Bifurcation examples in neuronal models

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Outline

Most figures from textbook of Izhikevich

Reminder on the $I_{Na,p} + I_K$ model

This is a simplified 2-dimensional simplification of the Hodgkin-Huxley model where we assume

- a leak current
- a persistent *Na*-current with instantaneous kinetics
- a persistent *K*-current with slower kinetics

$$C\frac{dV}{dt} = I - \overbrace{\bar{g}_K n(V - E_K)}^{I_K} - \overbrace{\bar{g}_{Na} m_\infty(V)(V - E_{Na})}^{I_{Na}} - g_L(V - E_L)$$

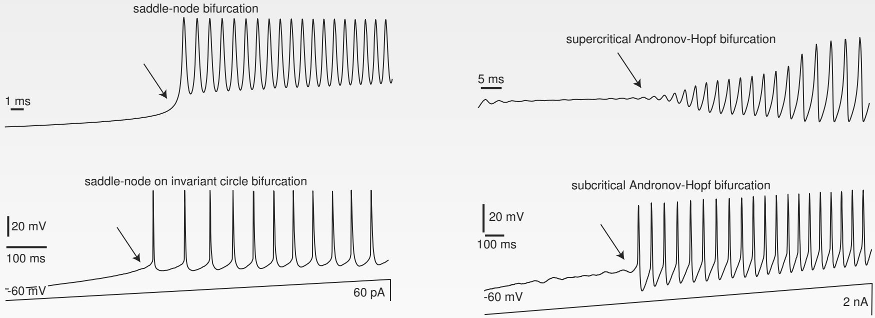
$$\frac{dn}{dt} = \frac{n_\infty(V) - n}{\tau(V)}$$

where

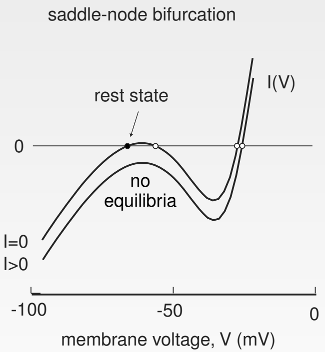
$$(m, n)_\infty = \frac{1}{1 + exp[(V_{1/2} - V)/k]}$$

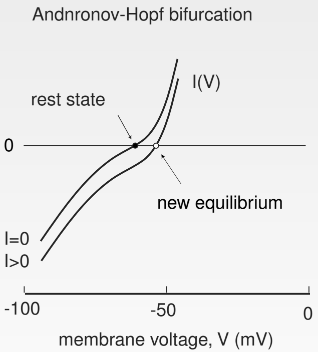
4 examples of codim 1 bifurcations

Figures from Izhikevich



I-V curves in the $I_{Na,p} + I_K$ model





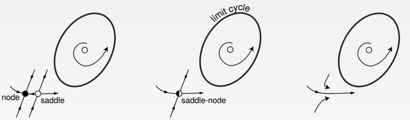
Neural properties of bifurcations

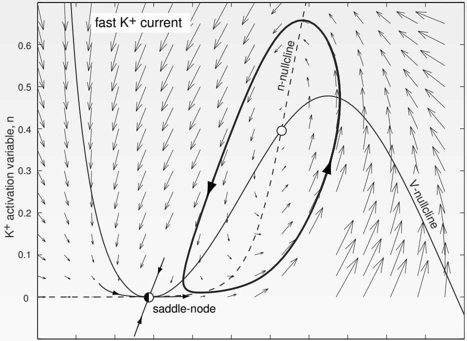
Quasi-static change in I, bifurcations?

Bifurcation of an equilibrium	**Fast subthreshold oscillations**	**Amplitude of spikes**	**Frequency of spikes**
saddle-node	no	nonzero	nonzero
saddle-node on invariant circle	no	nonzero	$A\sqrt{I - I_b} \to 0$
supercritical Andronov-Hopf	yes	$A\sqrt{I - I_b} \to 0$	nonzero
subcritical Andronov-Hopf	yes	nonzero	nonzero

Saddle-node bifurcation 1/2

Figures from Izhikevitch, $I_{Na,p} + I_K$ model with high threshold, $\tau(V) = 0.152$





Saddle-node bifurcation 2/2

- the bifurcation occurs at $I_p = 4.51, (V_p, n_p) = (-61, 0.0007)$
- We can compute the center manifold
- we check that

$$a = \frac{1}{2} f_{VV}(V_p, I_p) \neq 0 \quad c = f_O(V_p, I_p) \neq 0$$

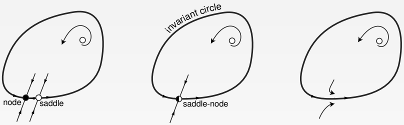
- We have the normal form

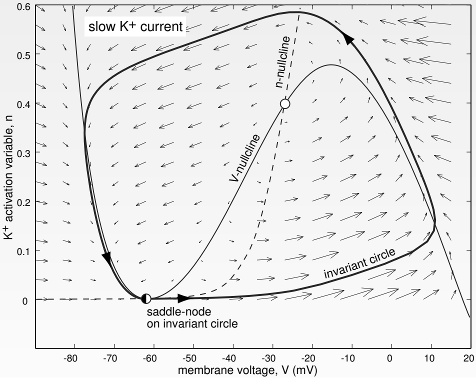
$$\dot{V} = c(I - I_p) + a(V - V_p)^2 \quad a = 0.1887, c = 1$$

Saddle-node bifurcation on limit cycle 1/2

Figures from Izhikevitch, $I_{Na,p} + I_K$ model with high threshold, $\tau(V) = 1$

