

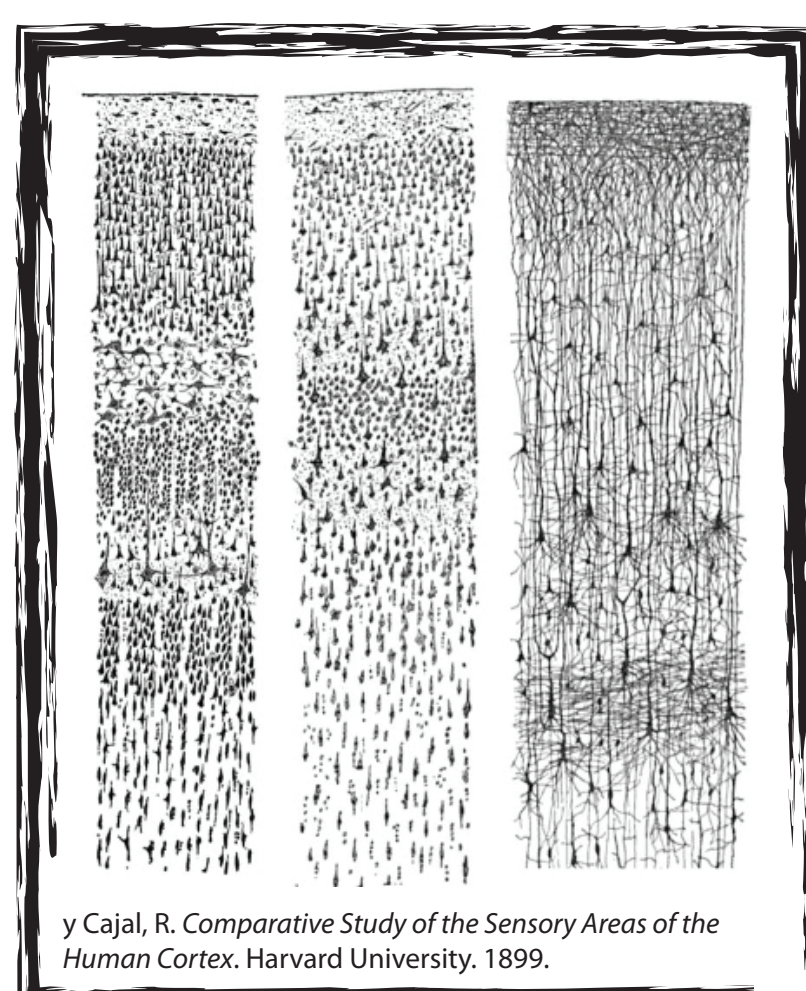
Introduction

Chaotic behavior in a spatially extended system is often referred to as **spatiotemporal chaos**. The trajectories of a system as it evolves through state space are described by **irregular spatial and temporal patterns**.

In mathematical biology, spatiotemporal chaos has been demonstrated in chemotaxis models (Painter & Hillen, 2011) predator-prey models (Sherratt, J. & Fowler, A., 1995) and the Hodgkin-Huxley neural model (Wang, Lu, & Chen, 2006).

Transient chaos is a special case of chaotic dynamics in which the system dynamics collapses without external perturbation. Rather, collapse is an intrinsic property of the system.

Here, we diffusively couple many **spiking neurons** into a ring network and find that the network dynamics can collapse on to two different species of attractor: the **limit cycle** and the **steady-state** solution.



The Morris-Lecar Model

$$C \dot{V} = I_{app} - I_{Ca} - I_K - I_L$$

$$\dot{n} = \frac{n - n_{ss}}{\tau_n}$$

$$I_{Ca} = g_{Ca} M_{ss} (V - V_{Ca})$$

$$I_K = g_K n (V - V_K)$$

$$M_{ss} = \frac{1}{2} \left(1 + \tanh \frac{V - V_1}{V_2} \right)$$

$$n_{ss} = \frac{1}{2} \left(1 + \tanh \frac{V - V_3}{V_4} \right)$$

$$\tau_n = T_0 \operatorname{sech} \left(\frac{V - V_3}{2V_4} \right)$$

The Morris-Lecar model was derived empirically from the barnacle giant muscle fiber (Morris & Lecar, 1981). The **system equations** describe the *membrane potential* (V) of the neuron as a function of ion currents and the *state of the potassium channel* (n). The *applied current* (I_{app}) is the **bifurcation parameter**.

The **channel equations** describe each current's value across the membrane as it depends on each channel's *Nernst potential* (V_{Ca} and V_K).

Each channel has a **voltage-dependent activation function** associated with it. The potassium channel has an additional term, τ_n , describing the *time-course* of potassium channel activation.

Parameters: $C = 20$ [uF/cm²] - Membrane Capacitance, $g_K = 8$ [uS/cm²] - Potassium conductance, $g_{Ca} = 2$ [uS/cm²] - Leak Conductance, $V_L = -60$ [uS/cm²] - Leak Equilibrium Potential, $V_{Ca} = 120$ [mV] - Ca Equilibrium Potential, $V_K = -80$ [mV] - K Equilibrium Potential, $V_1 = -1.2$ [mV] - Potential when $M_{ss} = .5$, $V_2 = 18$ [mV] - reciprocal slope of M_{ss} voltage dependence, $T_0 = 15$ [s] - time constant, $g_{Ca} = 4$ [uS/cm²] - Class I Calcium Conductance, $V_3 = 14.95$ - Potential when $n_{ss} = .5$, $V_4 = 17.4$ [mV] - reciprocal slope of n_{ss} voltage dependence

