## Invertebrate Pattern Generation: Overview

## **Detailed Description**

Central pattern generators (CPGs) are networks of neurons in the central nervous system (CNS) that produce patterned activity, usually as coherent oscillations, in the absence of external timing cues. CPGs provide timing input to motor neurons whose discharge dictates movements of muscles that control rhythmic behavior such as respiration or locomotion (Marder and Calabrese 1996). The long-held debate between scientists who believed half a century ago that rhythmic motor activity is generated by reflex chains and those who held the more radical view of centrally generated rhythms was resolved conclusively, in favor of the latter group, by demonstrating that neural networks generating rhythmic motor activity can do so in the isolated nervous system, in the absence of the body and therefore sensory feedback. In the early 1960s, these "fictive" motor patterns were first demonstrated to govern rhythmic activation in two invertebrate model systems: the movement of flight wings in locusts and the beating of swimmerets in crayfish (Wilson 1961; Ikeda and Wiersma 1964). The demonstration of fictive motor activity led to the development of in vitro preparations in search of the underlying CPG circuits. Although CPG networks have been traditionally described in the context of controlling motor activity, a more contemporary viewpoint of CPGs includes networks that subserve brain oscillations connected to sensory, cognitive, and memory tasks (Yuste et al. 2005).

CPGs have historically led systems neuroscience in the understanding of neural circuit interactions, partly because of the ease of identification of neurons and networks whose activity correlates with a rhythmic motor activity. The identification of neural circuits has been more successful in invertebrates where the number of neurons involved in neural processing is lower, sometimes by orders of magnitude, and the ability of identifying synaptic connections among neurons is facilitated by dual recordings. Vertebrate and especially mammalian neural circuit analysis was, until recently, performed with cruder techniques such as lesions, but in the past decade or so, genetic tools and the identification of molecular markers have allowed for more precise circuit analysis in the large networks of vertebrate systems (Han 2012; Arrenberg and Driever 2013). However, neural circuits have been identified only in a few vertebrate model systems and simple behaviors (Issa et al. 2011; Cangiano and Grillner 2005). The knowledge of the neural circuits and the ability to record functionally identified neurons in invertebrates have allowed for the in-depth analysis of the mechanisms underlying circuit dynamics and plasticity (Marder et al. 2005) as well as a rigorous description of the computations performed by the neural circuits (Selverston 2010).

The computational description of pattern-generating circuits evolved in parallel with the in vitro experimental studies of cellular and synaptic mechanisms. The complexities of circuit analysis of invertebrate CPGs have led to numerous modeling studies, some of which have been influential in shaping our conceptual understanding of both single-neuron and network operations. For example, the computational description of bursting oscillations, led by models of invertebrate CPG neurons (Plant and Kim 1976), paved the way for the complete mathematical analysis of bursting mechanisms in neurons and other excitable cells (Rinzel 1987; Rinzel and Lee 1987). This section of the Encyclopedia of Computational Neuroscience provides an overview of the contributions of invertebrate pattern generators in the context of computational models.

## **Cross-References**

Automated Parameter Search in Small Network Central Pattern Generators Bifurcations Dynamics of Single Neurons and Small Networks Bursting in Neurons and Small Networks Gap Junctions in Small Networks Half-Center Oscillators in Small Networks Invertebrate Neuromuscular Integration Neuromodulation in Small Networks Sensory Input to Central Pattern Generators Short-Term Synaptic Plasticity in Central Pattern Generators Stability and Homeostasis in Small Network Central Pattern Generators

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