Also called Saddle-node homoclinic bifurcation

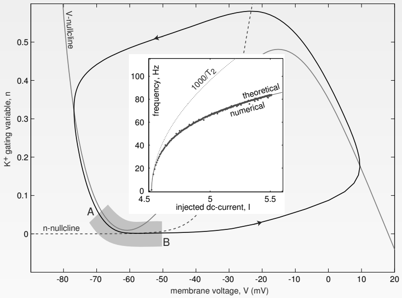




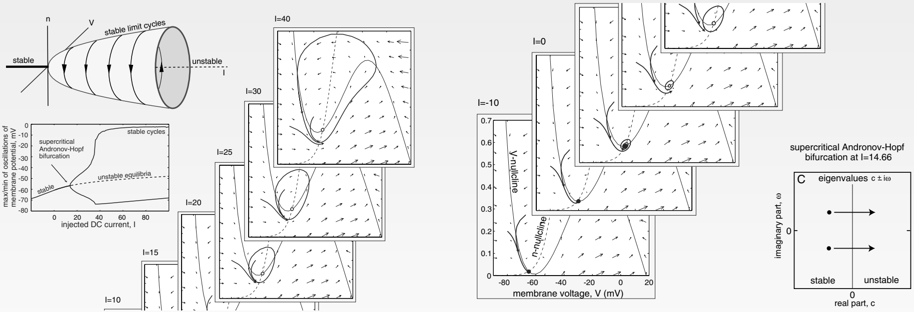
Saddle-node bifurcation on limit cycle 2/2

Saddle-node homoclinic bifurcation

- Time from A to B
  $T_2 \approx \frac{\pi}{\sqrt{ac(I - I_p)}}$
- Action potential duration
  $T_1 \approx 4.7ms$
- Firing frequency $\omega = \frac{1000}{T_1 + T_2}$

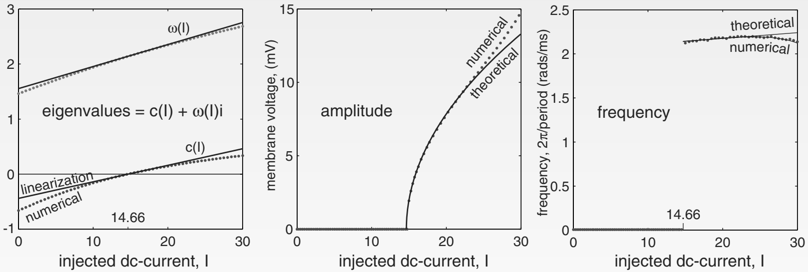


Supercritical Andronov-Hopf bifurcation

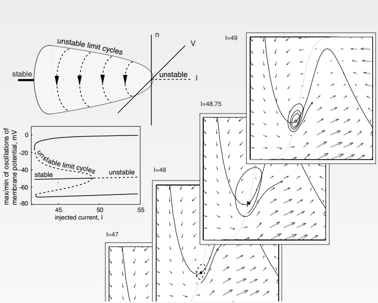


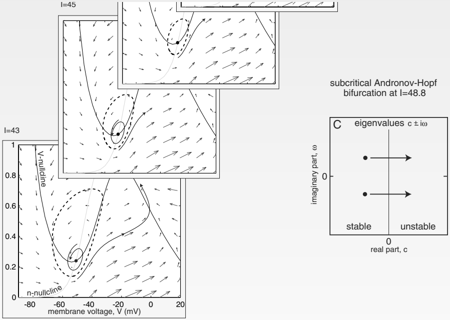
Supercritical Andronov-Hopf bifurcation

$I_{Na,p} + I_K$ model with low threshold



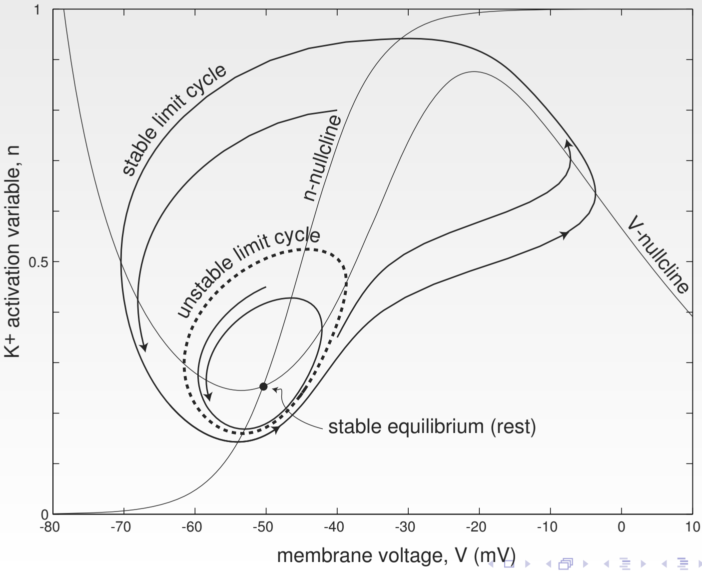
Subcritical Andronov-Hopf bifurcation





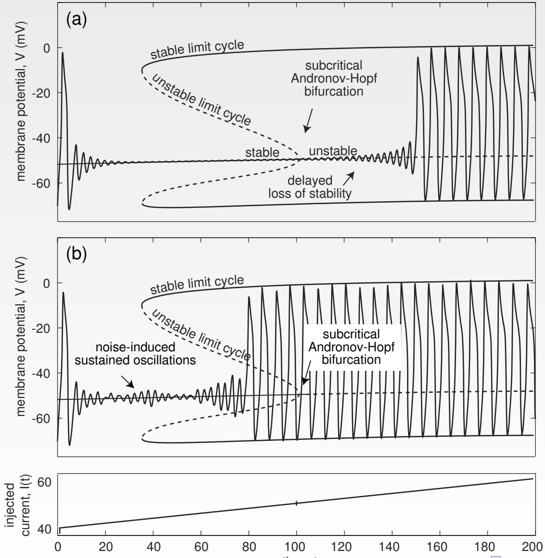
Bistability in the $I_{Na,p} + I_K$ model

To be explained later



Delayed loss of stability

To be analyzed later (also)...



