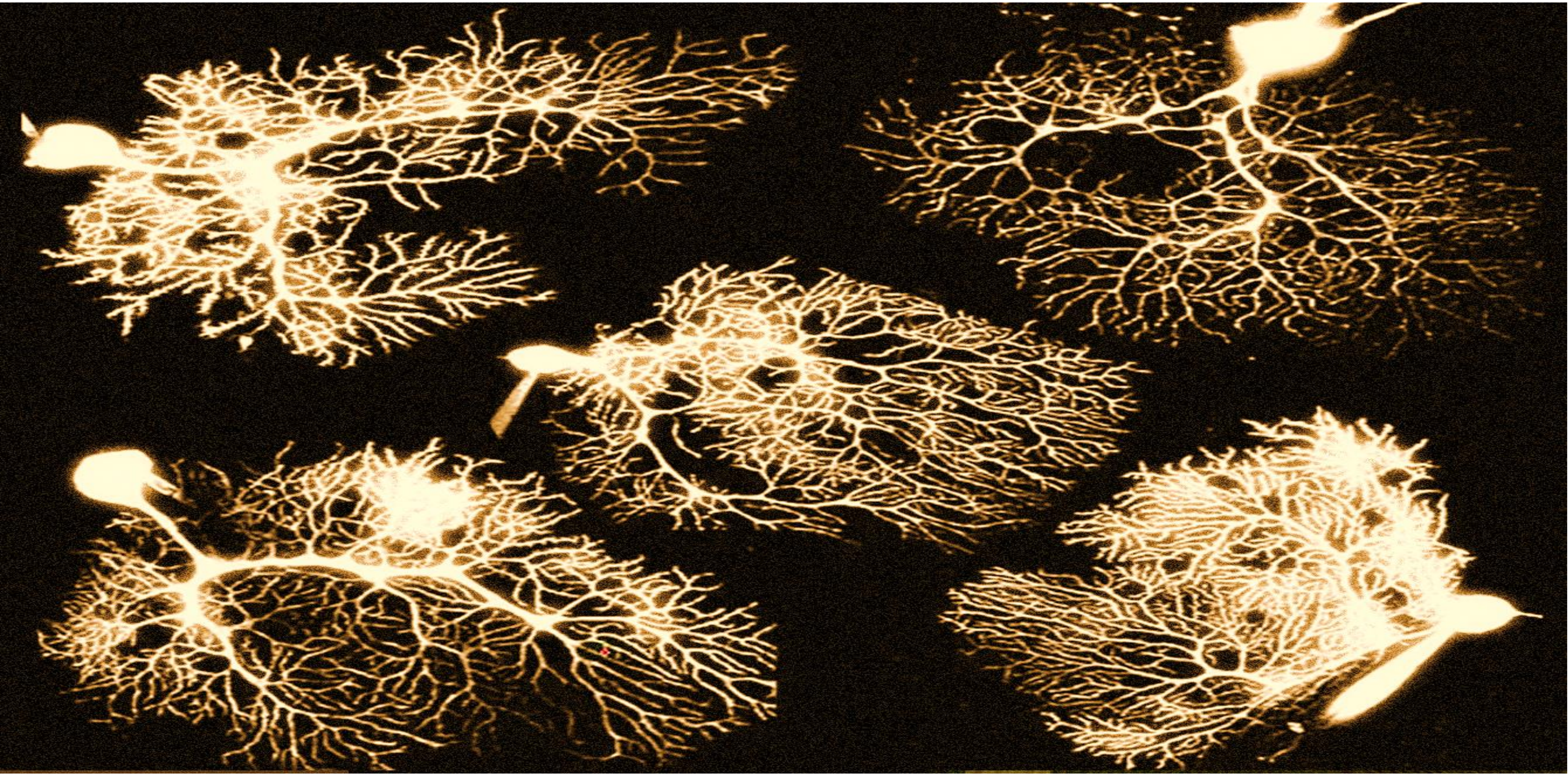
Neuroscience of Learning, Memory, Cognition

Part I: Neuronal Networks



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Neuron Models

Set III

Outline

- Sensing & perception
- Neurons & spikes
- The Hudgkin-Huxley equation
- Modeling neuronal dynamics

Some slides credit:

- Adrienne Fairhall, Rajesh Rao, UW course material 2013-2017
- Wulfram Gerstner, EPFL course material 2018

Other credits as noted on slides

Cover slide drawing: Santiago Ramon Y Cajal

Textbooks:

- Peter Dayan & Larry Abbott "Theoretical Neuroscience", 2005
- Wulfram Gerstner "Neuronal Dynamics", 2014
- Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Reference book:

- Paul Miller "An Introductory Course in Computational Neuroscience", 2018

Outline

- Sensing & perception
  - Neurons in the brain
  - Visual cortex & receptive fields
  - Vision & perception
- Neurons & spikes
  - Electrical personality of a neuron
  - Ionic channels
  - Action potential
- The Hudgkin-Huxley equation
  - The passive membrane
  - Voltage-gated channels
  - Anatomy of a spike
- Neuronal dynamics
  - **Phase portrait models**
  - **Fixed points and their stability**
  - **Bifurcation (saddle-node / Hopf)**
  - **Simplified 2D models**

Phase Portrait Models

Capturing The Basic Dynamics of Neurons

- Let's start with the simplest model:
  - Write down an equation for V that does something like a neuron does:

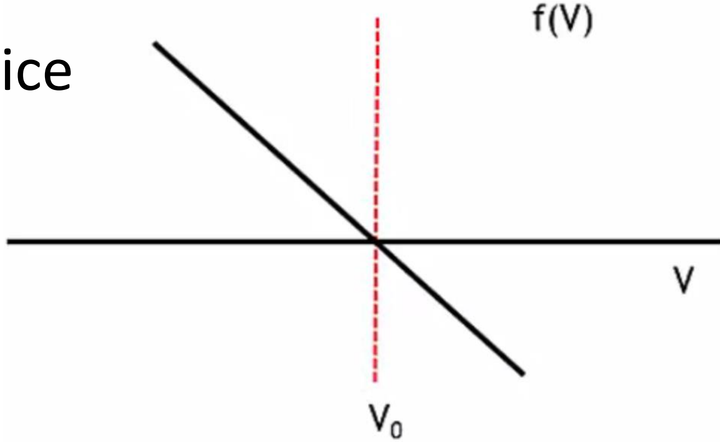
$$\frac{dV}{dt} = f(V) + I(t)$$

  - We want to find a function $f(V)$ to model the neuron's activity

$$\boxed{f(V) = -a(V - V_0)}$$

  - A linear function may be a good choice as long as we are not close to the spiking events:

