# Excitable cells as dynamical systems

## Part 2: excitability and bursting

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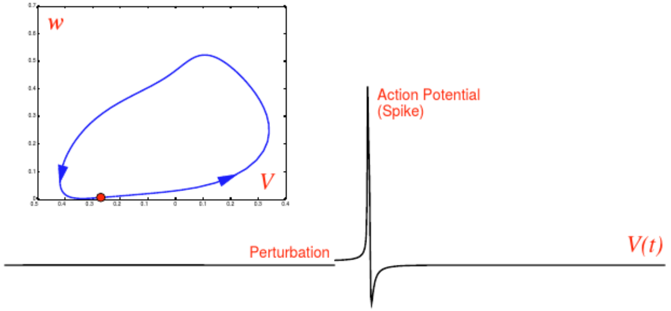
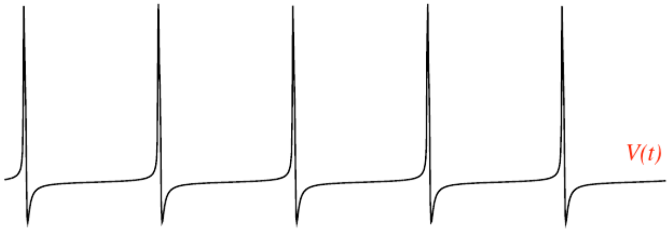
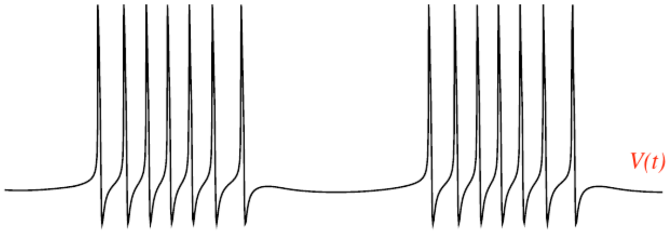
# Excitability, spiking and bursting



Neural Excitability

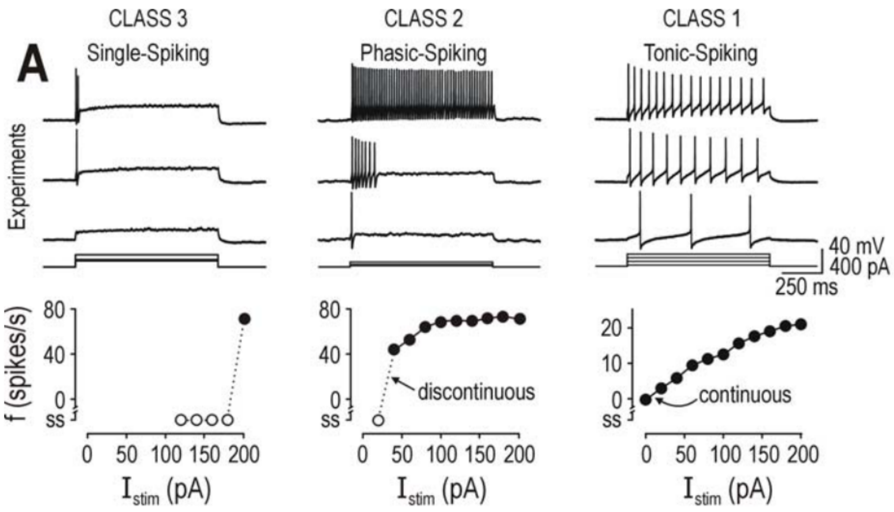


Periodic Spiking



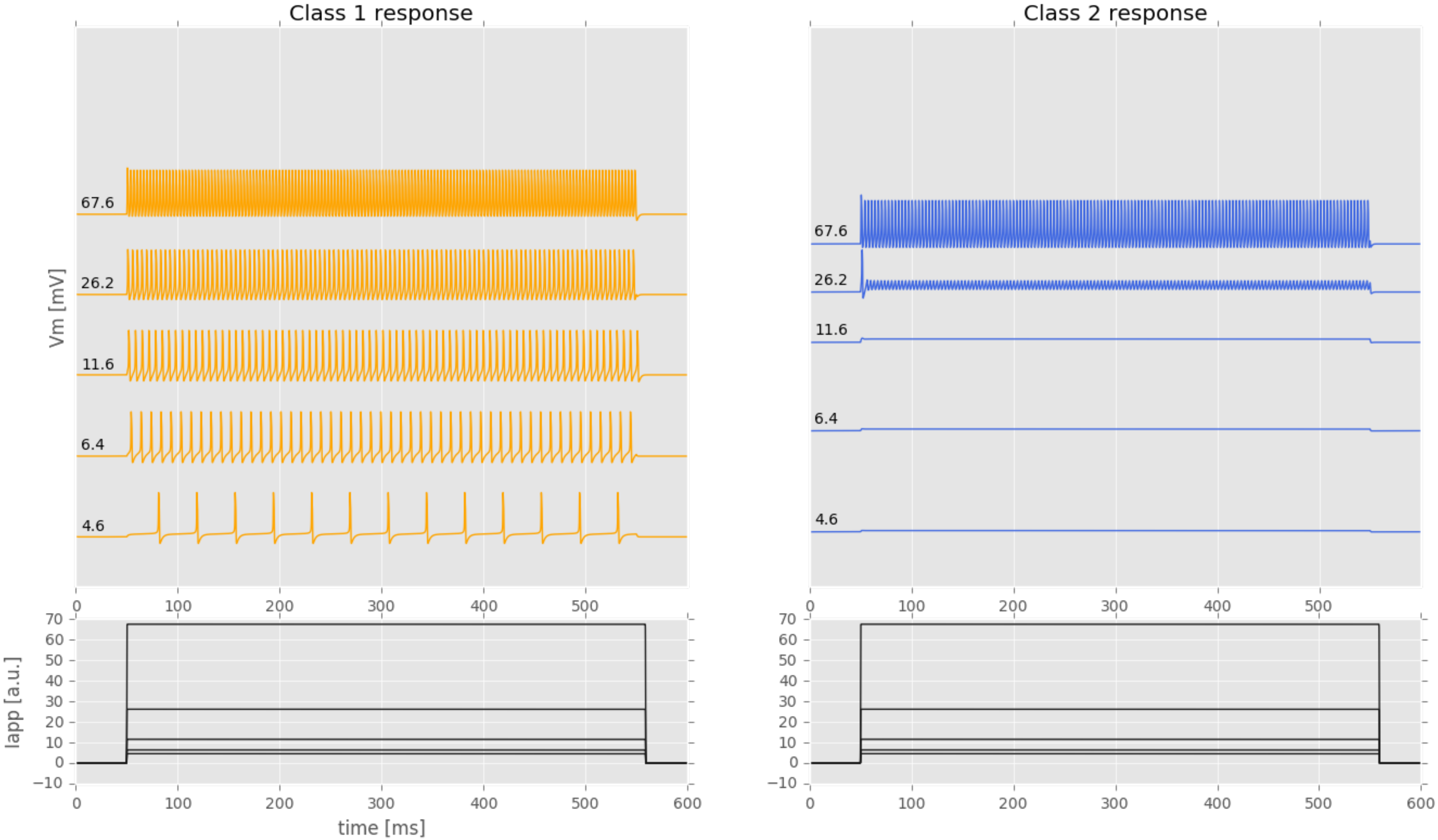
Periodic Bursting

E. Izhikevich *International Journal of Bifurcation and Chaos,* **10:** 6 (2000) 1171–266 (c) World Scientific Publishing Company