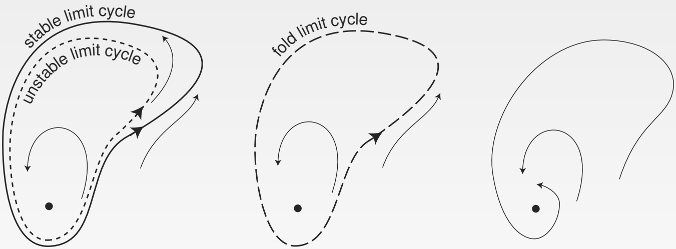
Outline

Transitions from spiking to resting.
(SNIC, superAH,SN-LC,Saddle homoclinic)

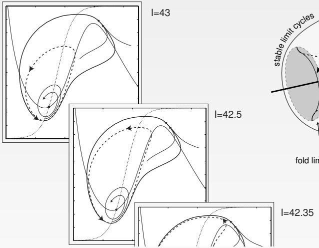
Neural properties of bifurcations

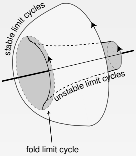
Bifurcation of a limit cycle attractor	**Amplitude**	**Frequency**
saddle-node on invariant circle	nonzero	$A\sqrt{I-I_b} \to 0$
supercritical Andronov-Hopf	$A\sqrt{I-I_b} \to 0$	nonzero
fold limit cycle	nonzero	nonzero
saddle homoclinic orbit	nonzero	$\frac{-A}{\ln\|I-I_b\|} \to 0$

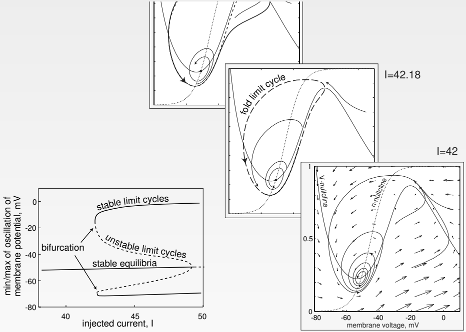
Saddle node of limit cycle bifurcation 1/2



Saddle node of limit cycle bifurcation 2/2



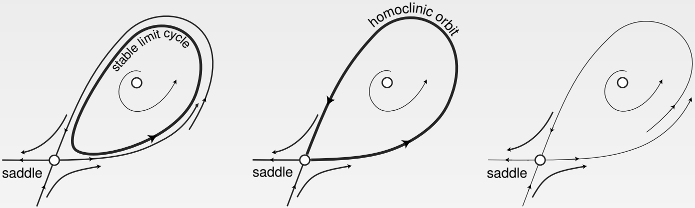




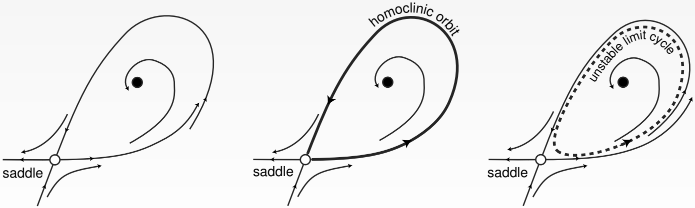
Saddle-Node homolinic bifurcation 1/4

Andronov-Leontovich 1939

Typically $W^u \cap W^s = \emptyset$.



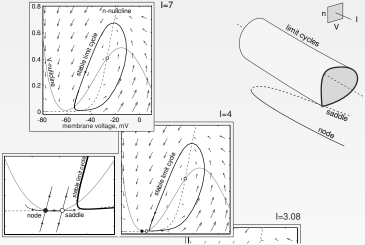
a. supercritical saddle homoclinic orbit bifurcation

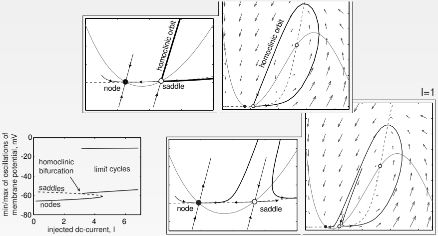


b. subcritical saddle homoclinic orbit bifurcation

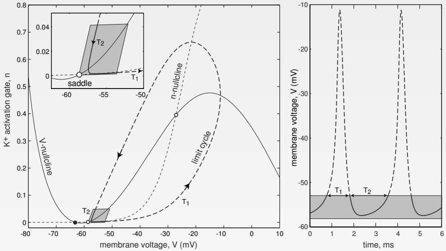
Saddle-Node homolinic bifurcation 2/4

Estimate of period: $T \propto -\ln(\mu - \mu_c)$

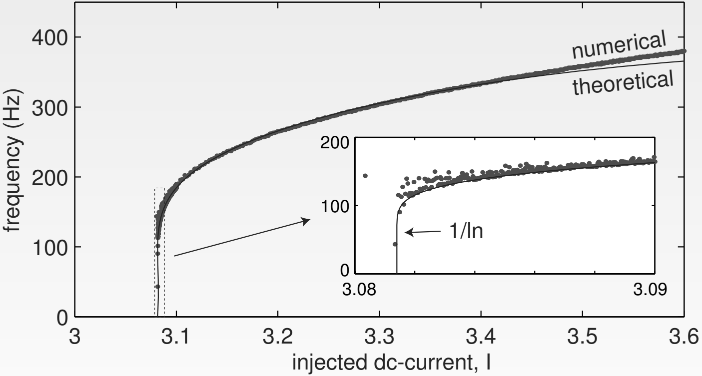




Saddle-Node homolinic bifurcation 3/4



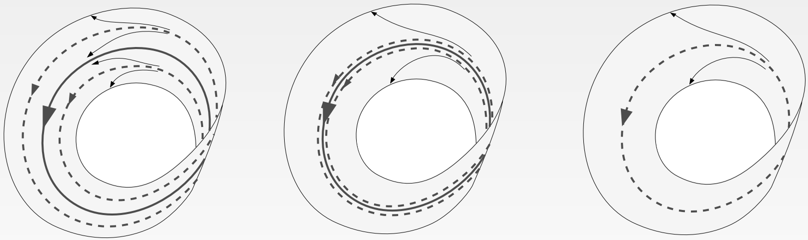
Saddle-Node homolinic bifurcation 4/4



Outline

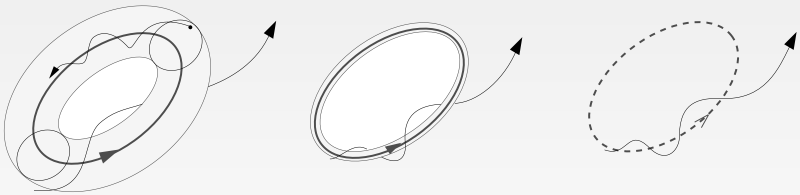
Subcritical Flip bifurcation

Period doubling



Neimark-Sacker bifurcation

Invariant torus creation



Bogdanov-Takens bifurcation

Theorem

Consider the DS $\dot{x} = f(x;\mu) \in \mathbb{R}^2$, f smooth, $f(0;0) = 0$ with two zeros eigenvalues $\lambda_{1,2} = 0$. If

