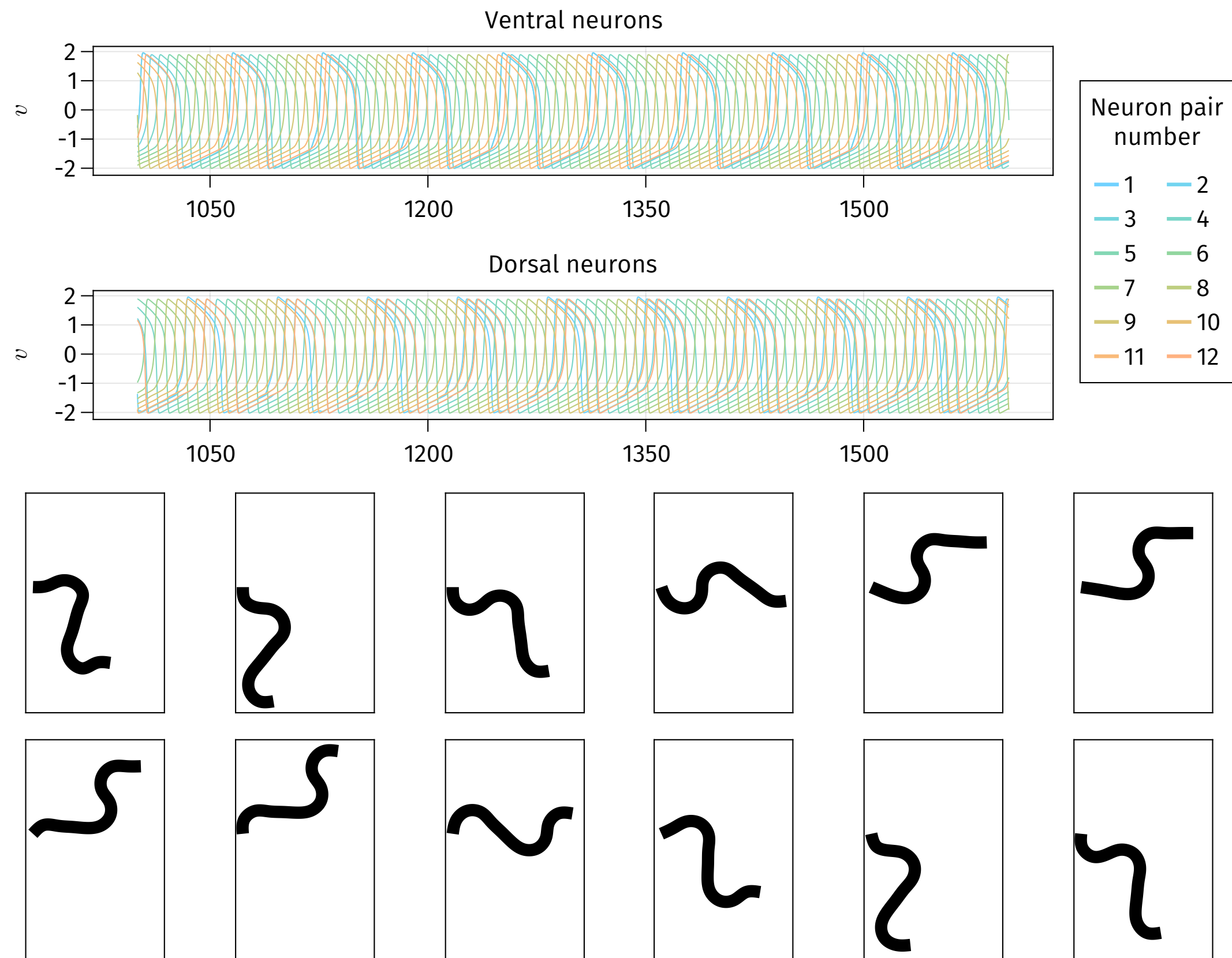


Figure 2. A comparison between simulation and analog implementation. Coupled systems of neurons can be used to describe all relevant dynamics of the CPG; in this instance, we use the head oscillator (mutually inhibitory coupling) and a single pair of ventral neurons with positive coupling, to simulate impulse propagation along the descending pathway.



