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Classic model, new dynamics

Physical Review Letters **86,** 4278-4281 (7 May 2001)

In a seminal paper[1] published in 1967, Art Winfree proposed a model for the spontaneous synchronization seen in large populations of biological oscillators, such as flashing fireflies or cardiac pacemaker cells. He discovered that in a system of weakly coupled, nearly identical oscillators, increasing the coupling strength can lead to the temporal analogue of a phase transition. As the coupling strength increases beyond a threshold value, the oscillators start to synchronize, until finally they exhibit locked amplitudes and phases.

Fireflies exhibiting spontaneous synchronization. Image © SPL.

As Joel Ariaratnam and Steven Strogatz recount in a paper in this week's *Physical Review Letters*, Winfree's model has since been refined and applied to an incredible range of systems, from arrays of semiconductor lasers or Josephson junctions to bubbly fluids and neutrino flavour oscillations. Yet the dynamics of Winfree's original model have gone largely unexamined, owing to its mathematical intractability.

Ariaratnam and Strogatz rectify this omission by identifying a special case of Winfree's model that can be solved exactly — one in which the influence of each oscillator on another takes the form of a smooth, pulse-like function ($1 + \cos q_i$, where q_i is the phase of the influencing oscillator), modulated by a sinusoidal response function ($-\sin q_j$, where q_j is the phase of the oscillator receiving the stimulus). Although this response function is chosen for its tractability, the authors point out that certain biological rhythms exhibit roughly sinusoidal resetting in response to weak pulses of light.

In the limit of weak coupling and a narrow range of oscillator frequencies, Ariaratnam and Strogatz's model reduces to a well understood refinement of Winfree's model, the Kuramoto model, which is known to exhibit locked, partially locked or incoherent behaviour, depending on the values of the coupling strength k and frequency distribution width g. But the *PRL* authors' examination of the full k-g phase diagram for their special case reveals previously unrecognized, hybrid states, in which subsets of the oscillators behave differently, according to their natural frequencies. For example, in one such hybrid state, a collection of oscillators in the middle of the frequency range are locked together, while the slower ones are intermittently locked and the faster ones drift incoherently.

Ariaratnam and Strogatz relate their model to recent work on 'pulse-coupled oscillators', which are of interest as possible model neurons. But the authors unashamedly declare their interest to be "more mathematical than biological", and clearly revel in the discovery of "a fascinating wealth of dynamics that, curiously, escaped notice for over thirty years".

Phase Diagram for the Winfree Model of Coupled Nonlinear Oscillators
JOEL T. ARIARATNAM & STEVEN H. STROGATZ
In 1967 Winfree proposed a mean-field model for the spontaneous synchronization of chorusing crickets, flashing fireflies, circadian pacemaker cells, or other large populations of biological oscillators. Here we give the first bifurcation analysis of the model, for a tractable special case. The system displays rich collective dynamics as a function of the coupling strength and the spread of natural frequencies. Besides incoherence, frequency locking, and oscillator death, there exist hybrid solutions that combine two or more of these states. We present the phase diagram and derive several of the stability boundaries analytically.
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1. Winfree, A. T. Biological rhythms and the behavior of populations of coupled oscillators. *J. Theor. Biol*. **16,** 15-42 (1967).

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