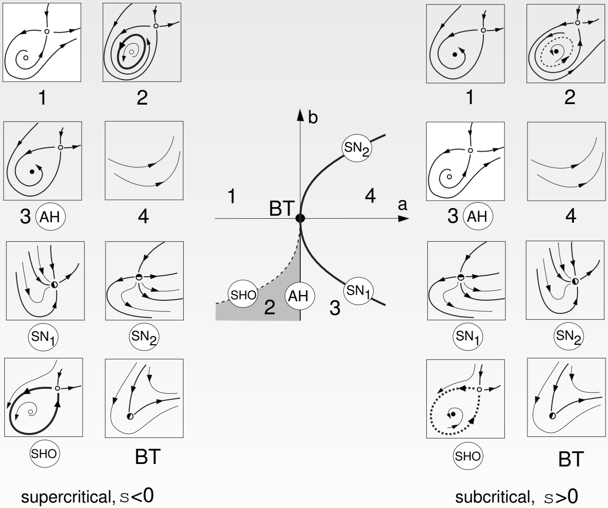
- $A(0) \equiv f_x(0,0) \neq 0, a_{20}(0) + b_{11}(0) \neq 0, b_{20} \neq 0$
- the map $(x,\mu) \to \left(f(x,\mu), tr\left(\frac{\partial f}{\partial x}\right), det\left(\frac{\partial f}{\partial x}\right)\right)$ is smooth in $(0,0)$,

then the DS is locally topologically equivalent to the DS

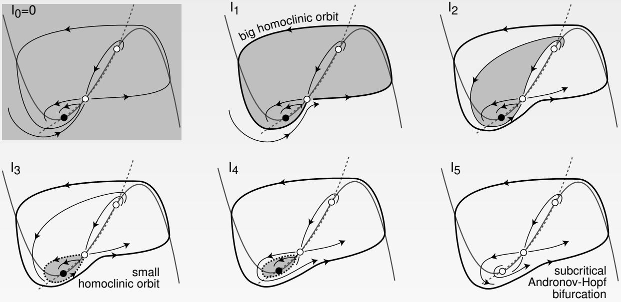
$$\begin{aligned} \dot{\eta}_1 &= \eta_2 \\ \eta_2 &= \beta_1 + \beta_2\eta_1 + \eta_1^2 + s\eta_1\eta_2 \end{aligned} \qquad \text{where } s = sign\frac{a_{20}(0) + b_{11}(0)}{b_{20}(0)}$$

Truncation does not change the dynamics.

BT bifurcation diagram



Example of a subcritical bifurcation



Neuronal Excitability

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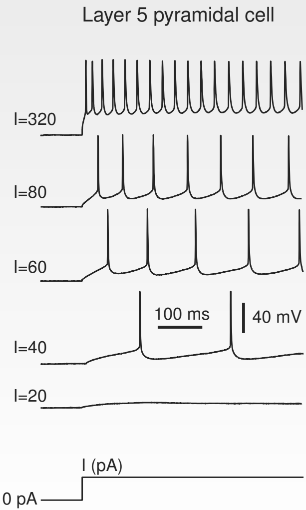
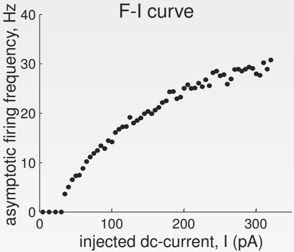
ENS - Master MVA / Paris 6 - Master Maths-Bio (2013-2014)

Outline

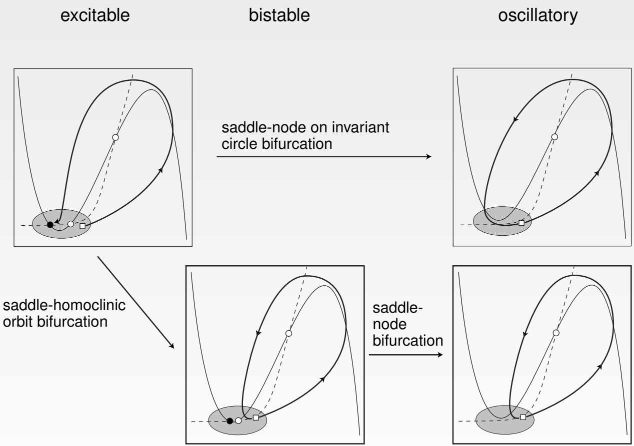
Hodgkin's Classification
Class I (Figures from Izhikevich)





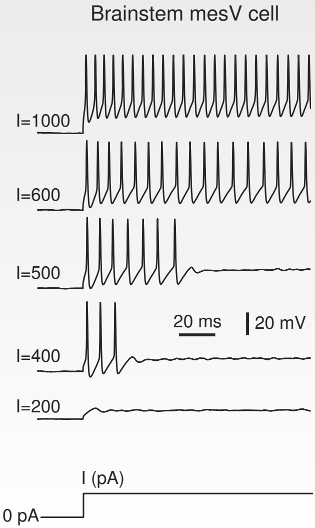
- Action potentials can be generated with arbitrarily low frequency, depending on the strength of the applied current.

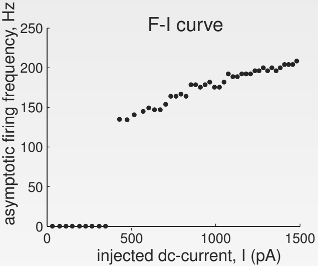
Hodgkin's Classification: Class I



Hodgkin's Classification

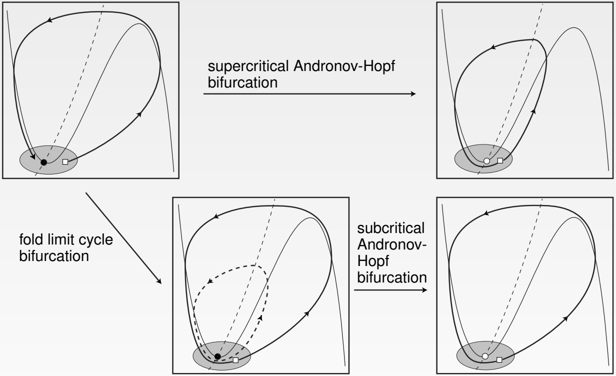
Class II (Figures from Izhikevich)





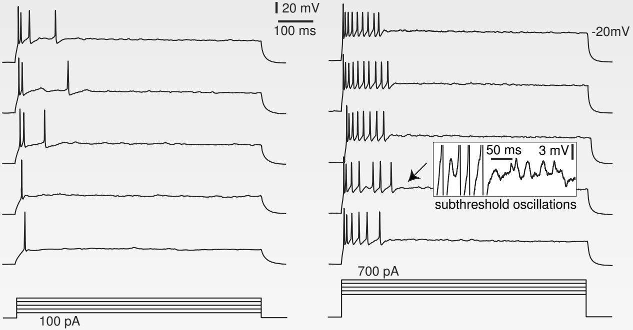
- Action potentials are generated in a certain frequency band that is relatively insensitive to changes in the strength of the applied current.