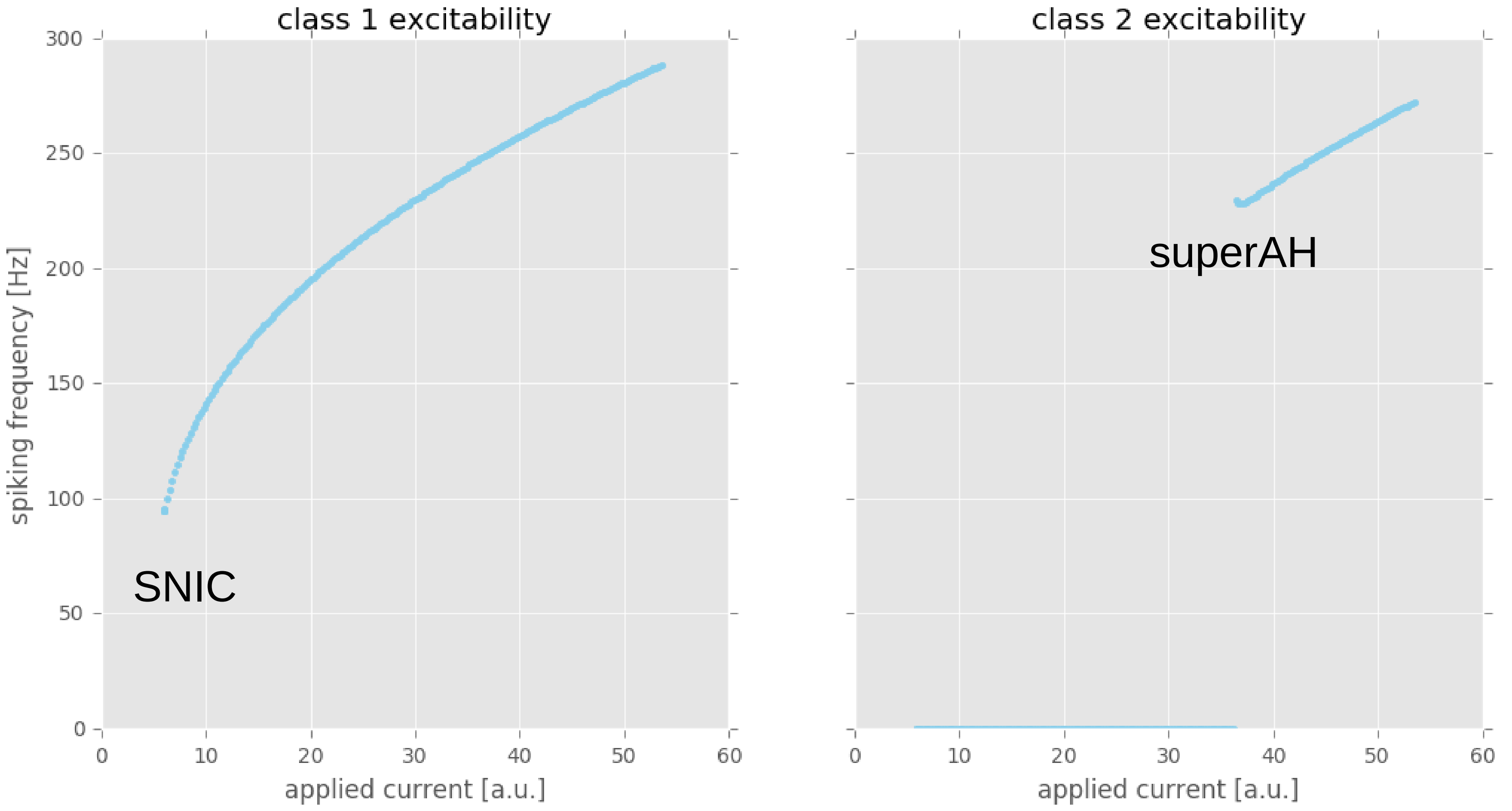


Prescott SA, De Koninck Y, Sejnowski TJ (2008) *PLoS Comput Biol* 4(10): e1000198. doi:10.1371/journal.pcbi.1000198

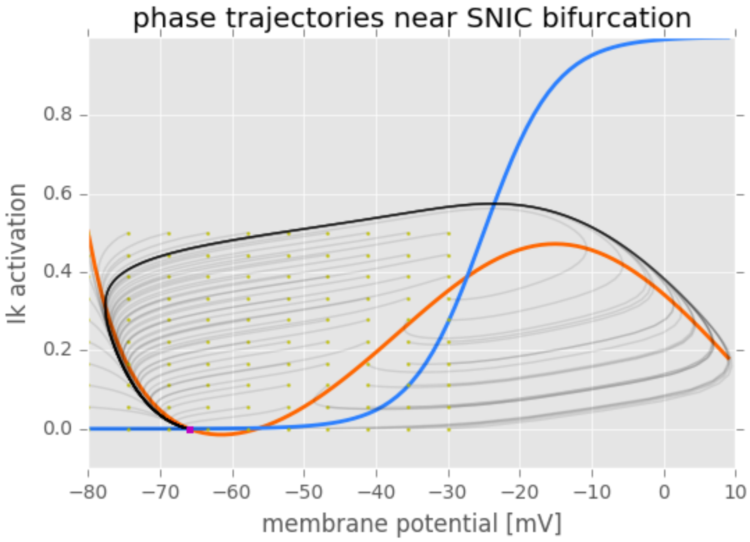
# Hodgkin classification of excitability ($I_{Na,p}+I_K$ model)