$$\frac{dV}{dt} = -a(V - V_0) + I(t)$$



Effect of $I(t)$ is not considered here

Capturing The Basic Dynamics of Neurons

$$\frac{dV}{dt} = -a(V - V_0) + I(t)$$

- A ***fixed point*** occurs where $\frac{dV}{dt} = 0$

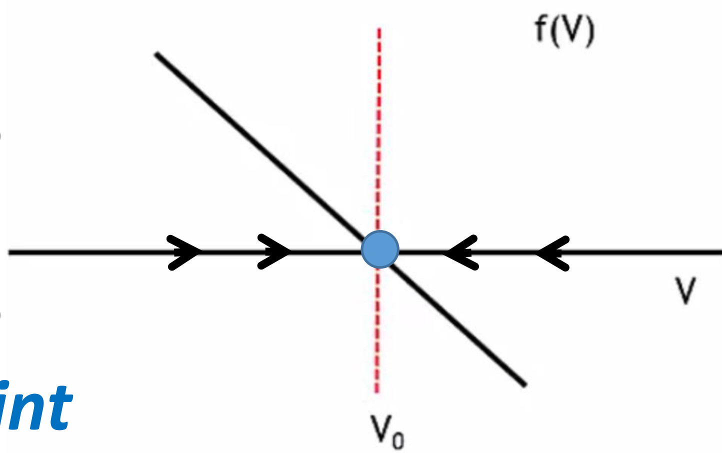
(Let's assume $I = 0$ so the fixed point is at $V = V_0$)

$$\boxed{\frac{dV}{dt} = -a(V - V_0) = 0}$$

- Examine the behavior on the two sides of the fixed point:
  - For $V > V_0$:

    $\rightarrow \frac{dV}{dt} < 0 \rightarrow$ Making V move towards V_0
  - For $V < V_0$:

    $\rightarrow \frac{dV}{dt} > 0 \rightarrow$ Making V move towards V_0



- This means V_0 is a ***stable fixed point***

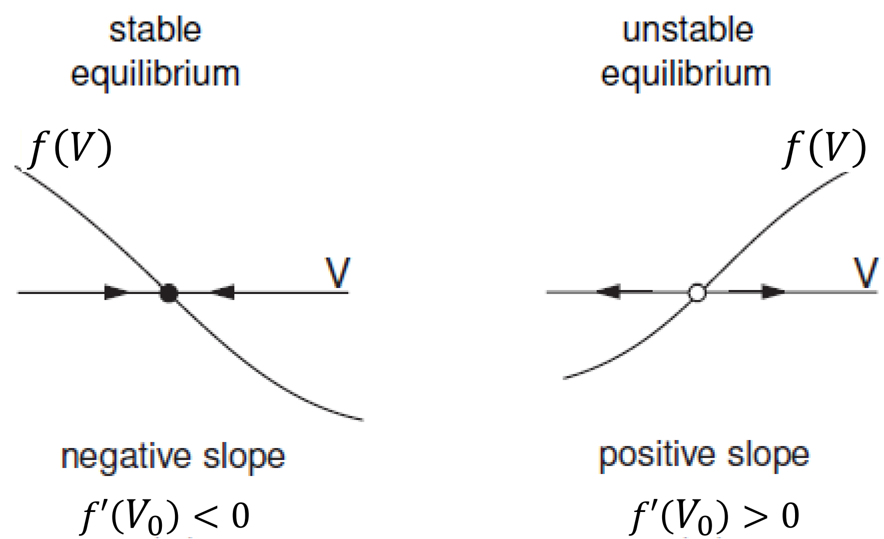
  ➢ **Let's briefly study fixed points of a 1D dynamic system and their stability**

Fixed Points and Their Stability

$$\frac{dV}{dt} = f(V)$$

Definition of a fixed point:

$$\boxed{\left.\frac{dV}{dt}\right|_{V_0} = f(V_0) = 0}$$



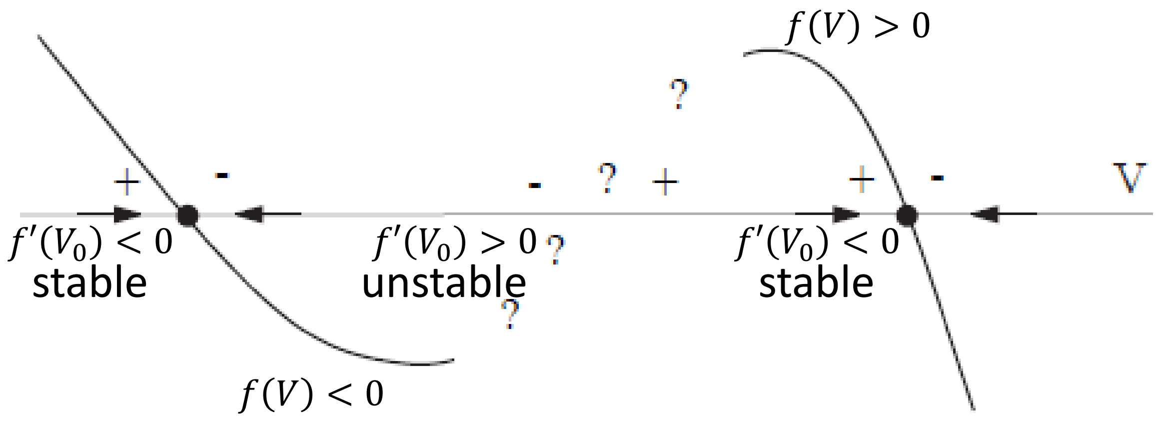
- The sign of the slope, i.e. $f'(V_0)$ determines the ***stability*** of the fixed point

- At point $V = V_0 + \varepsilon$ (for a small positive ε):

$$\frac{dV}{dt} = f(V) \approx f(V_0) + f'(V_0)(V - V_0) = 0 + f'(V_0)\varepsilon \begin{cases} > 0 \text{ if } f'(V_0) > 0 \rightarrow \mathit{Unstable} \\ < 0 \text{ if } f'(V_0) < 0 \rightarrow \mathit{Stable} \end{cases}$$