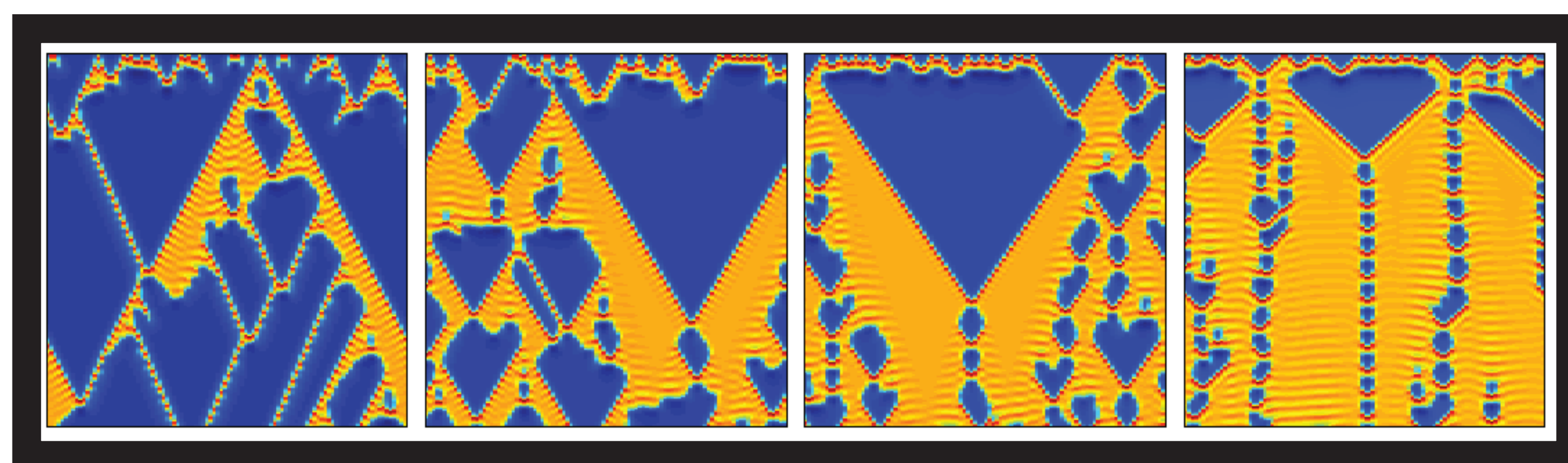
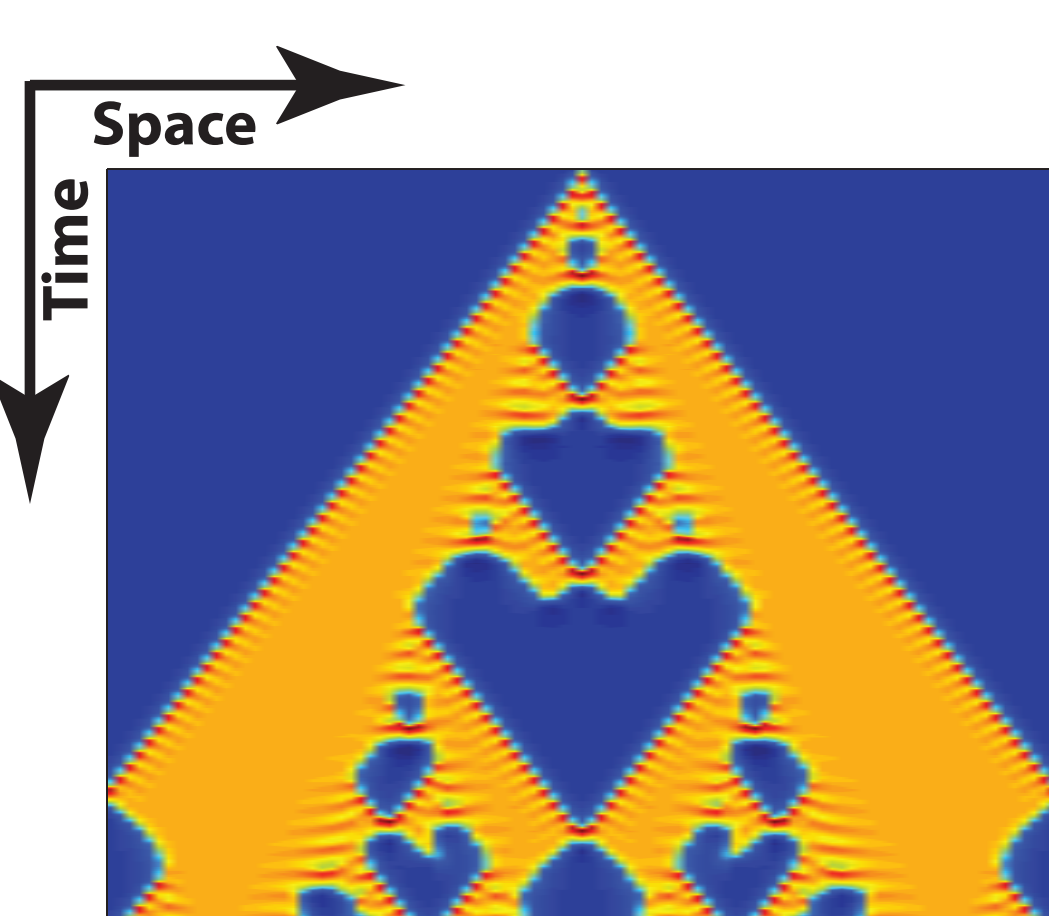
Electrically Coupled Neural Network

A coupled ring network consists of several Morris-Lecar neurons. Each neuron's membrane potential is coupled to the membrane potential of its neighbor through a **diffusive coupling term**:

$$\dot{V}_i = f(V, n) + D(V_{i+1} + V_{i-1} - 2V_i)$$

The coupling term allows information from one neuron to spread across the network through neighboring interactions. In a network at resting potential, neurons moved to the excitable region are called **kicker neurons**.

Figures: a **single kicker** neuron spreads activity through the network (**right**). The vertical axis represents time (descending). The horizontal axis represents individual neurons in the network. The membrane potential is described by the color (blue: resting potential). **Below:** the effect of **several kickers** as the bifurcation parameter is increased. Starting from the left, $I_{app} = 28.5, 30, 32, 38$.