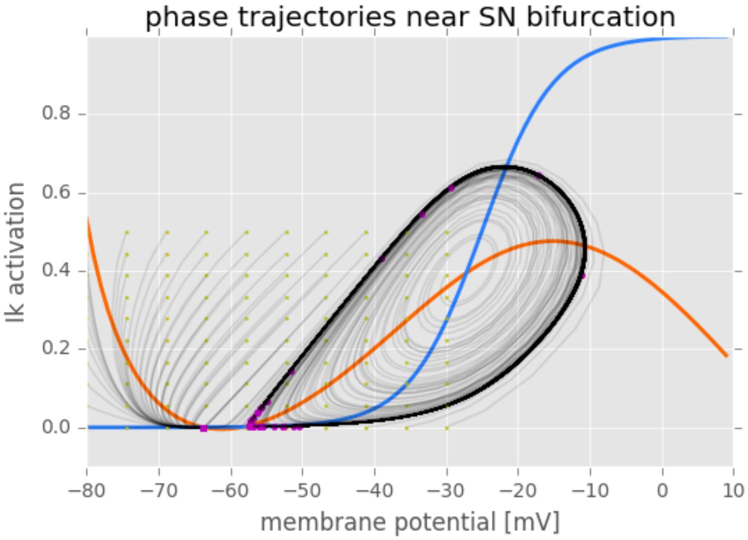


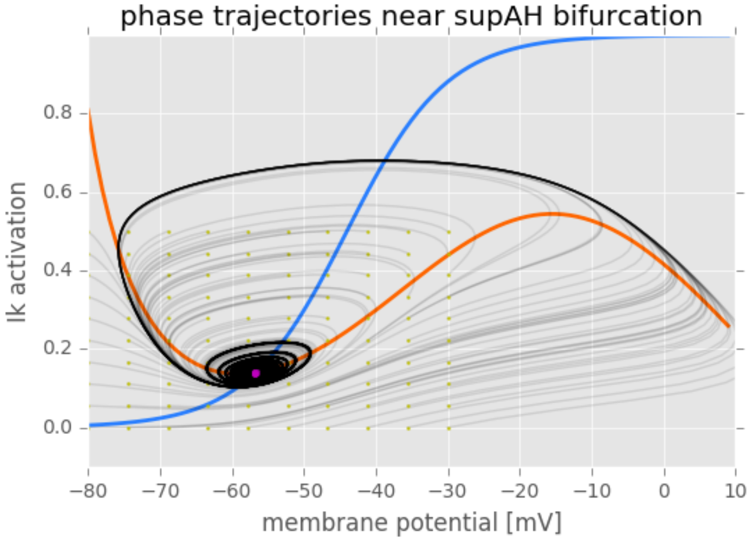
# Hodgkin classification of excitability ($I_{Na,p}+I_K$ model)

