

## “Experimental and computational analysis of an intersegmental coordination circuit”

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Many behavioral tasks require synchronization of distributed neural circuits, but details of the neural mechanisms that synchronize them are largely unknown. In the crayfish CNS, the modular local circuits that control swimmerets are distributed in four segments, but when the swimmeret system is active, the motor output from these modules are synchronized with a stable intersegmental phase-difference of 0.25, an example of metachronal synchronization. This phase difference is unaffected by changes in the system's period, an example of phase-constancy.

In each module, coordinating neurons encode detailed information about each cycle of the module's motor output as bursts of spikes, and export this information to modules in other segments. In a comprehensive set of recordings, we mapped the synaptic connections of two types of coordinating neurons onto their common target neurons in other segments – the intersegmental coordinating circuit. Each axon made its strongest synapse onto the target neuron in the nearest neighboring segment. Its synapses onto homologous targets in more remote segments were progressively weaker, a segmental gradient of synaptic strength. The shape-indices of these synaptic potentials (EPSPs) are tuned to transmit the coordinating information from each axon precisely. In each target neuron's own module, these bursts of EPSPs modified the phase of the module's motor output. Each target neuron decodes information from several coordinating axons, and the strengths of their synapses differ systematically. These differences in synaptic strength weight information from each segment differently, which we postulate can account for features of the system's characteristic metachronal synchronization.

The pattern-generating kernel of each swimmeret module has properties of a “half-center oscillator” in that it contains two sets of reciprocally-inhibitory local neurons that establish the key features of the module's output. In one approach to understanding the system's phase-constant properties, we modeled it as a chain of local circuits constructed with conductance-based neuron models. First, we examined the phase-response properties of these circuits for two fundamentally different mechanisms that produce anti-phase activity in individual circuits: the "escape" and "release" mechanisms. We demonstrated that these different mechanisms give rise to very different phase-response properties, and we used phase-plane arguments to explain the different shapes of the phase-response curves. We then compare properties of these models to properties of the swimmeret system's coordinating circuit, and consider the system's synchrony and phase constancy.