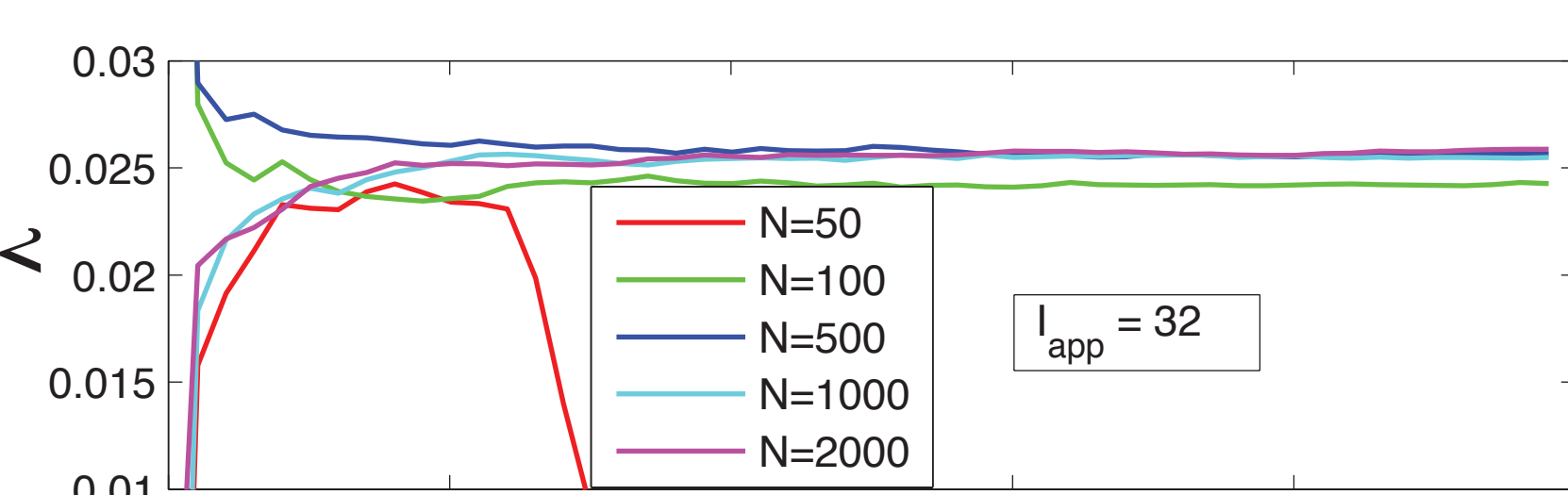
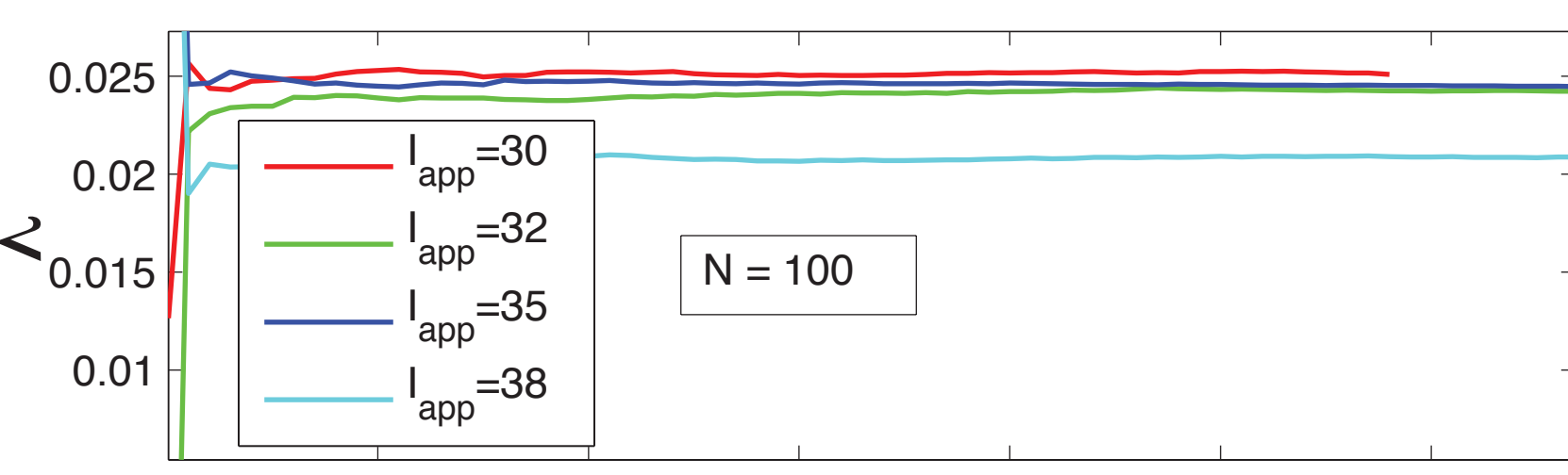


Applied Current

Existence of Chaos

The Morris-Lecar ring network is a **chaotic system**. Measurements of the maximum **Lyapunov exponent** (λ) result in a positive number, showing that solutions that start near each other in phase space diverge exponentially.