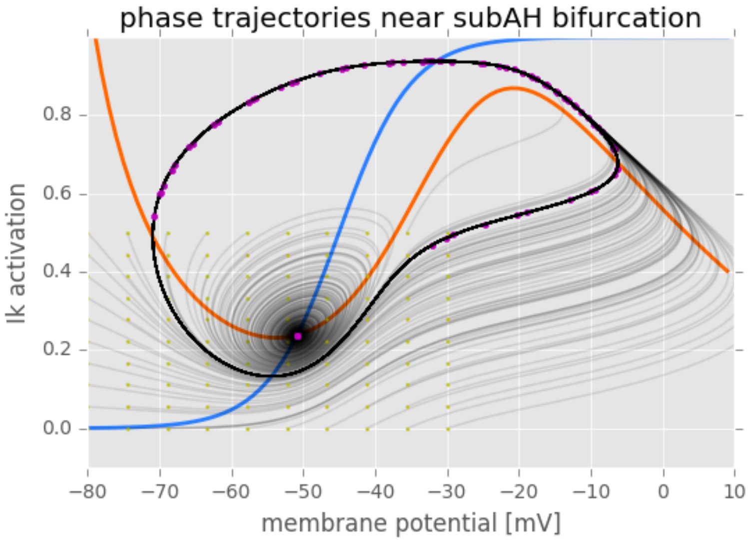


# Excitability and bistability in $I_{na,p}$+$I_K$-model near the 4 bifurcations of the resting state

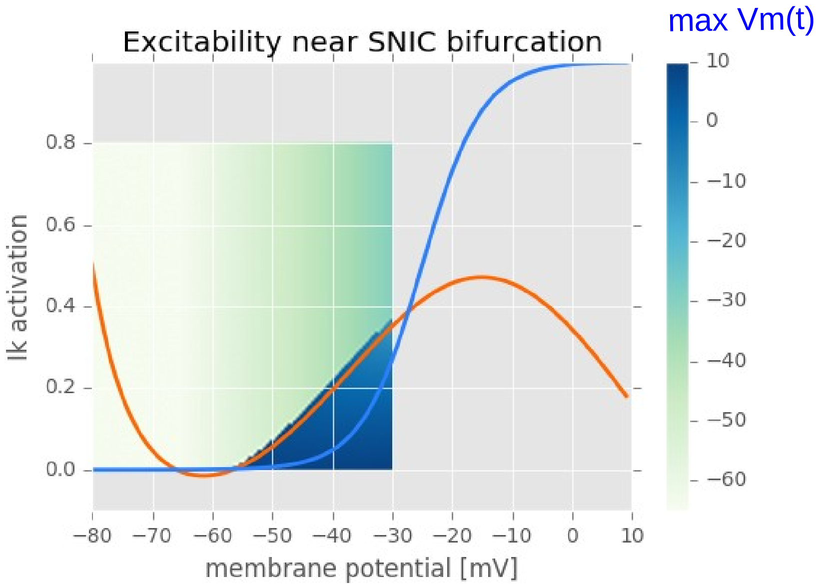

phase trajectories near SNIC bifurcation

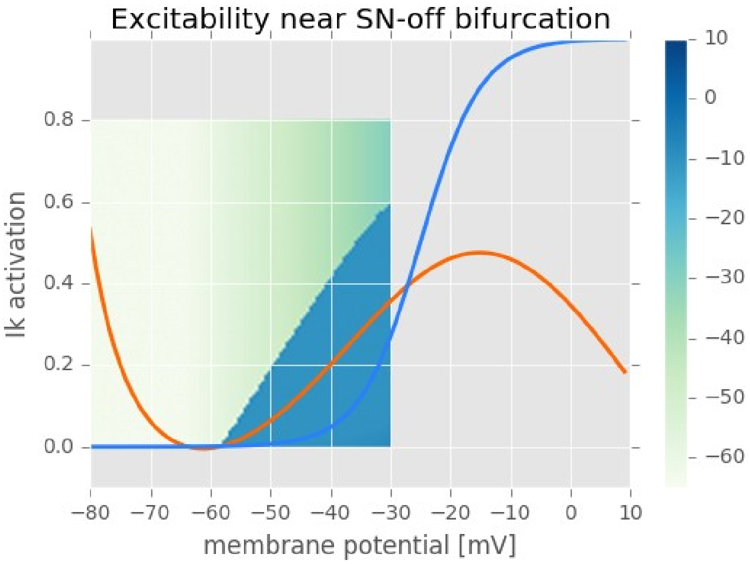

phase trajectories near SN bifurcation

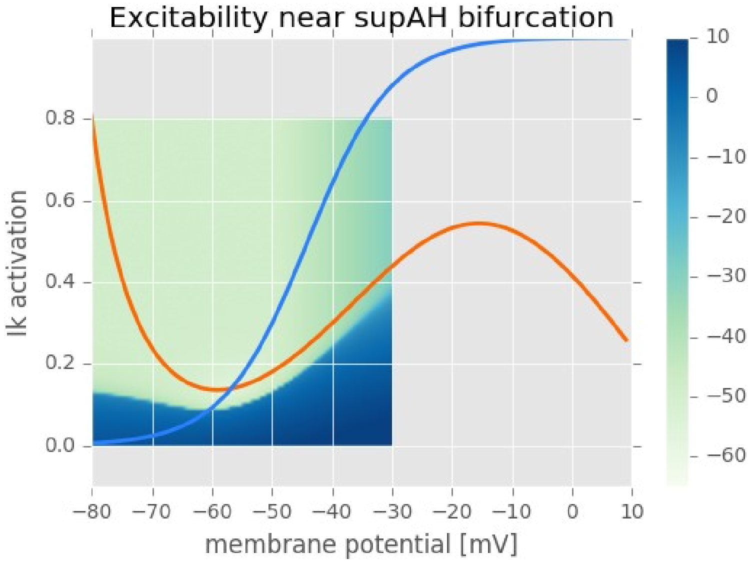

phase trajectories near supAH bifurcation

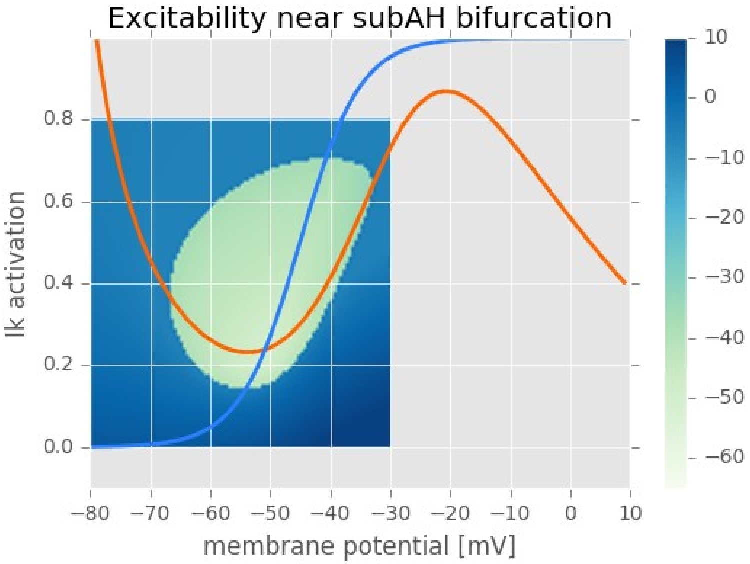

phase trajectories near subAH bifurcation

# Threshold maps for the 4 bifurcations resting → spiking

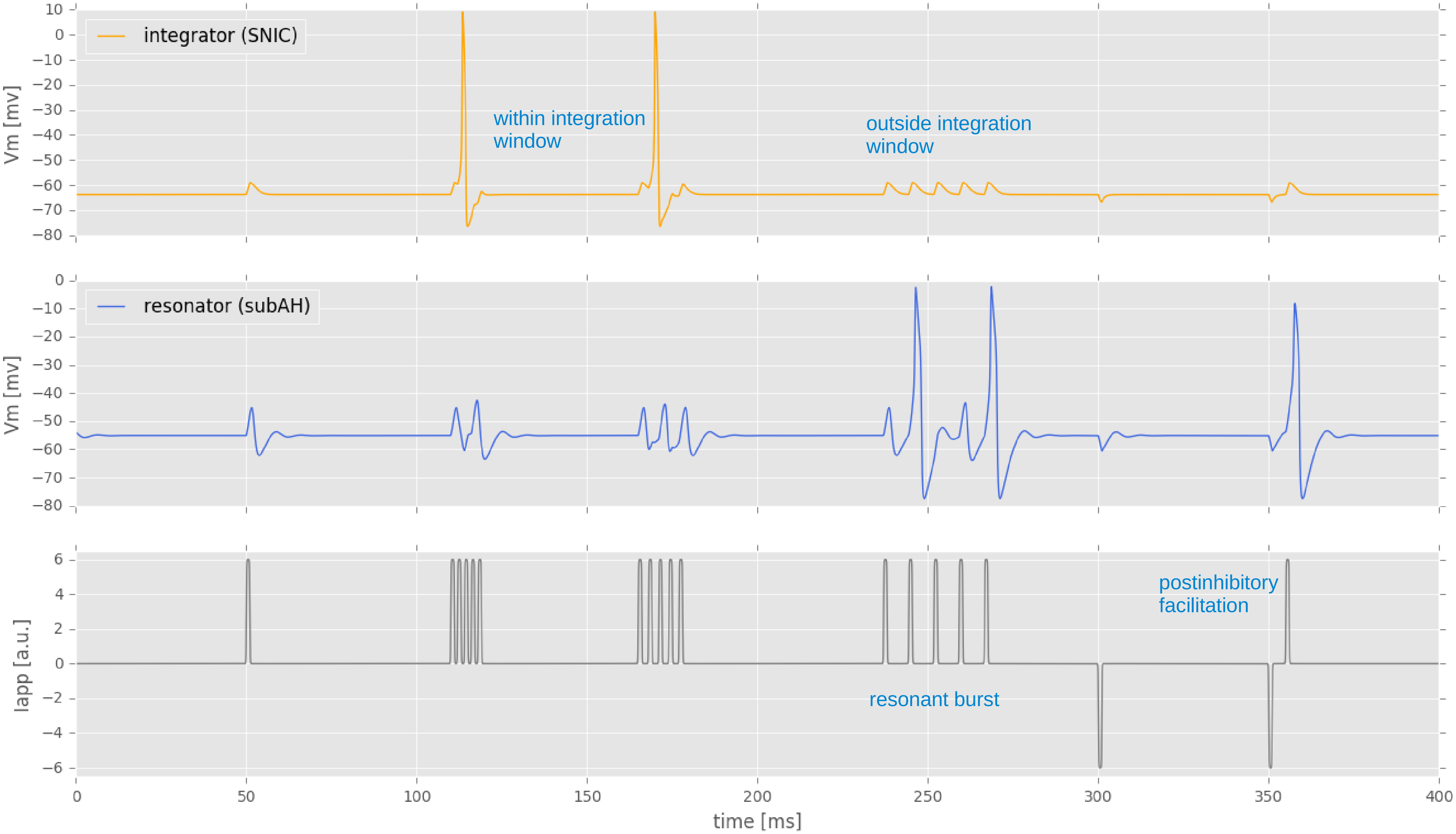