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

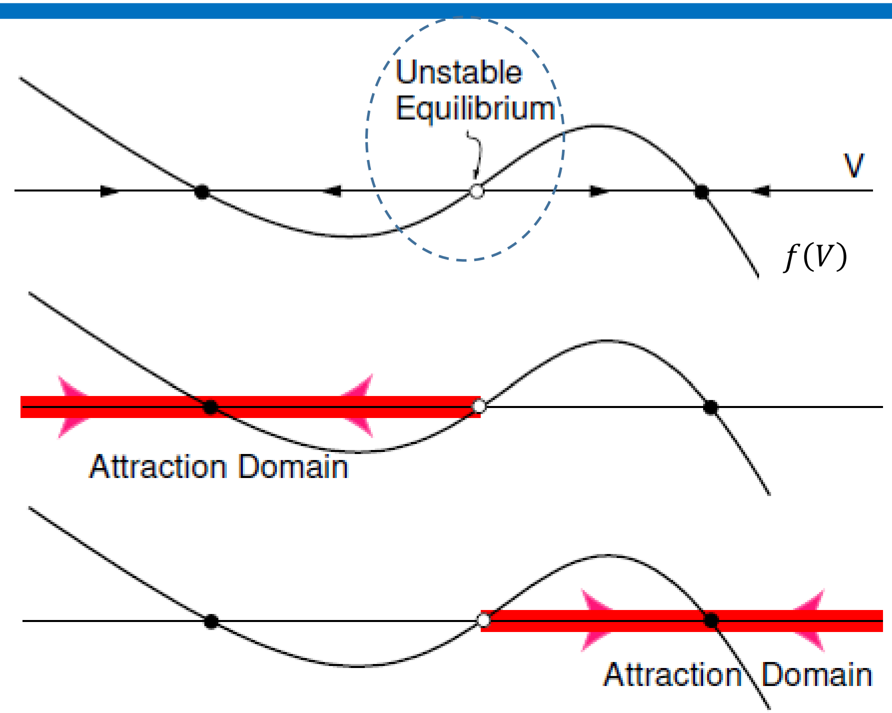
Fixed Points and Their Stability



- Two stable fixed points must be separated by at least one unstable fixed point
  - Because $f(V)$ has to change signs from minus to plus (continuity)

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability



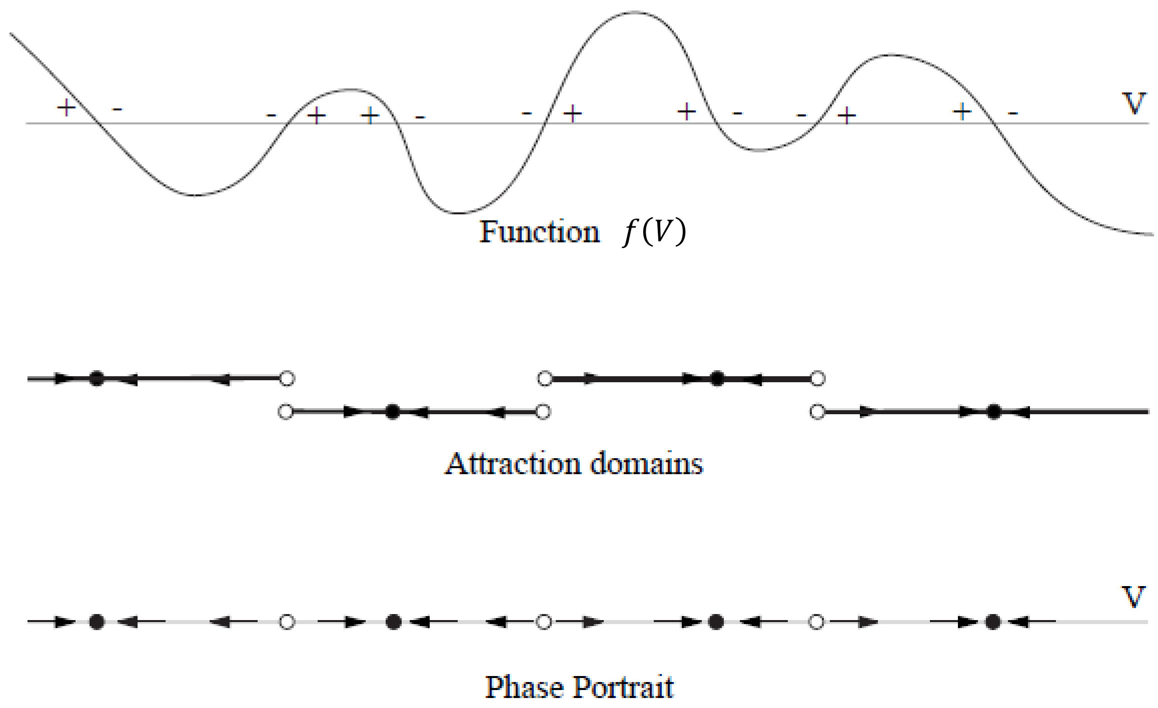
- Two ***attraction domains*** in a 1D system are separated by an **unstable** fixed point

  → An unstable fixed point can serve as a ***threshold***

  (This is an important point which we shall discuss soon)

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Fixed Points and Their Stability



- ***Phase portrait*** of a 1D system shows the dynamics of its variables in graphical form

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Fixed Points and Their Stability

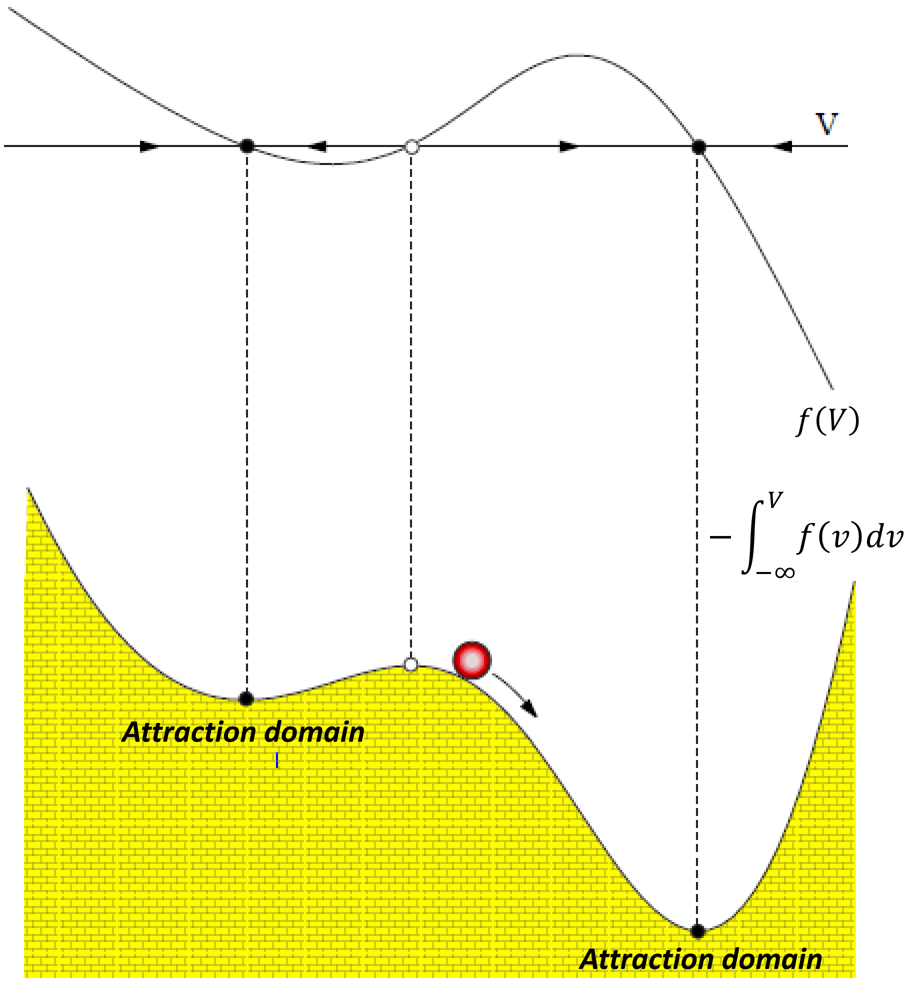
Mechanistic interpretation of stable and unstable fixed points