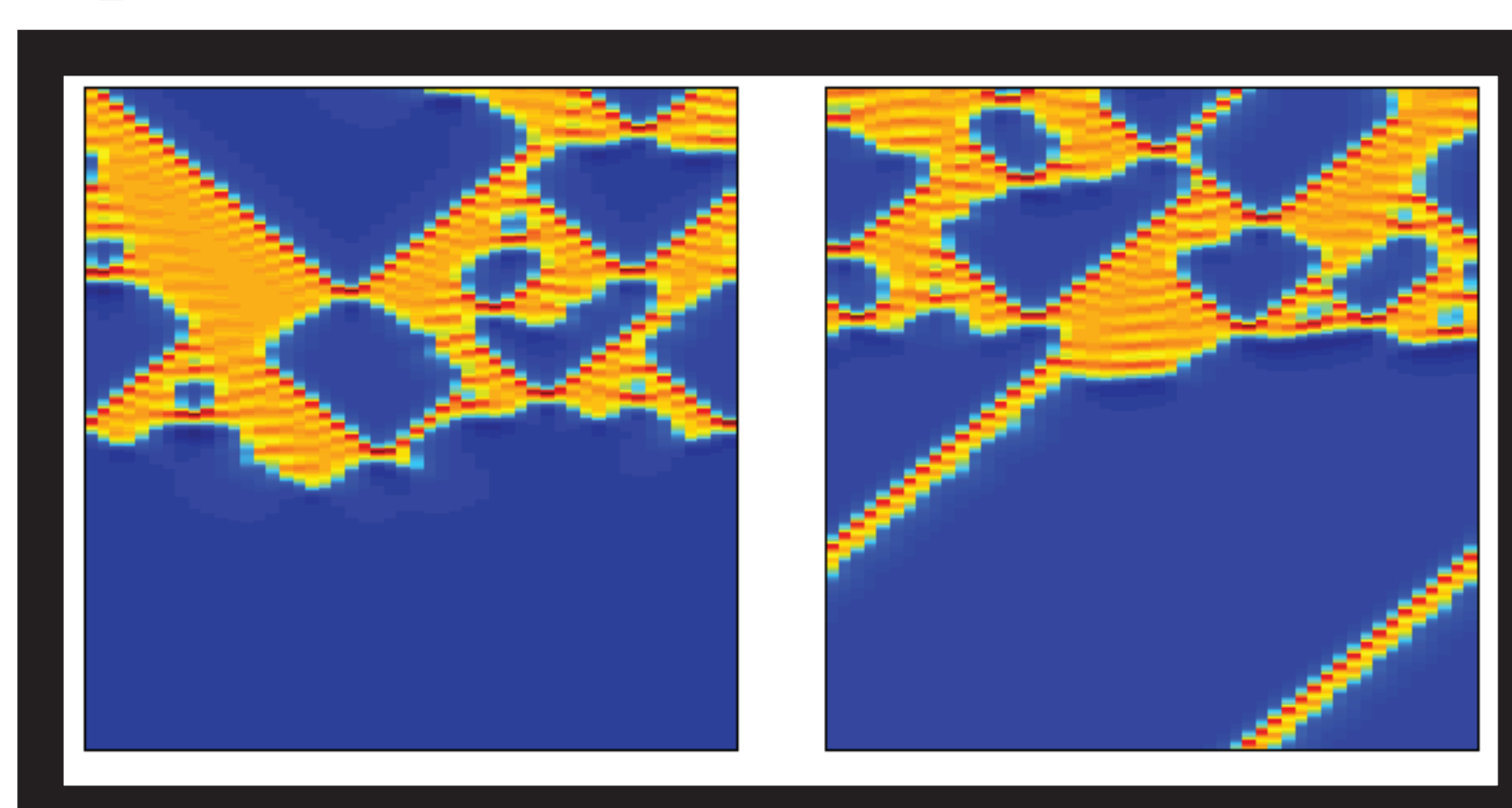
As the bifurcation parameter is increased (**top**) the Lyapunov exponent **decreases**. When the network size increases (**bottom**), the Lyapunov exponent **increases**.



Collapse of Chaos

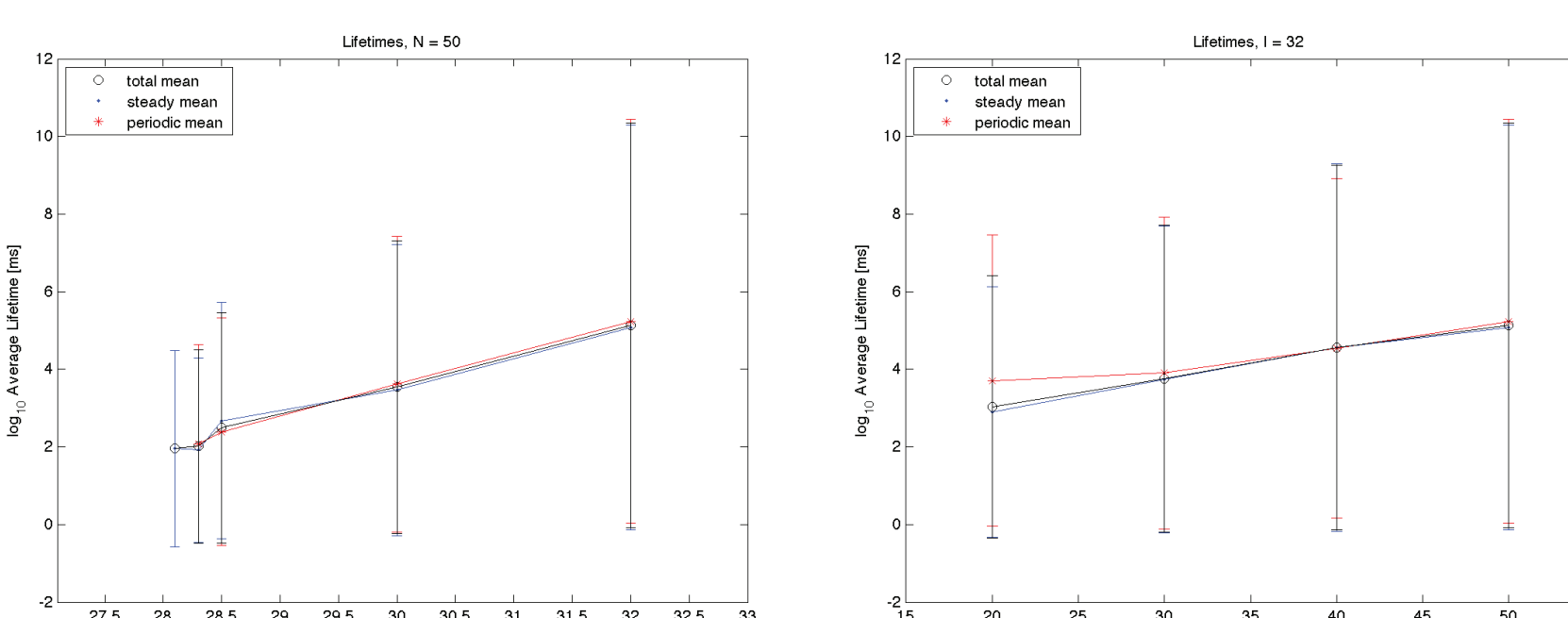
Transient chaos is characterized by a sudden collapse of chaotic dynamics in the absence of external perturbations, indicating that collapse is an intrinsic property of many deterministic systems.