Excitability near SNIC bifurcation


Excitability near SN-off bifurcation


Excitability near supAH bifurcation

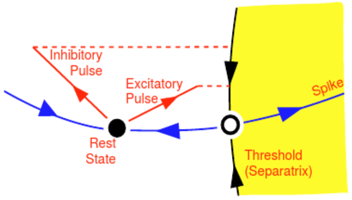

Excitability near subAH bifurcation

# Responses to short pulses: integrators *vs* resonators

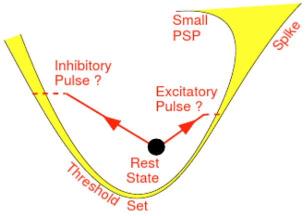


# Implications of subthreshold oscillations: excitation by hyperpolarization

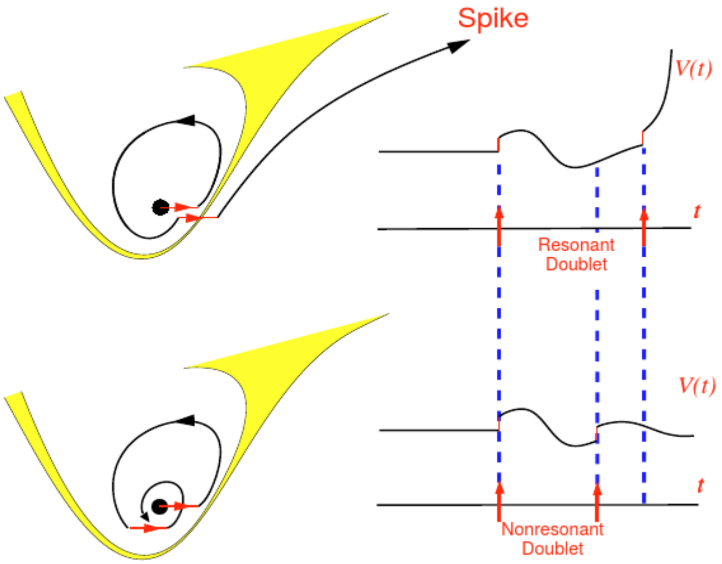
integrator



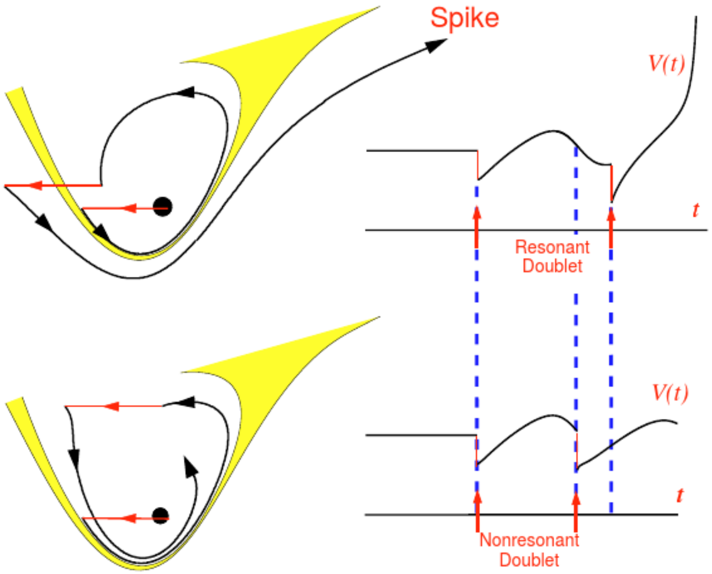
resonator



"Excitatory" Pulses

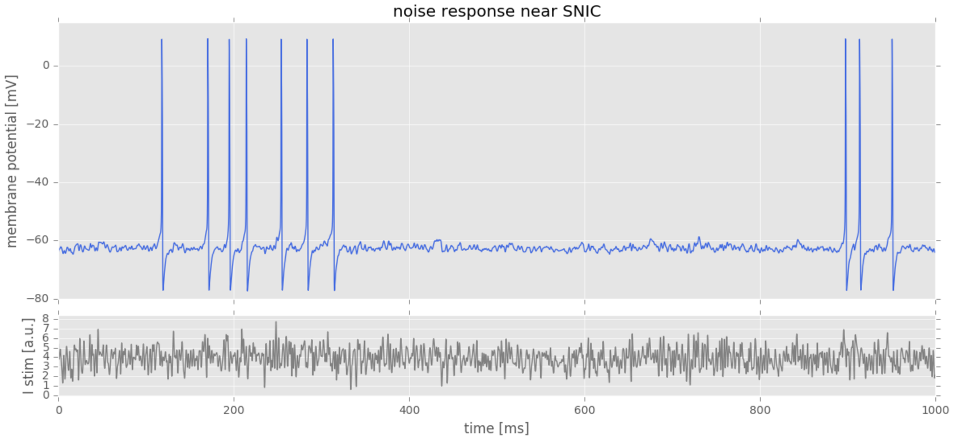


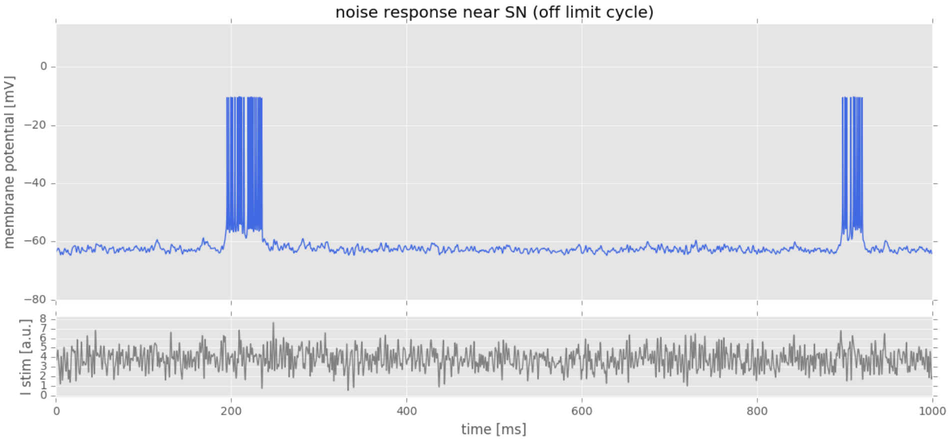
