

Title:

NETWORKS OF PLANAR NEURAL ORGANIZING CENTERS

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Category:

A. Theory and Analysis



☐ Theme:

Theme:

## Excitable membranes and synaptic mechanisms















## **ABSTRACT:**





It has been found that a codimension-three focus type degenerate Bogdanov-Takens bifurcation at a cusp organizes the Type I excitability of neural membranes and also has parameter regions for Type II. We derive and analyze a canonical model for weakly connected neural networks of multiple such bifurcations, and apply the canonical model to study the emergence of synchrony and the dynamics of associative memorization in some cases of certain biologically motivated circuits. We also simulate strongly connected neural oscillators and two-component models of mixed types constructed from this model, and bursting from periodic variation of parameters.

**Keywords:** bifurcation; canonical model; nonhyperbolic neural network; synchrony; type I excitable membrane; weakly connected neural network;

## SUMMARY:

### 1. Introduction:

As a stimulating current that is being applied to a patch of excitable membrane is slowly increased, the membrane resting state typically will be perturbed from its resting potential by one of only two ways: the equilibrium state disappears by merging with a saddle point at a saddle-node or fold bifurcation (which is a "turning point" on the current-potential  $I$ - $V$  diagram), or loses stability at a Andronov-Hopf bifurcation. If in the first case there is a nearby saddle-node on a limit cycle, perhaps due to a saddle-node separatrix loop, an action potential is formed and the membrane is called Type I. If in the second case the Hopf bifurcation is subcritical and near a double-limit cycle bifurcation, repetitive firing ensues and the membrane is called Type II [2,6,8]. In Type I, action potentials emerge with a fixed amplitude within a narrow range of amplitudes, but arbitrarily low frequencies which depend upon the strength of the applied current. In the sub-critical Type II scenario above, the repetitive spiking emerges with a fixed amplitude and a fixed frequency within a narrow range of frequencies, relatively insensitive to the strength of the stimulating current.

Whenever in a neural model the inward current equilibrates fast in comparison to a outward potassium current so that one may consider only the two-dimensional dynamic system involving just the membrane potential and the single slow outward current, these two methods of initiating active membrane properties -- saddle-nodes and Hopf points -- are only merged at Bogdanov-Takens bifurcation points. This is because the linearized system has a zero eigenvalue at a saddle-node (where the implicit function fails), and a purely imaginary conjugate pair of eigenvalues at a Hopf point whose magnitude is the frequency of the small amplitude emerging self-sustained oscillations. These two points can merge in the plane when the frequency vanishes at a Bogdanov-Takens point which has double-zero eigenvalues. However, in Hodgkin-Huxley type models, saddle-nodes (as well as Hopf plus any saddle separatrix loops) always occur in pairs that arise from cusp or hysteresis points (and Hopf centers or homoclinic bifurcations).

The reason for this is that when the membrane potential (or applied current) is very large in absolute value, the ion gates are either almost completely closed or completely open ( $m, n = 0, 1$  and  $h = 0$ ) and the system becomes essentially linear with a globally stable equilibrium. As a result, for very positive or negative  $V$  and  $I$ , the curve of stationary solutions  $V$  vs.  $I$  is approximately linear with positive slopes. For all values of  $V$ , there exists a unique equilibrium with  $I$  given by a continuous function of  $V$  [5]. Thus turning points (folds) in the  $V$  vs.  $I$  equilibrium curve must occur in pairs which can be eliminated (smoothed out) at hysteresis (cusp) points. Similarly, because of the global asymptotically stable node at  $V, I = \pm\infty$ , a limit cycle arising from a Hopf bifurcation must be annihilated by another Hopf bifurcation or homoclinic orbit [7].



The simplest situation in which all of these various bifurcations and the two types of neural excitability can and do occur is in the neighborhood of a focal type degenerate Bogdanov-Takens-cusp codimension-three bifurcation [1,4], which we have shown by normal form theory and numerics to be present in several neural models, including Hodgkin-Huxley and Morris-Lecar [3]. At this bifurcation, a Bogdanov-Takens point merges with a cusp, which are remarkably close in multi-parameter bifurcation diagrams of Type I systems. Much of the possible dynamic behavior of these neural systems is topologically conjugate to the dynamics that occur in the normal form of this bifurcation, which has an unfolding as the second-order cubical equation

$$x'' = \mu_1 + \mu_2 x + \alpha x^3 + (\mu_3 + x - x^2)x'$$

with  $\alpha < -\frac{1}{8}$ . For the reasons discussed above, we believe it to be simplest possible

planar organizing center for Type I neural excitability and thus a canonical model. Here, there is a codimension-two separatrix loop at a saddle-node, and the "ghost" of this saddle-node near a codimension-one saddle separatrix loop causes the slow relaxation dynamics responsible for the characteristic long flat intermediary voltage trace due to A-type currents in Type I spiking pacemaker neurons. Moreover, there are also parameter regions of Type II excitability in this model.

## 2. Applications:

Although this model has very complex dynamics, it has a relatively few parameters and a simple form that is amenable for some analysis and simulation. One application that we have made of this model is in strongly connected neural oscillators and two-compartment models. We considered a Type I compartment driving a Type II compartment, such as an axon hillock with an A-current stimulating an axon without one. Results include complex finite pulses, quasiperiodic and chaotic spikes, and spiking where the amplitude and the frequency both increase as the applied current is increased.

We have also regarded the effect of varying periodically the parameter that controls the type of excitability and recurrent excitation. Results include complex bursting and chattering, and the appearance of three-dimensional Shil'nikov saddle-focus homoclinic bifurcations [9].

## 3. Weakly Connected Networks of Planar Neural Organizing Centers

A local canonical model for multiple focal degenerate Bogdanov-Takens-cusp bifurcations (Theorem): Suppose a weakly connected neural network of the form

$$\begin{aligned} \frac{dx_i}{dt} &= y_i \\ \frac{dy_i}{dt} &= f_i(x_i, y_i, \mu) + \varepsilon g_i(x, y, \mu, \rho, \varepsilon) \end{aligned}$$

is near a multiple focal degenerate Bogdanov-Takens-cusp bifurcation at  $x = y = \mu = 0$ , and the internal unfolding parameter

$$\mu(\varepsilon) = (\mu_1, \mu_2, \mu_3)$$

with  $\mu(0) = 0$  satisfies the adaptation condition

$$\frac{D(f_i)}{d\mu} \cdot \mu'(0) + g_i = 0$$

(realized by  $\mu_1'(0) = \rho(0)$  for the external input  $\rho(\varepsilon)$  when the uncoupled system is in block normal form). Then the network has a local canonical model:

$$\begin{aligned} \frac{du_i}{d\tau} &= v_i \\ \frac{dv_i}{d\tau} &= \mu_2'(0)u_i + \alpha_i u_i^3 + \mu_i v_i + \sum_{j=1}^n c_{ij} u_j \\ &+ \sqrt{\varepsilon} \left( \mu_1''(0) + \mu_3'(0)v_i - u_i^2 v_i + \sum_{j=1}^n d_{ij} v_j + \rho'(0) + \sum_{j=1}^n \sum_{k=1}^n e_{ijk} u_j u_k \right) \end{aligned}$$

for  $i = 1, \dots, n$  where  $\alpha < -\frac{1}{8}$ , and  $\tau = \sqrt{\varepsilon}t$  is the slow time.

We analyze this canonical model and apply it to investigate the emergence (or lack) of synchronous oscillations in coupled pairs and chains of oscillators, and mutually or sequentially inhibitory circuits. We also look at the possibility of using such networks as attractor or oscillatory associative memories.

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