Figures: The Morris-Lecar ring network exhibits transient chaos that can collapse on to two species of attractor: the stable fixed point in which the whole network falls to the resting potential (**left**), or a limit cycle, in which activity cycles around the network periodically (**right**).



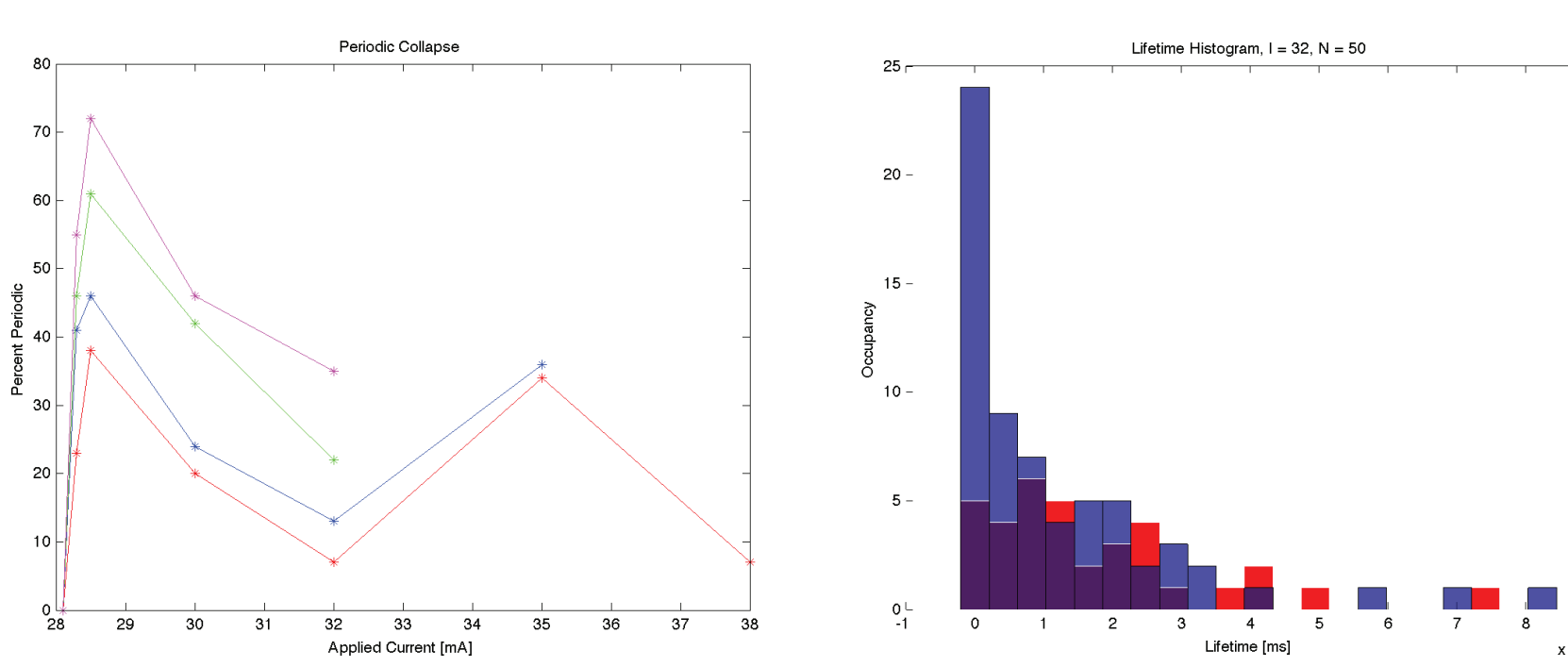
Lifetime analysis shows that prior to collapse, chaotic behavior can persist over large temporal scales. These lifetimes increase exponentially as the bifurcation parameter (**left**) is increased. Lifetimes also tend to increase as the network size (**right**) is increased, as is common for systems exhibiting transient spatiotemporal chaos (Wackerbauer & Showalter, 2003).

Figures: Lifetimes of transient chaotic behavior across I_{app} (**left**) and system size (**right**).



Periodic collapse behavior is more common near particular bifurcation parameter, and increases uniformly with the network size. Lifetime analysis (**above**) shows that both periodic and steady states have the same average lifetime, but the histogram details a wider distribution for the steady-state solutions.