"Inhibitory" Pulses

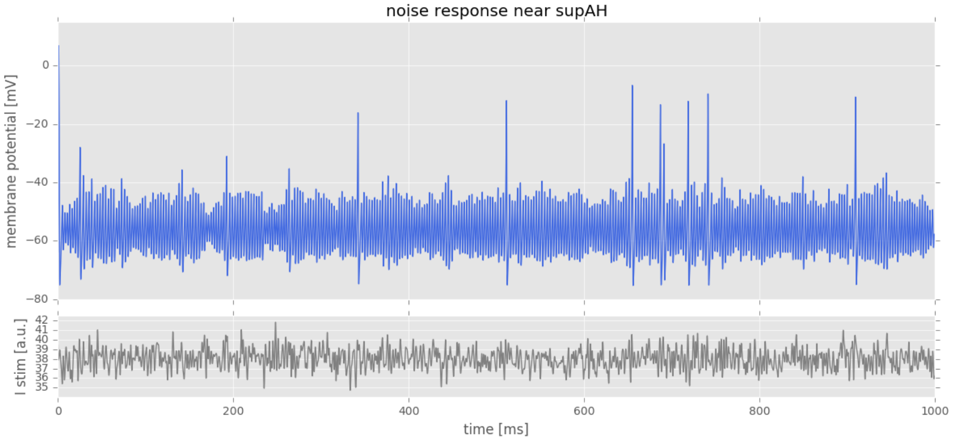


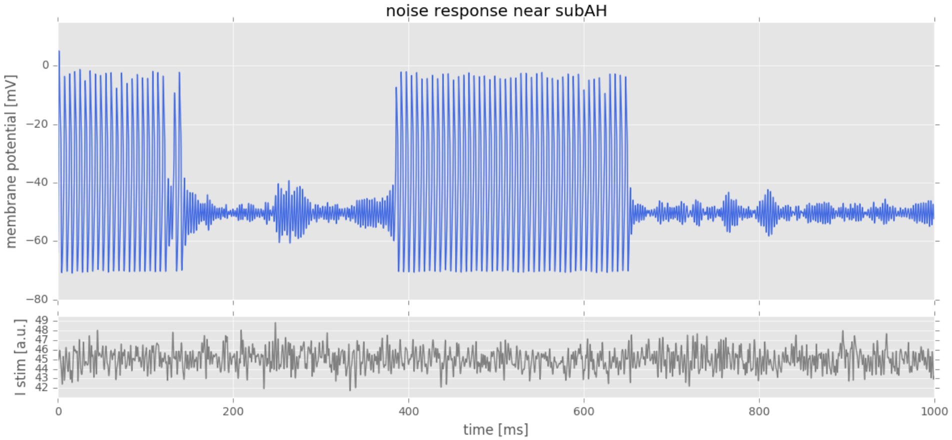
E. Izhikevich *International Journal of Bifurcation and Chaos,* **10:** 6 (2000) 1171–266 (c) World Scientific Publishing Company

# Response to noise









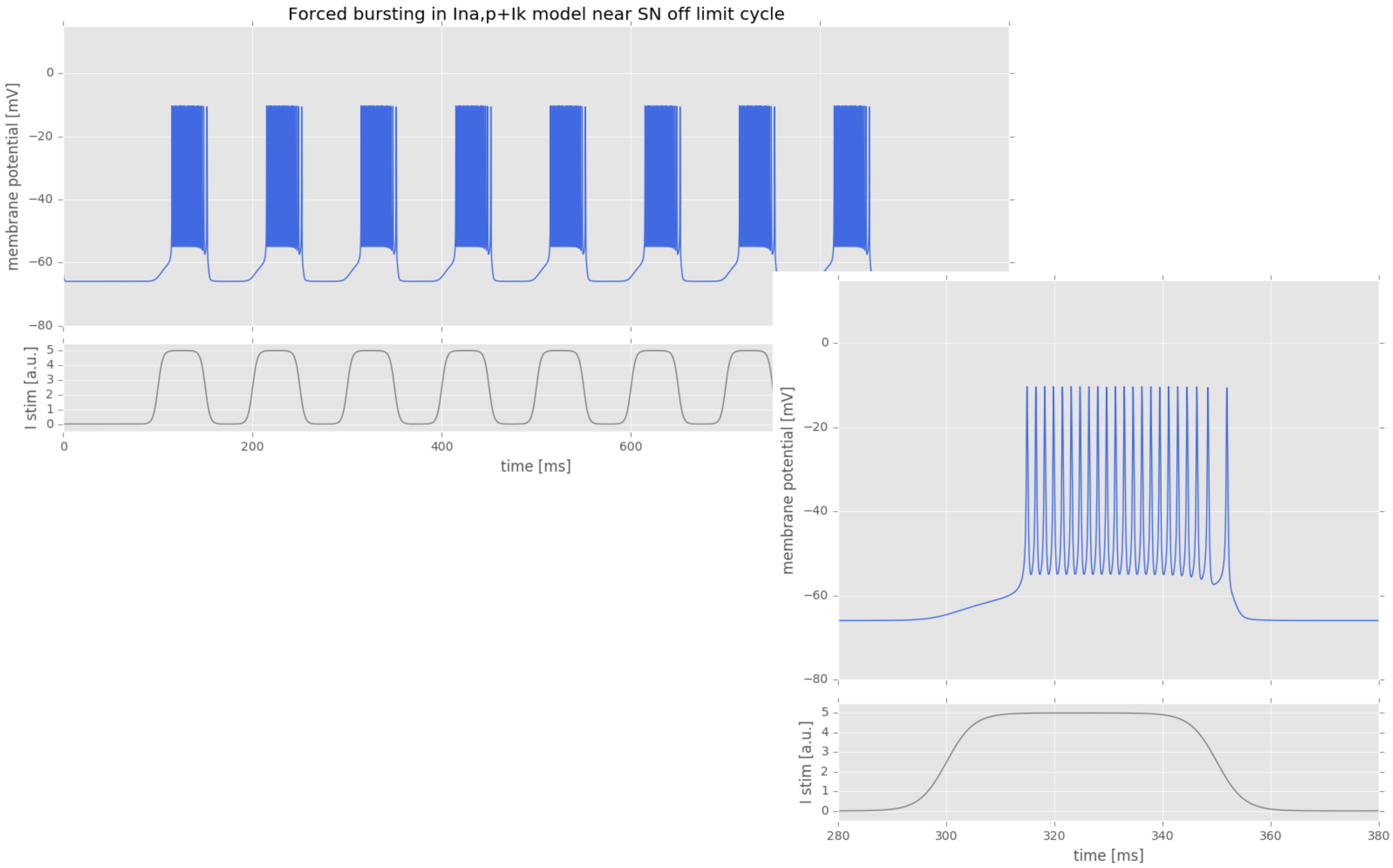
## Integrators

- Saddle-node bifurcations from resting state
- Arbitraty low-frequency firing
- Well-defined threshold manifold
- Distinguish between inhibitory and excitatory stimuli
- The higher the frequency of incoming EPSPs, the shorter the spike latency