Hodgkin's Classification: Class II



Hodgkin's Classification

Class III (Figures from Izhikevich)

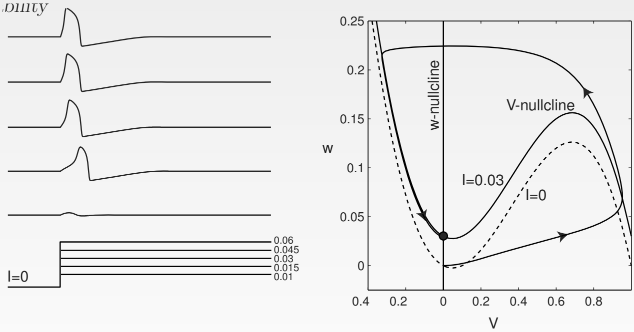


- L5 Pyramidal neuron in rat visual cortex. One spike is generated in response to a current step. Repetitive (tonic) spiking can be generated only for extremely strong injected currents or not at all.

Hodgkin's Classification

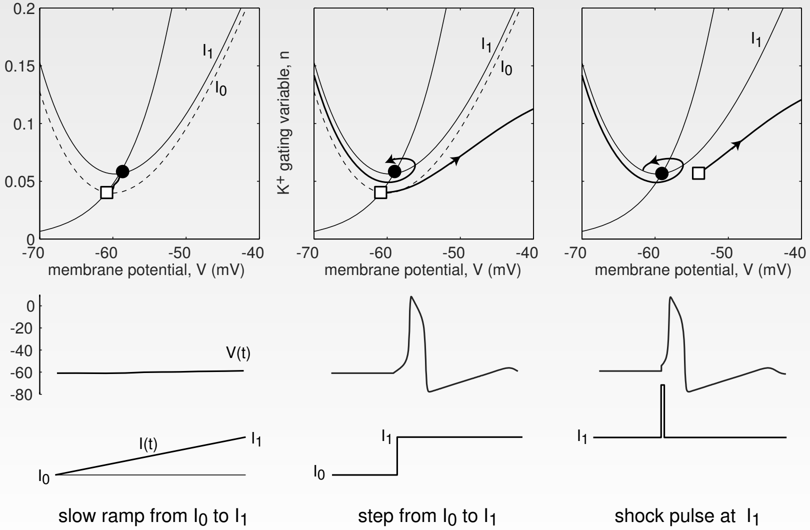
Class III (Figures from Izhikevich)

Class 3 neural excitability occurs when the resting state remains stable for any fixed I in a biophysically relevant range

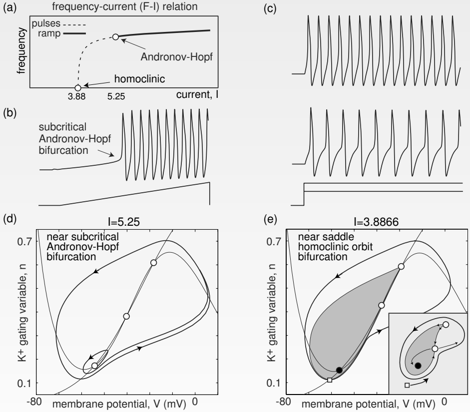


Example of the Fitzhugh-Nagumo model
$\dot{V} = V(a - V)(V - 1) - w + I, \;\; \dot{w} = bV - cw, \;\; a = 0.1, \;\; b = 0.01$

Ramps, Steps, and Shocks

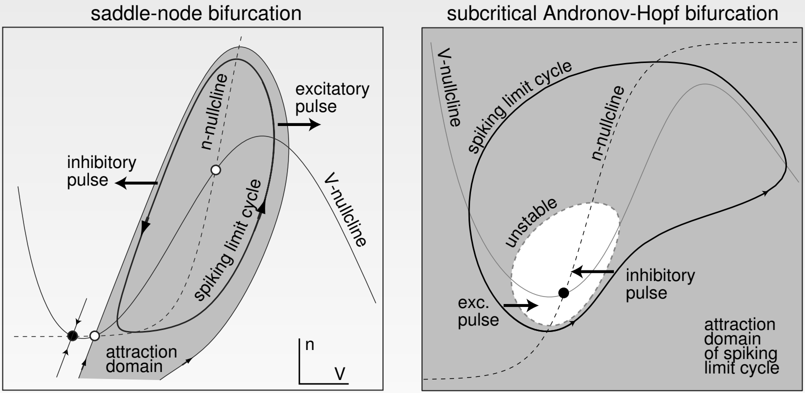


The $I_{Na,p} + I_K$ model, Class I or II?



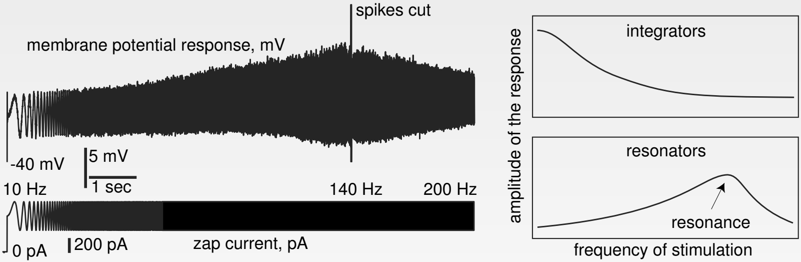
- Class II for ramps, I for Steps
- subcr. AH at $I = 5.25$ for ramps
- SN homoclinic for $I \approx 3.89$ for steps
- near BT