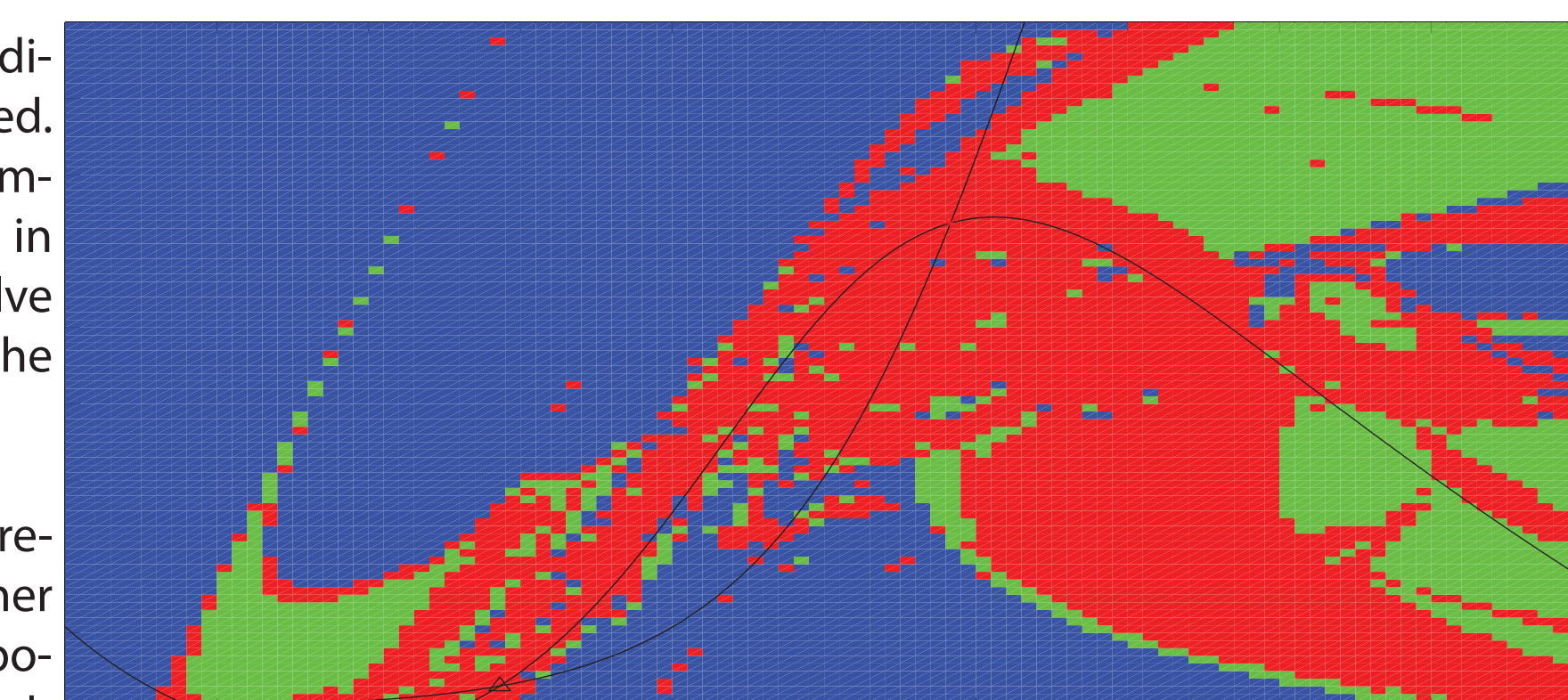
Figures: Probability of a collapse to periodic behavior (**left**) as a function of I_{app} . A histogram of lifetimes (**right**); steady (blue) and periodic (red) for $I_{app} = 32$.



Transient Basins of Attraction

A basin of attraction gives the set of initial conditions for which a particular attractor is reached. Here, the "transient" basin of attraction is computed. A set of neurons are moved to a point in phase space and the network is allowed to evolve deterministically for 1000ms. At that point, the state of the network is determined.

Only a particular subset of neurons are represented by the color of the phase point. All other neurons in the network are either at resting potential, or relaxed on the chaotic saddle, depending on the study (see **Basin Figures 2 & 3**).



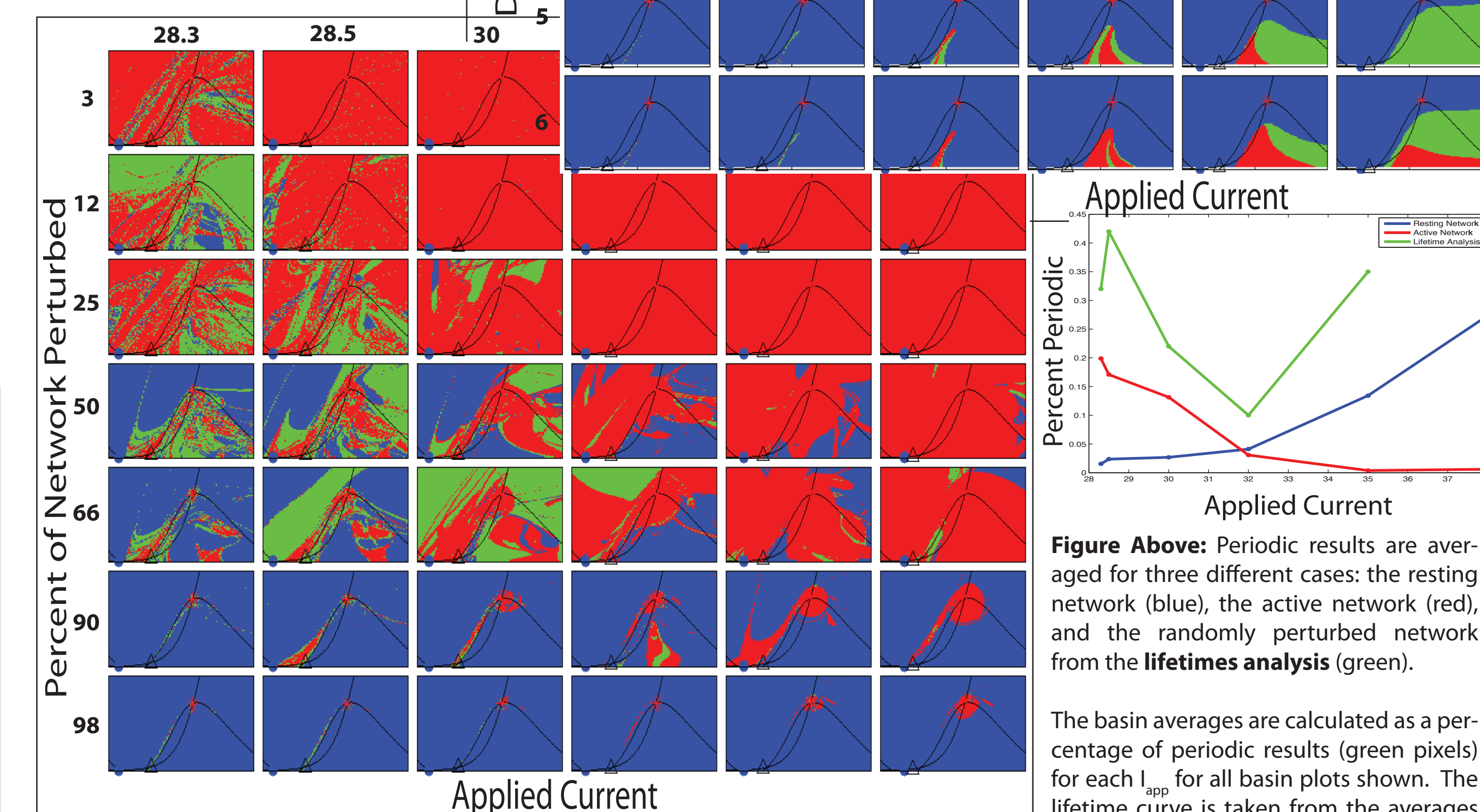
Basin Figure 1: The basin represents the initial conditions for which the system reached an attractor (**blue - steady state, green - periodic**) or those for which the system dynamics did not collapse (**red**).