- A massless (inertia free) ball moves toward ***energy minima*** with the speed proportional to the slope

- A 1D system $\frac{dV}{dt} = f(V)$ has the ***energy landscape***:

$$E(V) = -\int_{-\infty}^{V} f(v)dv$$

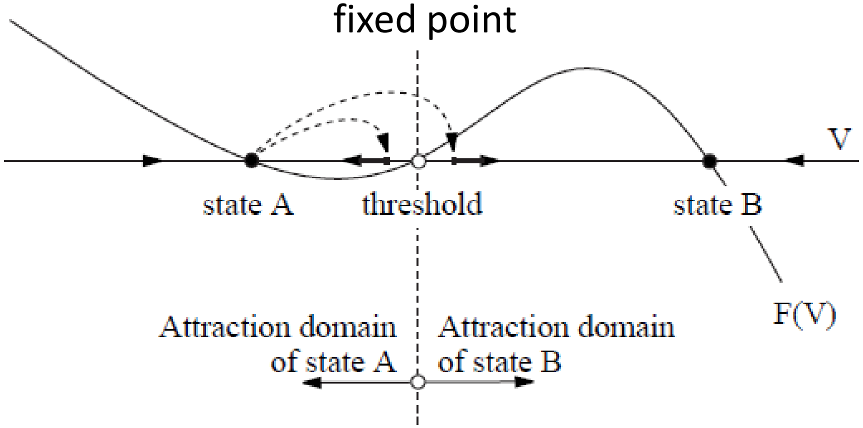
- Zeros of $f(V)$ with negative (/positive) slope correspond to minima (/maxima) of $E(V)$



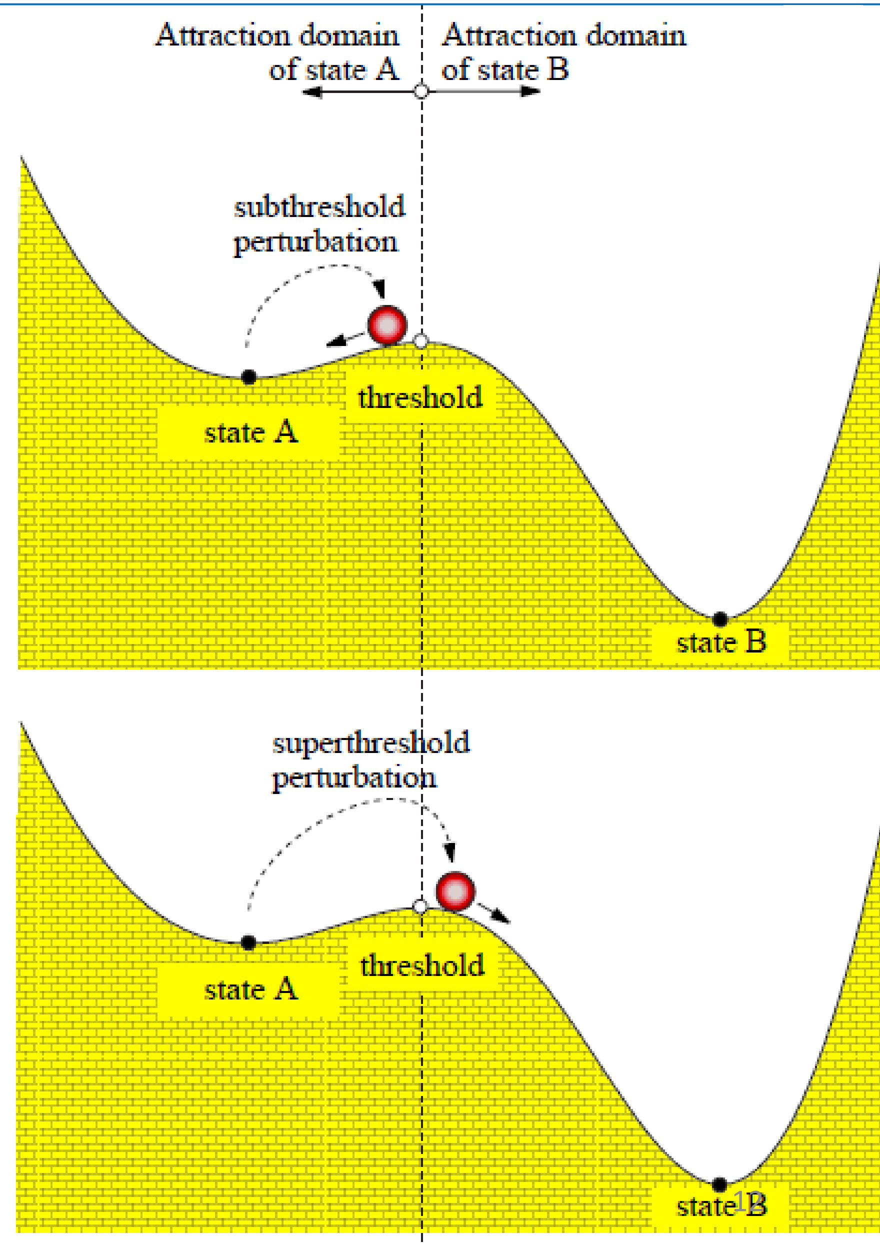
Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability

Unstable
fixed point



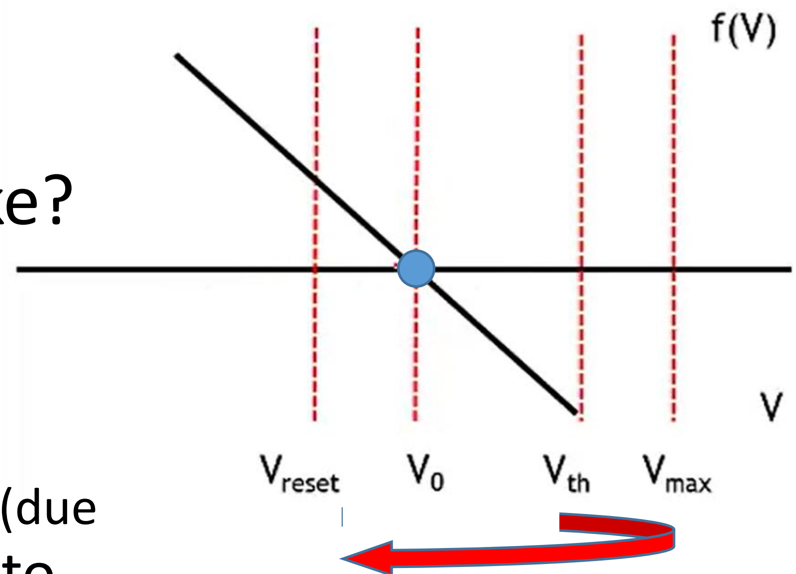
- An unstable fixed point plays the role of a ***threshold***:
  - A threshold separates two attraction domains



Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

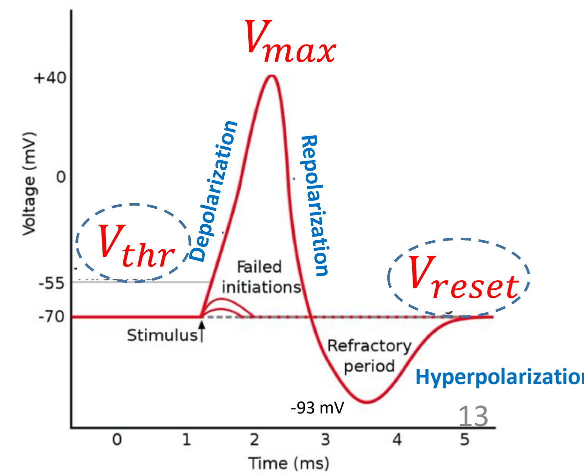
Back to Our Neural Dynamics – Making The Neuron Spike

$$\frac{dV}{dt} = -a(V - V_0) + I(t)$$



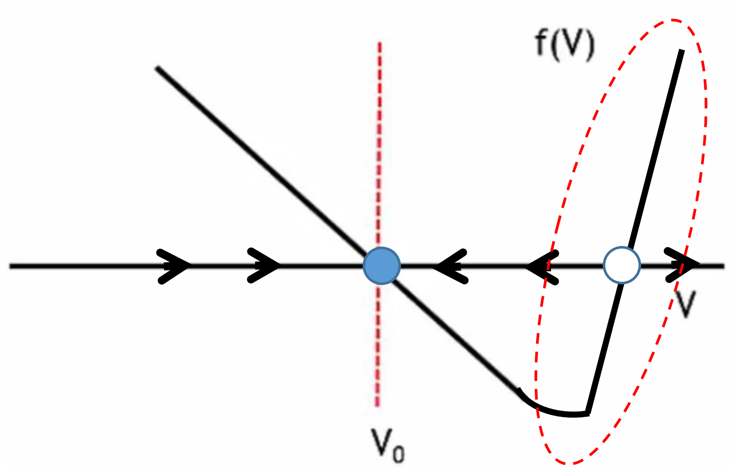
- How to make the neuron spike?
- Need to add two effects:

1. A ***threshold*** voltage V_{thr}:
   - So that if the voltage passes it (due to an input), it won't come back to V_0, but reaches a maximum value V_{max}
2. A ***reset*** voltage V_{reset}:
   - After reaching the maximum, the voltage resets to this voltage



Making The Neuron Spike

- Can we modify $f(V)$ so that the model is intrinsically excitable?
  - Let's add another fixed point (with a positive slope, so it serves as an ***unstable fixed point***, i.e. a ***threshold***)



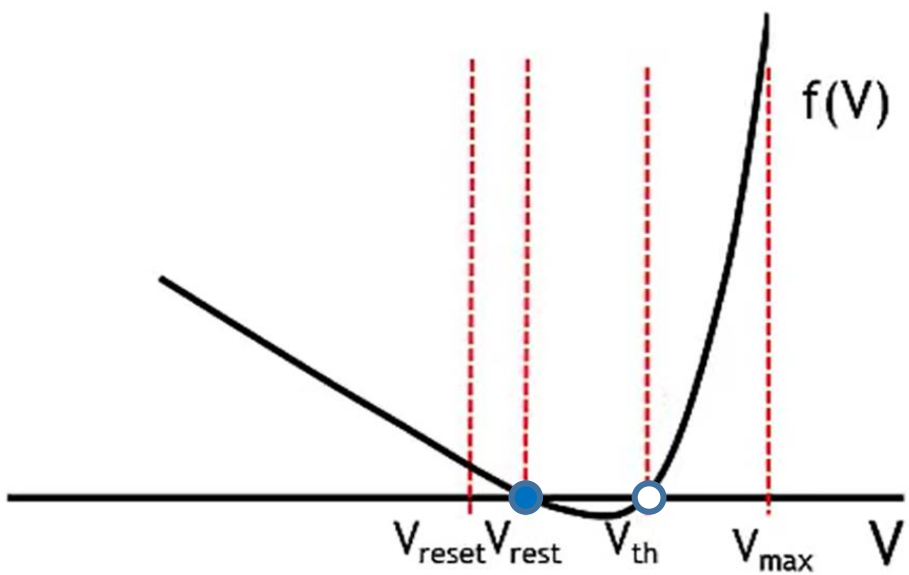
➢ If there is an input to take the voltage past the new fixed point, the voltage will further increase