The circuit

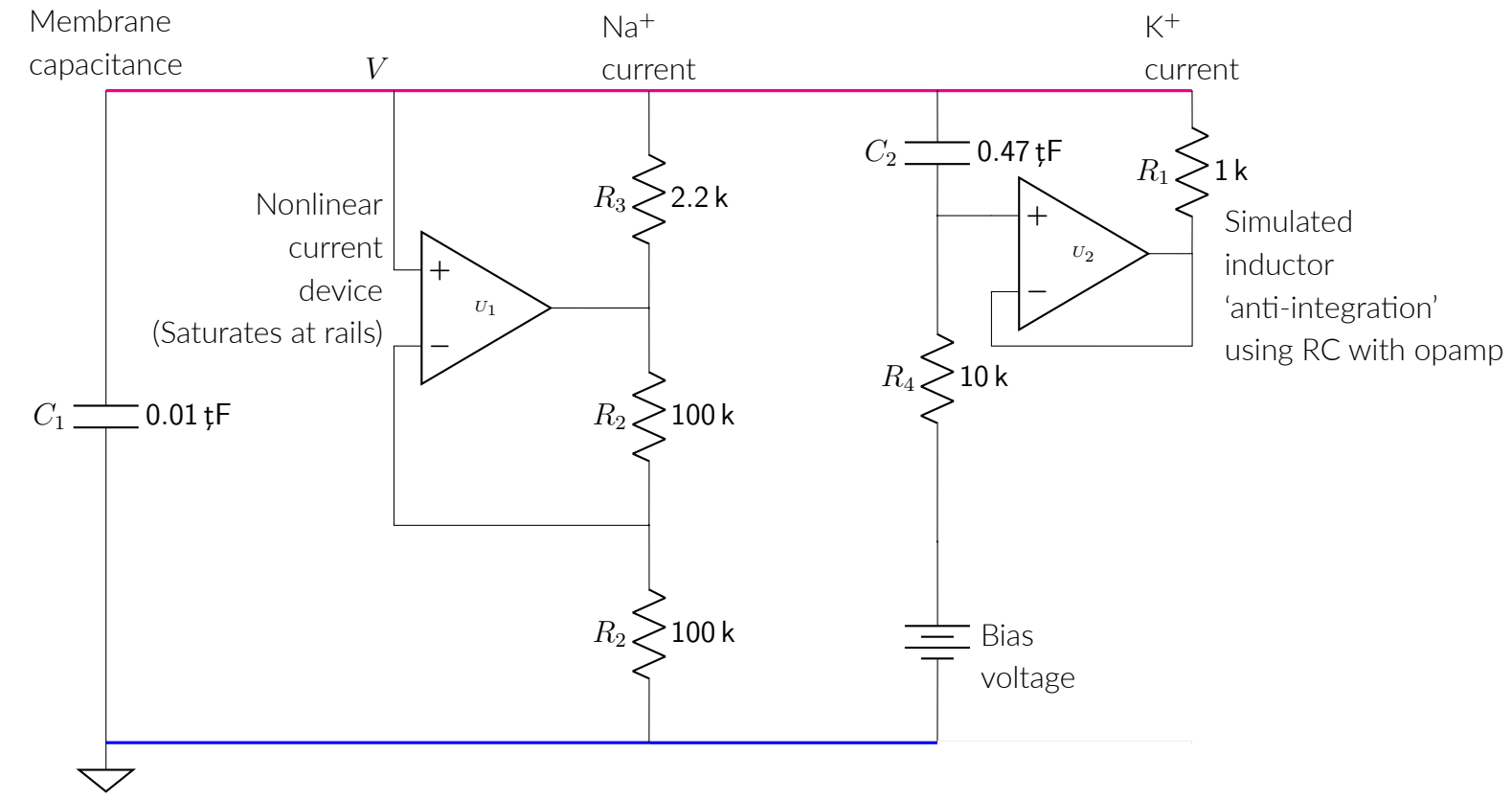


Figure 4. Our circuit (modified from [3]), simulating one Keener neuron.