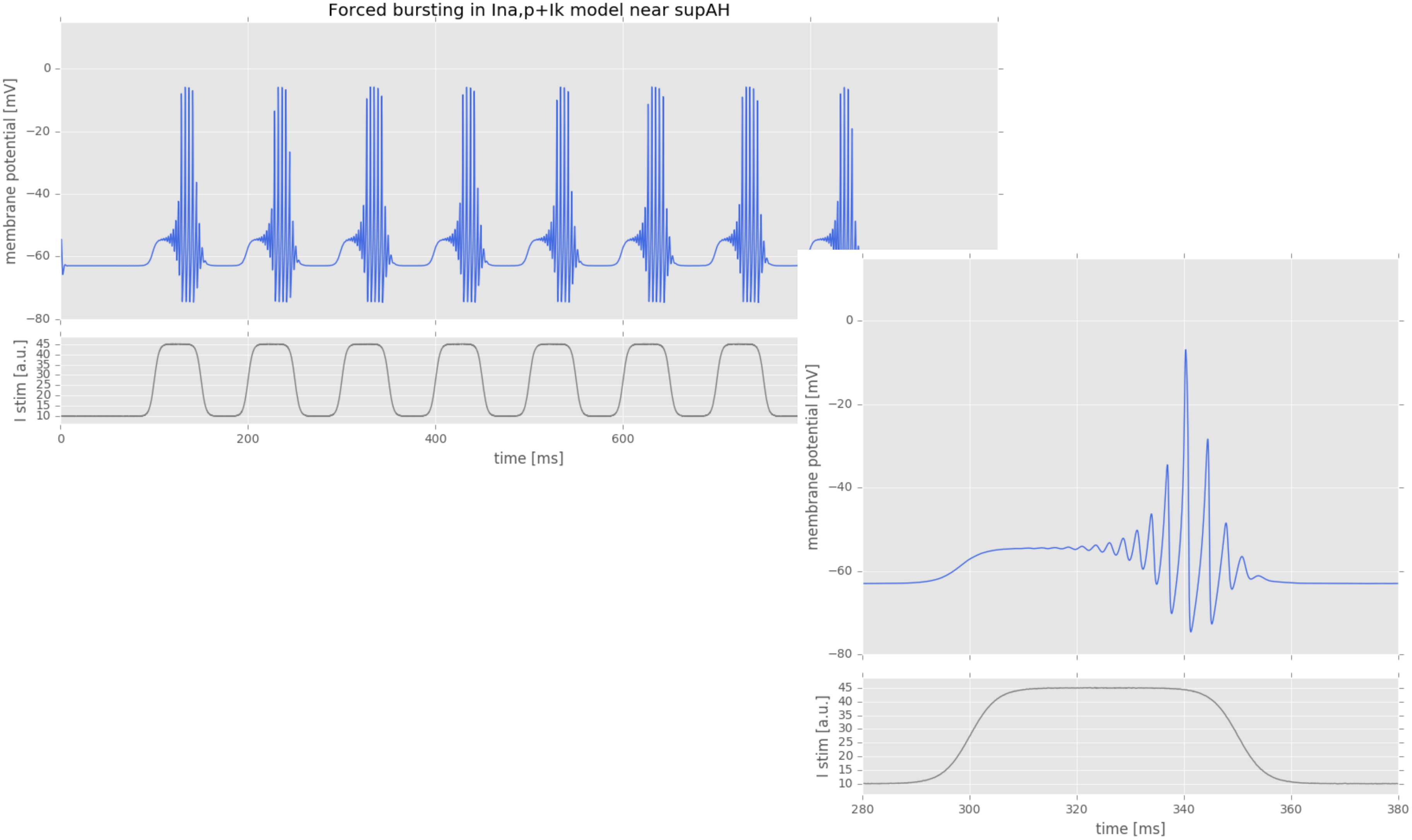
## Resonators

- AH bifurcation
- Fires within specific frequency range
- doesn’t have all-or none spikes
- No well-defined threshold manifold
- Can fire in response to inhibitory pulse train
- Increased input frequency can delay spike generation

# Slow modulation: forced bursting



# Slow modulation: forced bursting (supercritical AH)

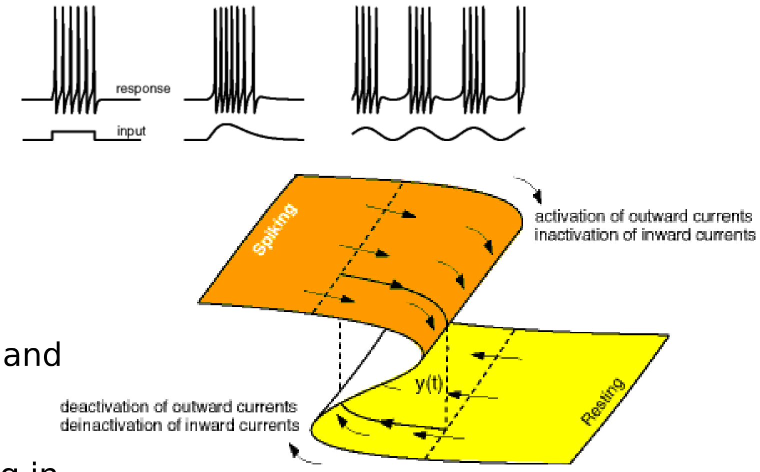


# Bursting

- Forced bursting
- Intrinsic bursting

  (additional slow membrane currents)

  - Slow wave: slow subsystem is insensitive to fast and is in oscillatory regime (must be at least 2D)
  - Hysteresis loop: *bistability* of resting and spiking in the fast subsystem