Bistability



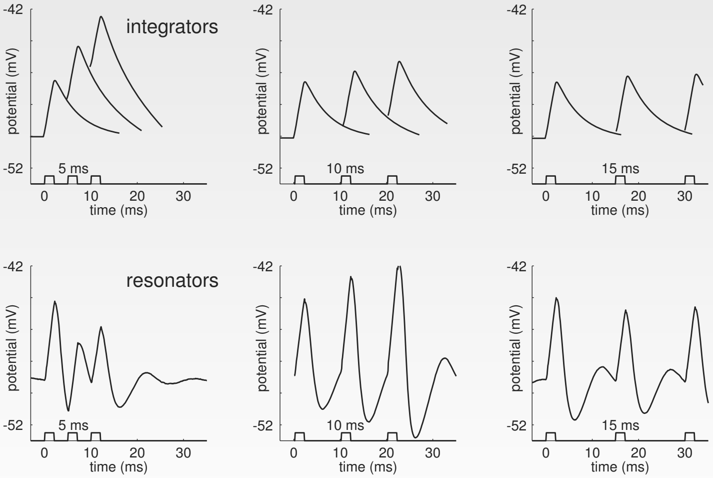
Excitatory / inhibitory pulses can shift the neuron from its resting state to repetitive firing.

Integrators vs. Resonators 1/2



1. Presence of sub-threshold oscillations
2. Exp. mechanism to test their presence

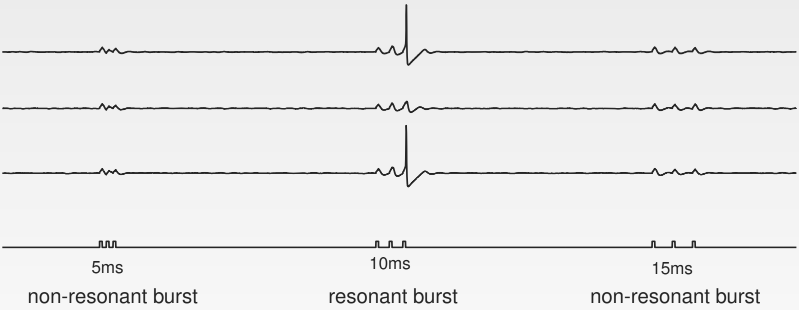
Integrators vs. Resonators 2/2



Integrators prefer high frequencies: detect coincidences.

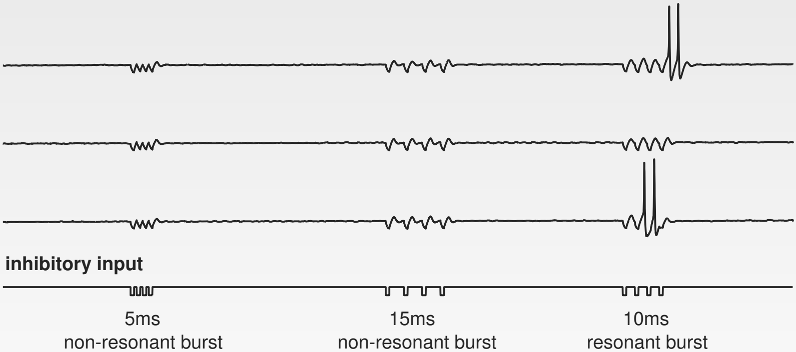
Resonators are selective in a frequency band.

Selective response: excitation or inhibition



Mesencephalic V neurons in brainstem having subthreshold membrane oscillations with a natural period around 9 ms Three consecutive voltage traces are shown to demonstrate some variability of the result

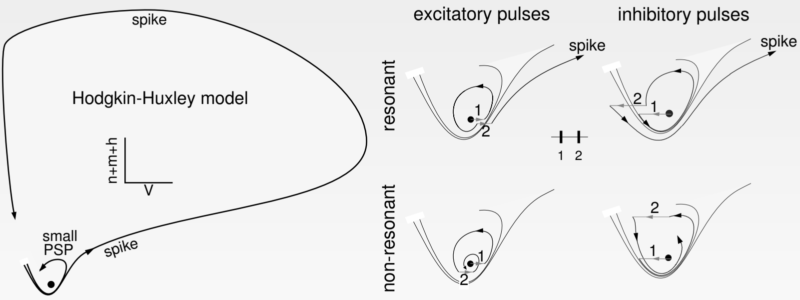
Selective response: excitation or inhibition



Experimental observations of selective response to inhibitory resonant burst in mesencephalic V neurons in brainstem having oscillatory potentials with the natural period around 9 ms. (Modified from Izhikevich et al. 2003).

Selective response: excitation or inhibition

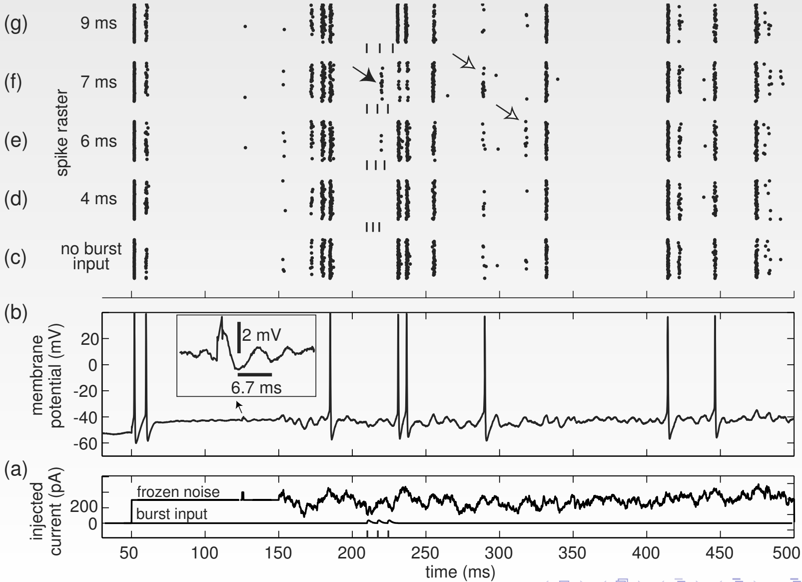
Geometrical explanation



Important temporal coherence of pulses.

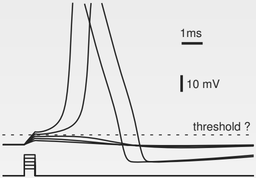
Influence of synaptic bombardment.