Making The Neuron Spike

- An example of the form of $f(V)$ that works well is the ***exponential integrate-and-fire*** model:

$$f(V) = -a(V - V_0) + \exp\left(\frac{V - V_0}{\Delta}\right)$$

  - Another example is the ***quadratic*** function



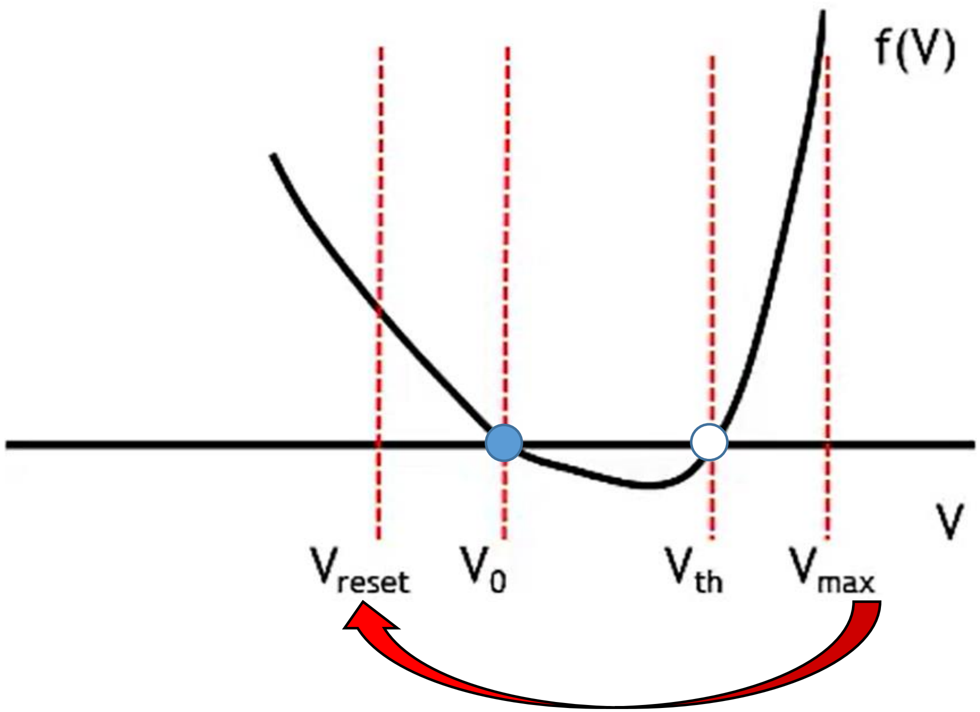
Fourcaud-Trocmé, Hansel, van Vreeswijk and Brunel

$$\frac{dV}{dt} = f(V) + I(t)$$

Δ controls the sharpness of the rise of the nonlinearity (smaller values of Δ result in sharper rises)

Making The Neuron Spike

- In addition to the second fixed point at V_{thr}, we will need a maximum voltage V_{max} (beyond which the voltage cannot continue to increase)
- And when we reach the maximum value V_{max}, we need a mechanism to return to the reset value V_{reset}

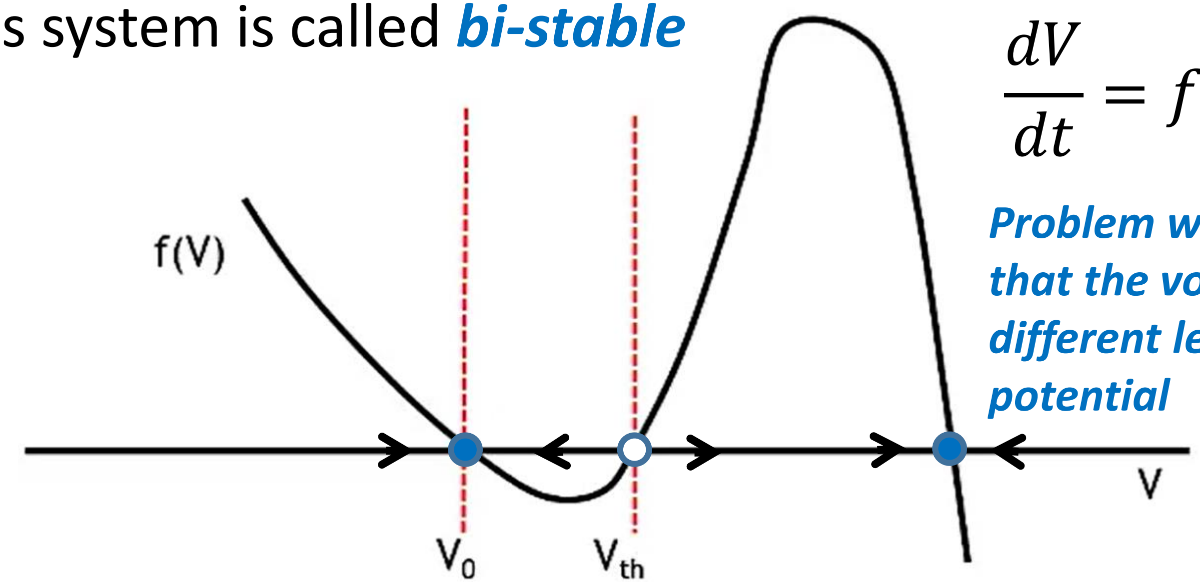


$$\frac{dV}{dt} = f(V) + I(t)$$

Making The Neuron Spike

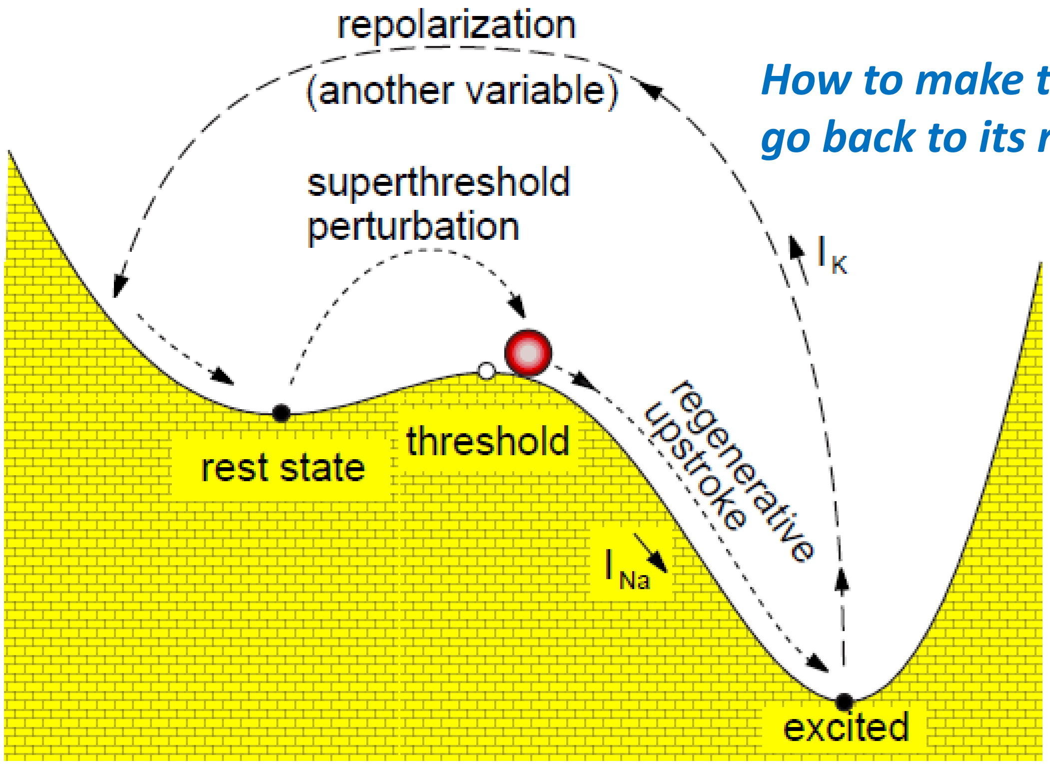
- For getting the voltage back to the reset value:
  - Let's add another fixed point by extending the curve back towards zero again
  - The new fixed point will be stable (Fixed points with negative slopes are stable, those with positive slopes are unstable)
  - After reaching the maximum value, the system goes to the new fixed point and stays there
  - This system is called ***bi-stable***

