

Multimodal regimes in chains of electrically coupled oscillators of Morris-Lecar type

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Abstract

We study chains of strongly electrically coupled oscillators of Morris-Lecar type. When individual oscillators are in the regime close to an Andronov-Hopf bifurcation, the coupled system exhibits a variety of oscillatory behavior. The structure and bifurcations of stable periodic solutions are investigated using numerical and analytic techniques. The work is motivated by the firing modes found in a compartmental model of a dopaminergic neuron [4].

Dopaminergic neurons (DNs) in substantia nigra and ventral tegmental area in mammalian brain exhibit distinct firing patterns: regular and irregular spiking, and bursting. These modes of firing are determined by intrinsic properties of the cell and are not altered by synaptic input. Wilson and Callaway suggested that the cell geometry was important for the generation of firing modes in DNs. This view was substantiated by calcium imaging experiments and mathematical modeling [4, 2]. In [4] a coupled oscillator model of a DN was proposed. Individual oscillators in this model represent compartments (not necessarily small) of the dendrite with approximately constant cross-sectional diameter. The intrinsic dynamics in each compartment is oscillatory and except for natural frequency of oscillations is identical for all compartments. The natural frequency of oscillations in individual compartments is set by the compartment diameter and is varied along the cell. The equations in the neighboring compartments are strongly electrically coupled. Despite a sharp gradient in the natural frequency of oscillations along the chain, the coupled system exhibits oscillations at a common frequency, which are preceded by pronounced transients in average calcium concentrations. The calcium transients can cause the variation in the firing rate of the coupled system. The Wilson-Callaway model reproduces all salient features of the rhythmic firing in DNs: synchronous oscillations, calcium transients, and spike frequency adaptation.

The mathematical analysis of the Wilson-Callaway model has revealed that the duration of calcium transients is determined by the interplay of two parameters: the strength of electrical

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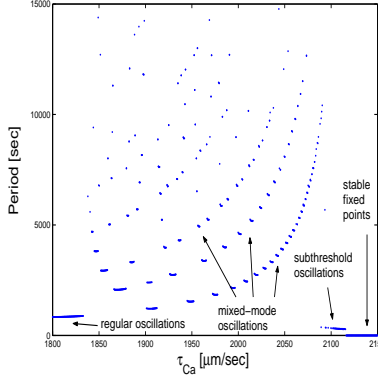


Figure 1: For a compartmental model of DN, the periods of stable solutions are plotted versus the rate of calcium efflux.

coupling and the rate of calcium extrusion from the cell [1, 2]. The latter dominates in the regime modeled in [4]. It turns out that the variation of the rate of calcium efflux also has a significant impact on the form and the frequency of the limit cycle oscillations of the coupled system. This is important because this suggests a possible mechanism for spike frequency adaptation and bursting in DNs. The study of these phenomena is the main motivation for the present work.

The individual oscillators in the Wilson-Callaway model are in the regime that is close to an Andronov-Hopf bifurcation. Small changes of the rate of calcium efflux or injected current in individual compartments result in a variety of stable multimodal solutions of the coupled system. These periodic solutions are composed out of small amplitude oscillations near an unstable fixed point and full amplitude relaxation oscillations. We use asymptotic and numerical methods to study the structure and bifurcations of the mixed-mode oscillators. As a first step, we propose a simplified model that captures the main features of chains of Morris-Lecar oscillators [3], but uses only essential nonlinearities. This allows us to simplify the calculations and to identify parameters responsible for various aspects of the system's dynamics. We have found that while the individual oscillators contribute equally to the generation of the frequency of full amplitude oscillations of the coupled system [1, 2], the frequency of the small amplitude oscillations may be determined by a single dominating oscillator. We show that the bifurcation diagram of the coupled system near the Andronov-Hopf bifurcation has an unexpected structure. Unlike the bifurcation diagrams for individual oscillators, that for the coupled system has an unusually long branch of small amplitude periodic solutions, and there is a family of stable mixed-mode periodic solutions nearby in the parameter space. The wave form and the period vary greatly across the family of mixed-mode solutions (see Figure 1). Similar situation may be encountered in a broader class of models.

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