The FitzHugh-Nagumo equations translate directly into a circuit that uses inductors, as $L = \frac{dI}{dt}$, however, that is an expensive and impractical solution due to mutual inductance effects. Keener’s circuit proposes a simulation of the inductors with operational amplifiers, which make the circuit considerably cheaper and stabler, and allow for a linear piecewise voltage response (from the op-amp) rather than a cubic one (from Nagumo’s tunnel diode), resolving the issue of long-term stability.

The frequency of oscillation changes with the values of the components, as well as the bias voltage, but is approximately 2 Hz with the circuit values here.

Coupling

We have implemented simple diffusion techniques, using a resistor to vary the coupling strength. Excitatory (positive-coefficient) coupling is implemented by a simple resistor, whereas inhibitory (negative-coefficient) coupling is implemented by an inverting amplifier, constructed using an operational amplifier and two resistors.

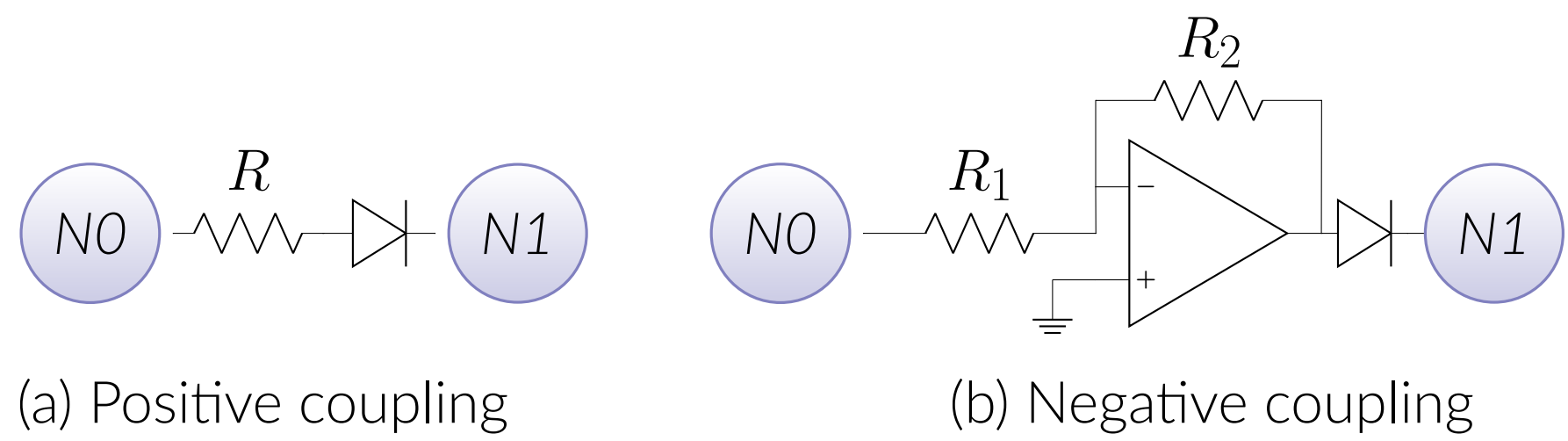


Figure 5. Different inter-neuronal coupling mechanisms.

References

¹ T. Xu, J. Huo, S. Shao, M. Po, T. Kawano, Y. Lu, M. Wu, M. Zhen, and Q. Wen, ”Descending pathway facilitates undulatory wave propagation in *Caenorhabditis elegans* through gap junctions”, PNAS (2018).
² E. Olivares, E. J. Izquierdo, and R. D. Beer, *A neuromechanical model of multiple network oscillators for forward locomotion in C. elegans*, preprint (July 22, 2019).
³ J. P. Keener, ”Analog circuitry for the van der Pol and FitzHugh-Nagumo equations”, IEEE Trans. Syst., Man, Cybern. (1983).
⁴ J. Gjorgjieva, D. Biron, and G. Haspel, ”Neurobiology of *Caenorhabditis elegans* Locomotion: Where Do We Stand?”,