$$\dot{x} = f(x, y) \qquad \text{fast subsystem} \qquad (1)$$

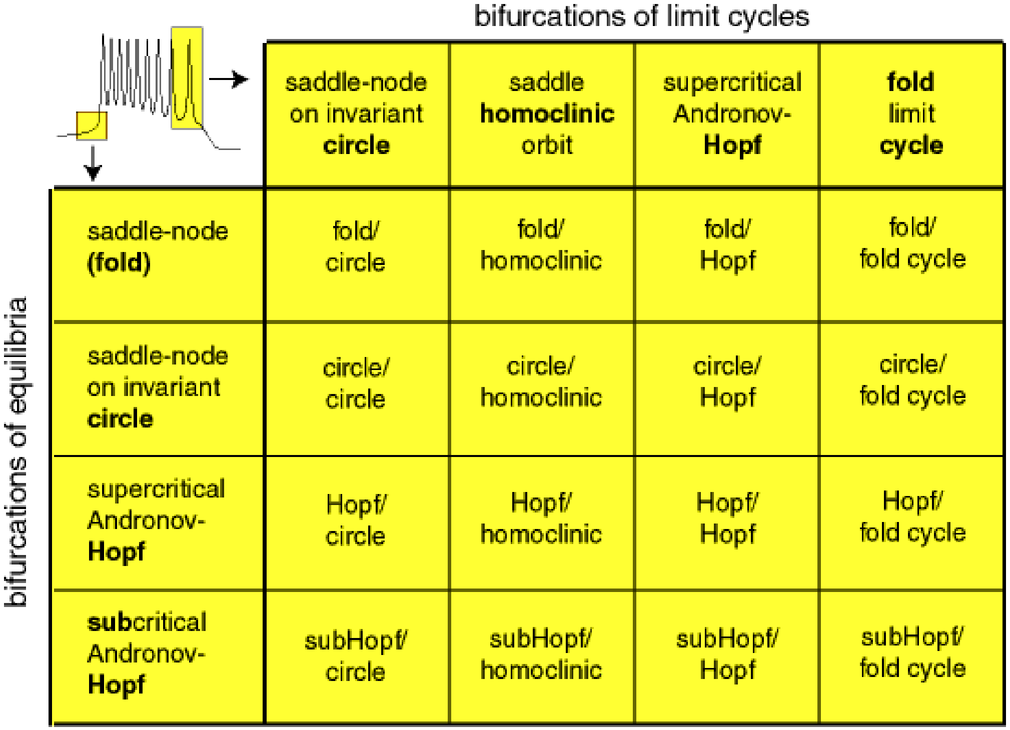
$$\dot{y} = \mu g(x, y) \qquad \text{slow modulation} \qquad (2)$$

$$\mu \ll 1$$

**To stop a burst, either:**

- activate outward current (e.g. $K^+$ M-current)
- Inactivate inward current (e.g. $Ca^{2+}$ T-current)

# Classification of bursters by bifurcations involved

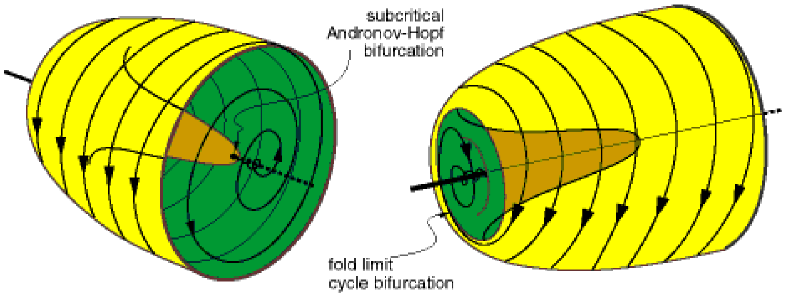


bifurcations of limit cycles

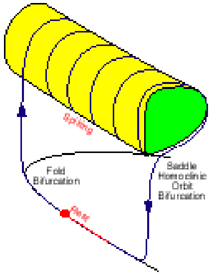
bifurcations of equilibria

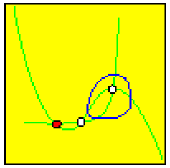
| | saddle-node on invariant **circle** | saddle **homoclinic** orbit | supercritical Andronov-**Hopf** | **fold** limit **cycle** |
|---|---|---|---|---|
| saddle-node **(fold)** | fold/ circle | fold/ homoclinic | fold/ Hopf | fold/ fold cycle |
| saddle-node on invariant **circle** | circle/ circle | circle/ homoclinic | circle/ Hopf | circle/ fold cycle |
| supercritical Andronov-**Hopf** | Hopf/ circle | Hopf/ homoclinic | Hopf/ Hopf | Hopf/ fold cycle |
| **sub**critical Andronov-**Hopf** | subHopf/ circle | subHopf/ homoclinic | subHopf/ Hopf | subHopf/ fold cycle |

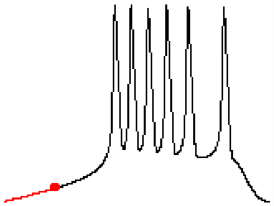
## subHopf/fold

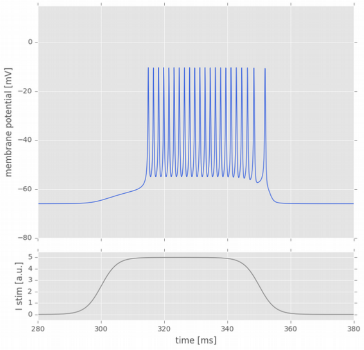


## Fold/homoclinic









# Some neurocomputational implications of burster classes: bistability

| | SNIC | Saddle homoclinic orbit | Supercritical Andronov-Hopf | Fold limit cycle |
|---|---|---|---|---|
| Saddle-node (fold) | fold / circle | fold / homoclinic | fold / Hopf | fold / fold cycle |
| SNIC | circle / circle | circle / homoclinic | circle / Hopf | circle / fold cycle |
| Supercritical Andronov-Hopf | Hopf / circle | Hopf / homoclinic | Hopf / Hopf | Hopf / fold cycle |
| Subcritical Andronov-Hopf | subHopf / circle | subHopf / homoclinic | subHopf/ Hopf | subHopf / fold cycle |

🟨 bistability at batch start 🟦 bistability at batch end

# Some neurocomputational implications of burster classes: frequency modulation within burst

| | SNIC | Saddle homoclinic orbit | Supercritical Andronov-Hopf | Fold limit cycle |
|---|---|---|---|---|
| Saddle-node (fold) | fold / circle | fold / homoclinic | fold / Hopf | fold / fold cycle |
| SNIC | circle / circle | circle / homoclinic | circle / Hopf | circle / fold cycle |
| Supercritical Andronov-Hopf | Hopf / circle | Hopf / homoclinic | Hopf / Hopf | Hopf / fold cycle |
| Subcritical Andronov-Hopf | subHopf / circle | subHopf / homoclinic | subHopf/ Hopf | subHopf / fold cycle |

🟨 increasing frequency at batch start 🟦 decreasing frequency at batch end

# Further reading

- Izhikevich E. *Dynamical Systems in Neuroscience: the Geometry of Excitability and Bursting.* MIT Press 2007

- Izhikevich E.  Neural excitability, spiking and bursting. International journal of bifurcations and chaos. 2000; **10**:6, 1171 —1266

- Prescott SA, De Koninck Y, Sejnowski TJ Biophysical Basis for Three Distinct Dynamical Mechanisms of Action Potential Initiation. *PLoS Comput Biol* 2008 **4**(10): e1000198.

- Rinzel J, Huguet G.  Nonlinear dynamics of neuronal excitability, oscillations and coincidence detection. *Communications on Pure and Applied Mathematics,* Vol. LXVI, 1464–1494 (2013)

# Acknowledgements

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