Mechanisms of Collapse

A transient basin study demonstrates two distinct mechanisms for collapse in the diffusively-coupled ring network. For a network mostly at rest, periodic solutions are more probable for higher current values, but for an active network relaxed on the attractor, the lower current values carry a higher probability of collapsing onto the limit cycle. As the perturbation size is increased, the probability of periodic collapse begins to spread to higher applied current. On the other hand, such large synchronized perturbations are unlikely in the closed system that experiences no external perturbation with the exception of a near collapse. In a near collapse, most neurons fall to the rest state except a small cluster of neurons that may either re-activate the network, or collapse its dynamics. This moves the network closer to the rest regime, where larger applied current is associated with a higher chance of collapse to the periodic state. These data suggest **distinct collapse mechanisms dominate interactions in different regions of the parameter space**.

Basin Figure 2: **Right:** the network at rest is perturbed with two kickers at varied distances from each other. The basin becomes indistinguishable from a single neuron perturbation around a distance of six.

Basin Figure 3: **Below:** an active network is initiated by randomly perturbing 1/5 of the neurons and letting the trajectories approach the vicinity of the chaotic saddle that drives the chaotic behavior. Then a fraction of neurons (vertical axis) are perturbed at random locations in the network.



Discussion

The empirically-derived Morris-Lecar neuron model makes a powerful element for a network study, allowing a compromise between complexity and computational efficiency. The system can express drastic changes over short temporal scales, shifting from an active chaotic state to simple periodic or steady-state behavior. Correlation studies reveal no long-term spatial or temporal correlation between members of the ensemble and collapse comes suddenly, without warning. System collapse is an intrinsic property, occurring in the absence of external influence.

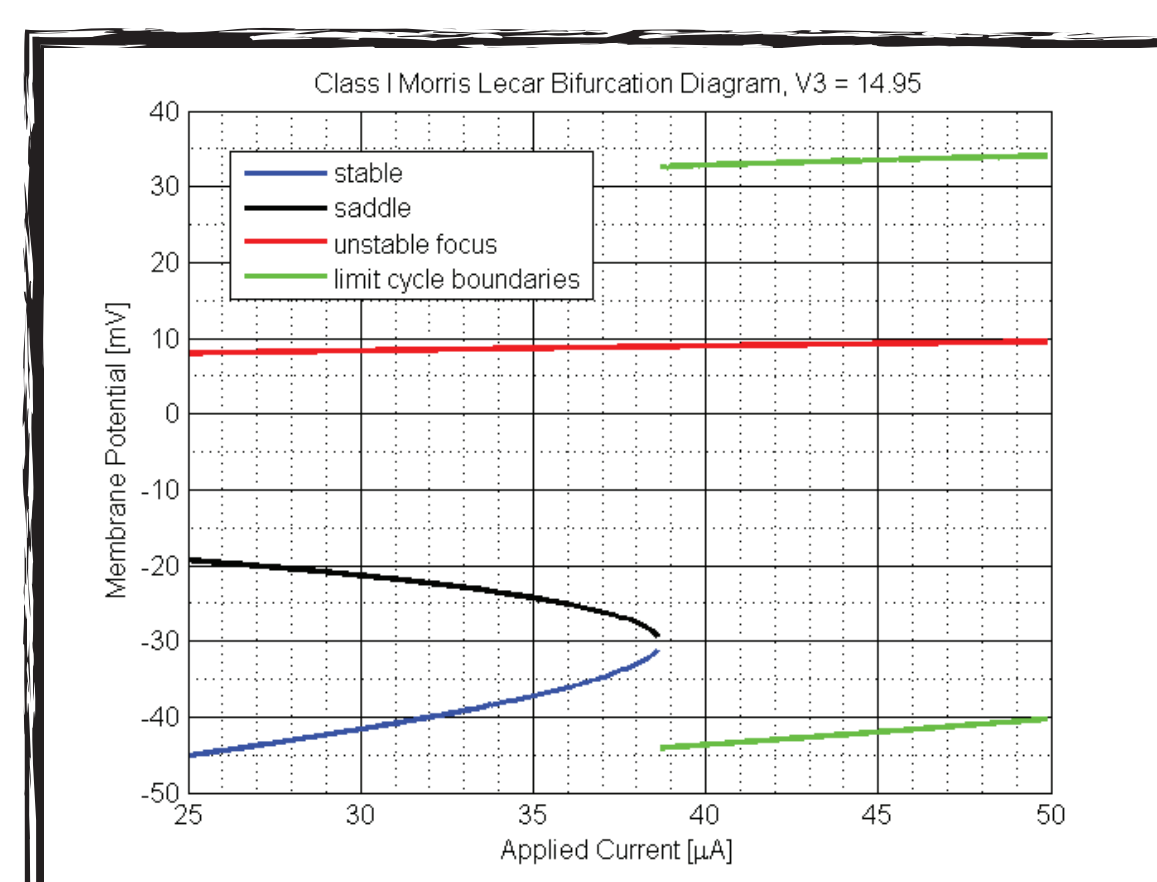
Chaos can persist in the network for long lifetimes, but the system always inevitably collapses to either a periodic (on) or steady (off) state. That complicated interactions with a binary result can occur in a diffusively-coupled system of spiking neurons implies a significant role for gap junctions in neural computation, especially with respect to lateral information transfer in parallel wired transmission. Gap junctions serve as gateways between cells. In the CNS, both astrocytes and neurons rely on gap junctions for intercellular communication. In neurons, gap junction coupling is sufficient to evoke action potentials and can synchronize activity across a network (Velazquez & Carlen, 2000). Gap junctions have been found connecting axons in the adult hippocampus (Hamzei-Schiani et al, 2007) and throughout the adult cerebral cortex (Nadarajah, et al, 1998). They have also been shown, in conjunction with inhibitory synapses, to modulate inspiratory motoneuron synchronization (Bou-Flores, C. & Berger, A., 2000).