$$\frac{dV}{dt} = f(V) + I(t)$$



Problem with this model is that the voltage stays at a different level from the rest potential

Making The Neuron Spike



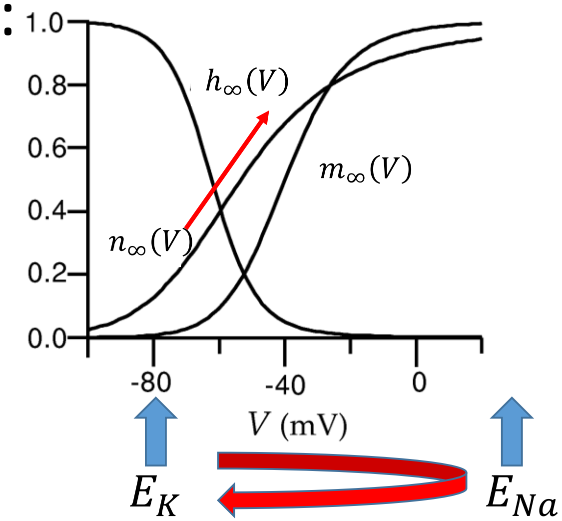
How to make the neuron go back to its rest state?

- Mechanistic concept of generation of an action potential
  - A second variable is needed for returning from the excited state to the rest state

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Two-Dimensional Models

- Recall there were 2 mechanisms in Hudgkin-Huxley which helped to restore the voltage back to rest:



1. The sodium drive towards E_{Na} (higher potentials) was switched off
2. The potassium channel activated to drive the voltage back towards E_K

- We need to do something similar to pull the voltage back towards rest:
  - ➢Include a second variable to take care of **inactivation**

$$\frac{dV}{dt} = f(V) + G(u) + I(t)$$
$$\frac{du}{dt} = -u + H(V)$$

➢***Let's study the ramifications of adding this new variable and its dynamics***

Two-Dimensional Models

$$\frac{dV}{dt} = f(V) + G(u) + I(t)$$
$$\frac{du}{dt} = -u + H(V)$$

- The new variable u ***decays linearly***: $\frac{du}{dt} = -u$

  (i.e. without an input $H(V)$, u decays exponentially to zero from an initial point)

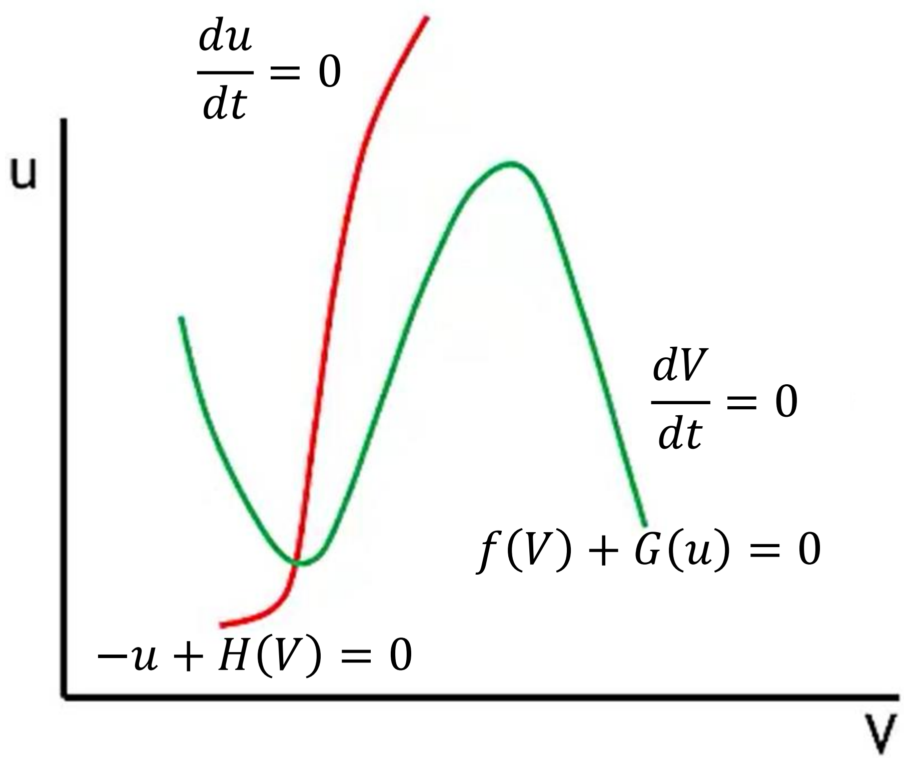
- But it also has a coupling with V through $H(V)$
  - ➢ When V gets large, u also becomes large

- The inactivation function u is also coupled with V through the function $G(u)$

  (which should be negative → So a large u pulls V down again)

Two-Dimensional Models

- With a 2-variable model, instead of plotting $f(V)$ against V, a 2D ***phase diagram*** is plotted
  - Instead of fixed points, the entire curve on which either variable has zero derivative is considered (called ***nullclines***)