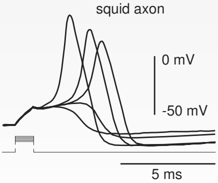
Frozen noise experiment

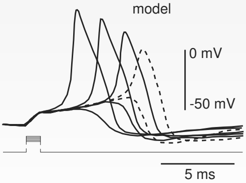


Threshold definition

Spike th. definiton not obvious



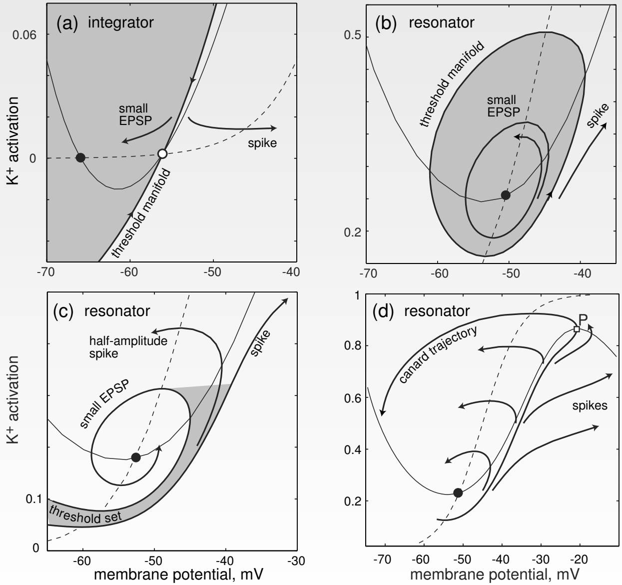




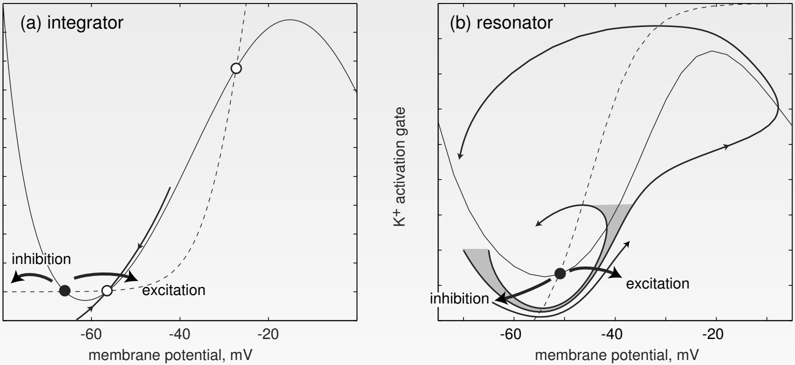
Threshold manifolds for the $I_{Na,p} + I_K$ model

- Integrators (close to saddle-node bifurcation) have a threshold manifolds, given by stable manifold of fold point.
- For resonators, it depends on bifurcation type
  - Bistable regime: (close to sub. AH): the unstable LC is a th. manifold.
  - In all other cases, there is no well defined th. manifold.

Threshold manifolds for the $I_{Na,p} + I_K$ model

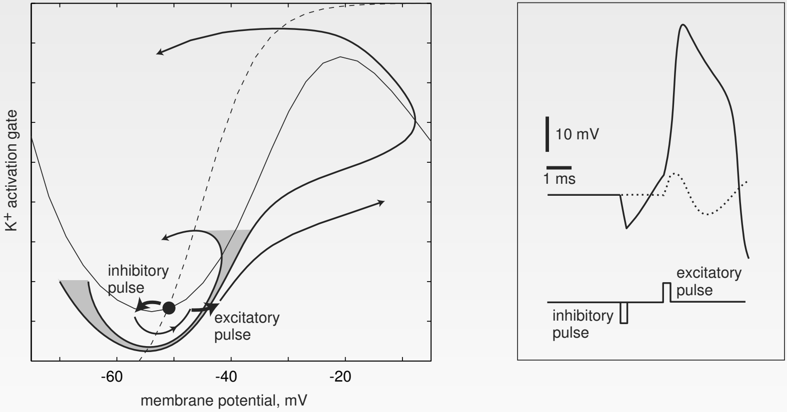


Spike emission: excitation or inhibition?



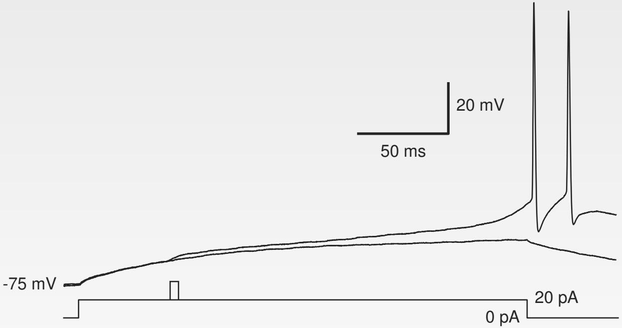
An integrator cannot spike in response to a hyper-polarizing current, a resonator can.

Spike emission: excitation or inhibition?



An hyper-polarizing current (inhib.) can enhance the effect of subsequent excitatory pulses.