Gap Junction References:
 Bou-Flores, C. & Berger, A. (2000). Gap Junctions and Inhibitory Synapses Modulate Inspiratory Motoneuron Synchronization. *Journal of Neurophysiology* 85 (4), 1543-1551.
 Hamzei-Schiani, F. et al (2007). Gap junctions on hippocampal mossy fiber axons demonstrated by thin-section electron microscopy and freeze-fracture replica immunogold labeling. *PNAS* 104 (30), 12548-12553.
 Nadarajah, B. et al (1998). Gap junctions in the adult cerebral cortex: Regional differences in their distribution and cellular expression of connexins. *The Journal of Comparative Neurology* 376 (2), 326-342.
 Velazquez, J.P. and Carlen P.L. (2000). Gap junctions, synchrony and seizures. *Trends in Neurosciences* 23 (2), 68-74.

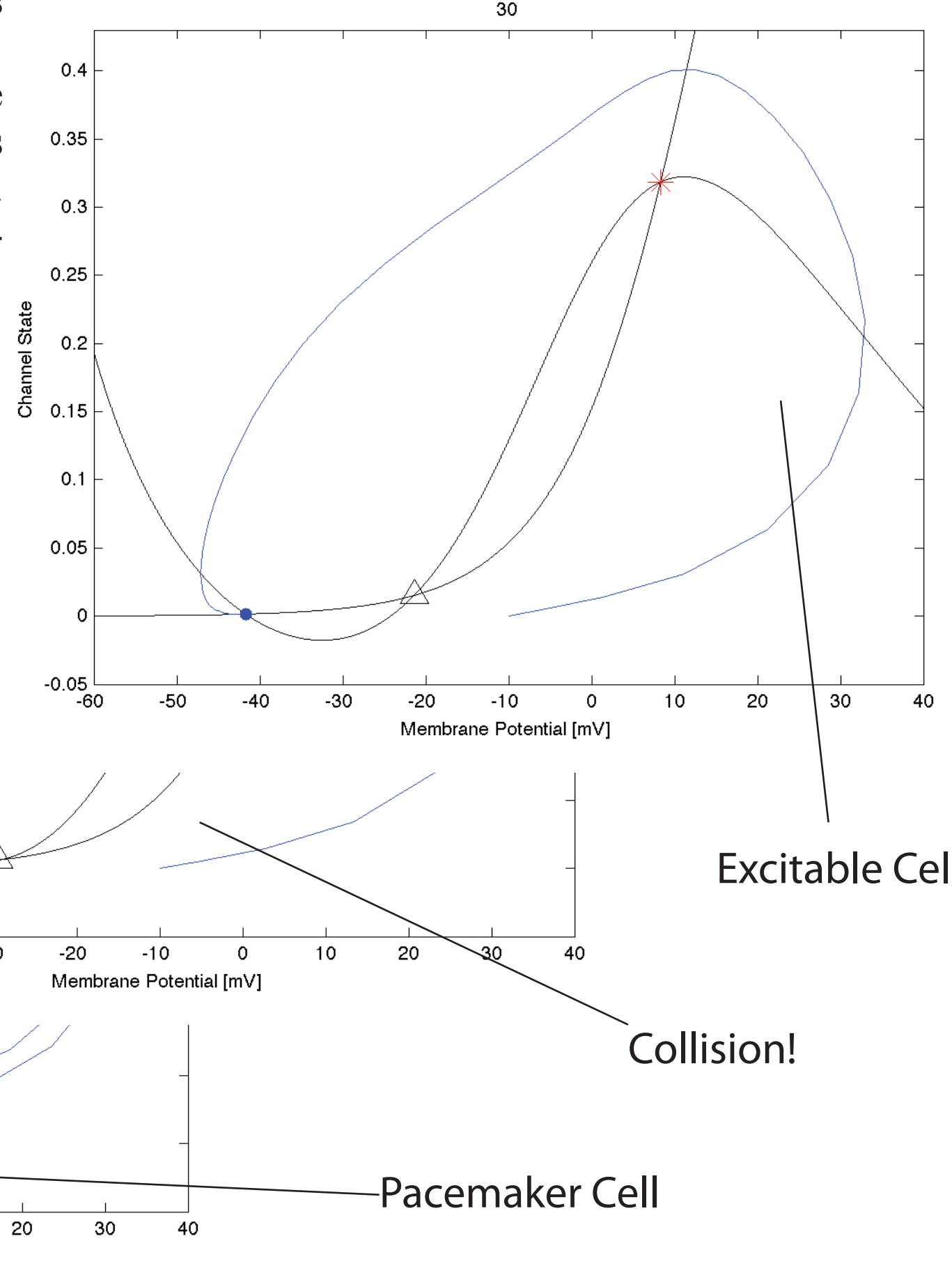
Stability Analysis

The **nullclines** of the system describe where each of the system equations equals zero, and thus no change in that variable occurs. At their intersection, the system is in equilibrium. If the equilibrium point is unstable, the slightest perturbation will push trajectories away.

Figure: A **bifurcation diagram** (**right**) demonstrates how the fixed points in the system change as a function of the bifurcation parameter. A **saddle-node bifurcation** occurs around $I_{app} = 38.8$ mA. This study is restricted to the **excitable** parameter regime $I_{app} < 38.8$, where the neuron remains at resting potential until acted upon by an external perturbation. Phaseplots (**below**) depict the nullclines.



In the parameter range of interest, the Morris-Lecar system has three fixed points. A **stable point** (blue dot) a **saddle-point** (black triangle) and an **unstable focus** (red asterisk). The **V-nullcline** shifts upwards as the bifurcation parameter (I_{app}) is increased and the **n-nullcline** is fixed in this parameter regime. This results in the intersection points colliding and annihilating each other as I_{app} approach 38.8 mA, where a stable limit cycle is born (**below**). The blue trace represents a typical trajectory for a single neuron.



Excitable Cell

Collision!

Pacemaker Cell