Latency to first spike

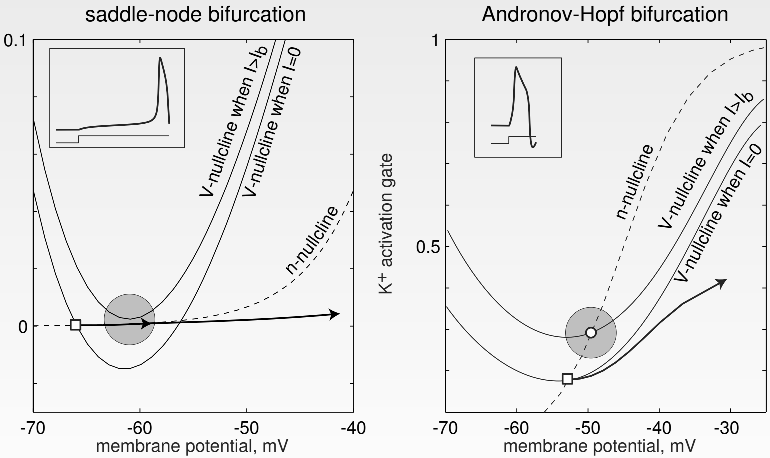


Property of integrators

Allow coding of input strengh in latency to first spike

Less sensitive to noise, since only prolonged inputs can cause spikes

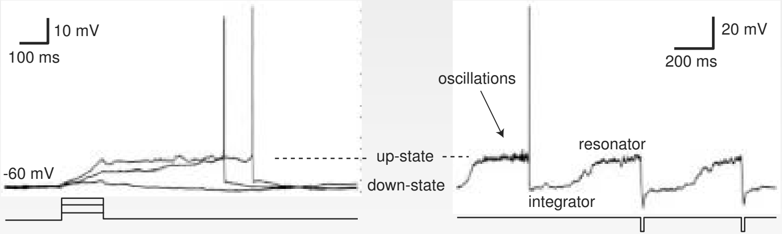
Latency to first spike



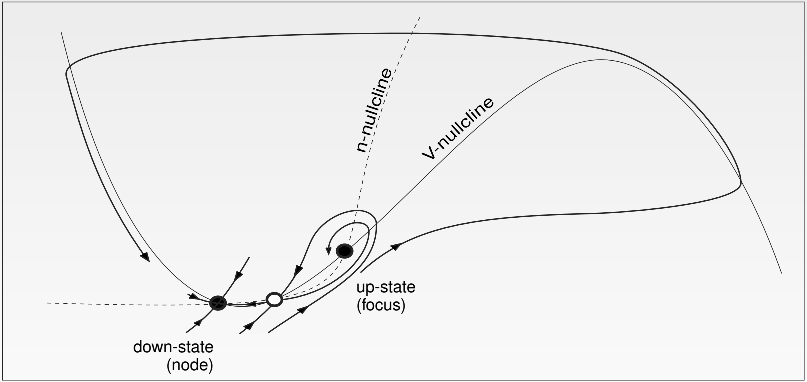
Flipping from an Integrator to a Resonator

- Mitral cells can be quickly switched from being integrators to being resonators by synaptic input.
- For resonators, it depends on bifurcation type
- high-states are attractive focus
- down-states are stable node

Integrator → Resonator 1/2

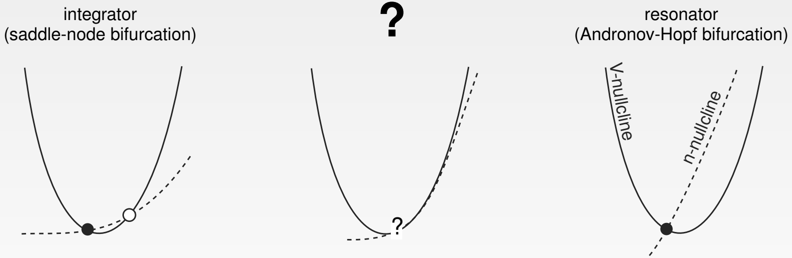


Integrator $\rightarrow$ Resonator 2/2



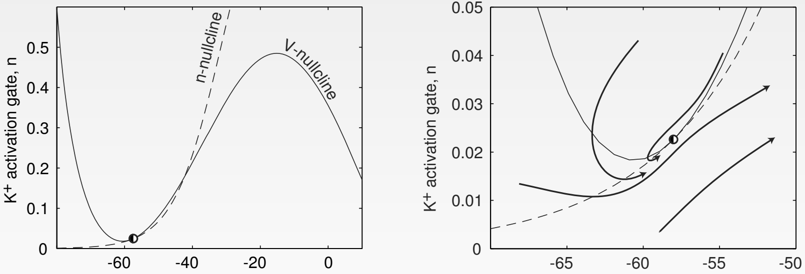
BT coming into play?

Need to combine in 2d a SN with a AH:

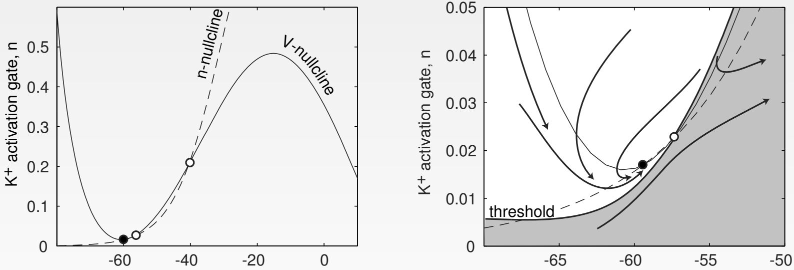


Bogdanov-Takens 1/3

In the $I_{Na,p} + I_K$ model (parameters E_L, $V_{1/2}$), the nullclines are parallel close to the left knee of the fast nullcline

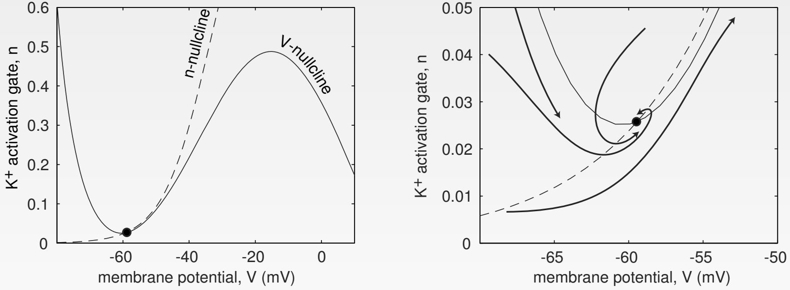


A small change in the parameter $V_{1/2}$ can give a Saddle-Node: i.e. an integrator



Bogdanov-Takens 3/3

or a resonator via a stable focus.



Summary 1/2

subthreshold oscillations \ coexistence of resting and spiking states	YES (bistable)	NO (monostable)
NO (integrator)	saddle-node	saddle-node on invariant circle
YES (resonator)	subcritical Andronov-Hopf	supercritical Andronov-Hopf

Summary 2/2

properties	integrators		resonators	
bifurcation	saddle-node on invariant circle	saddle-node	subcritical Andronov-Hopf	supercritical Andronov-Hopf
excitability	class 1	class 2	class 2	class 2
oscillatory potentials	no		yes	
frequency preference	no		yes	
I-V relation at rest	non-monotone		monotone	
spike latency	large		small	
threshold and rheobase	well-defined		may not be defined	
all-or-none action potentials	yes		no	
co-existence of resting and spiking	no	yes	yes	no
post-inhibitory spike or facilitation (brief stimuli)	no		yes	
inhibition-induced spiking	no		possible	