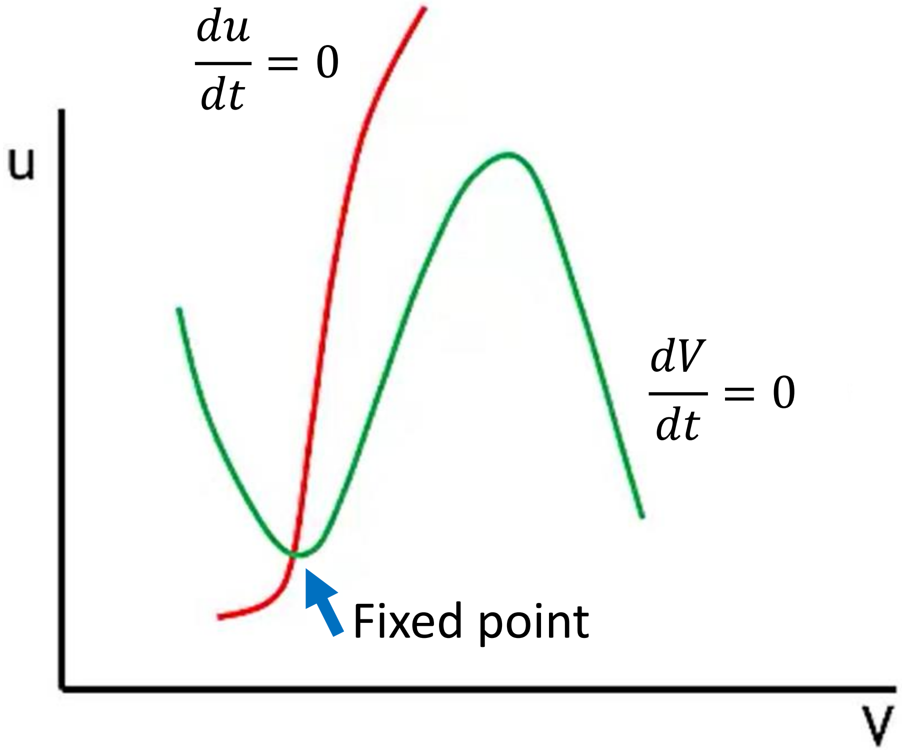


$$\frac{dV}{dt} = f(V) + G(u) + I(t)$$

$$\frac{du}{dt} = -u + H(V)$$

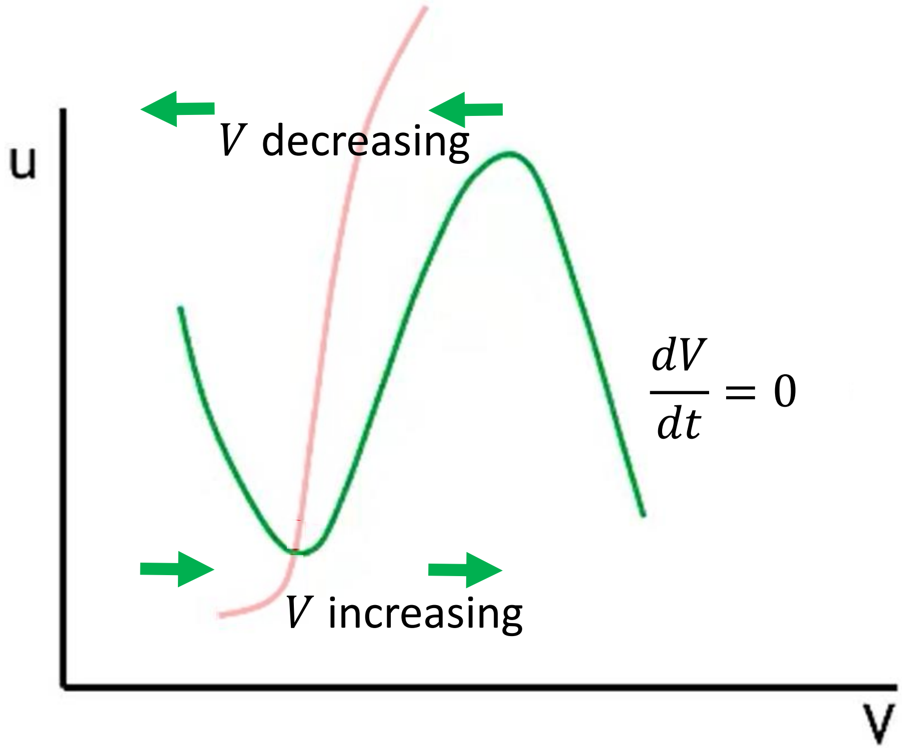
Two-Dimensional Models

- ***Fixed points*** of the plot occur where the nullclines collide
  - There is one fixed point in the plot below (the rest state)



Two-Dimensional Models

- Each nullcline curve divides the space into two parts:
  - On one side of $\frac{dV}{dt} = 0$ the variable V is increasing ($\frac{dV}{dt} > 0$) and on the other side it is decreasing ($\frac{dV}{dt} < 0$)



Two-Dimensional Models

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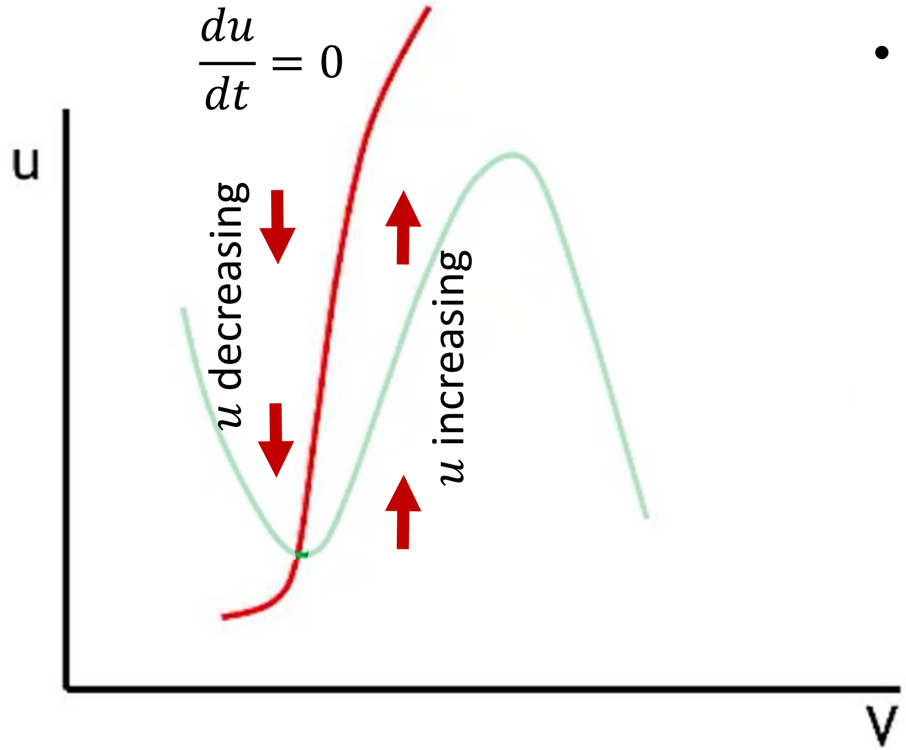
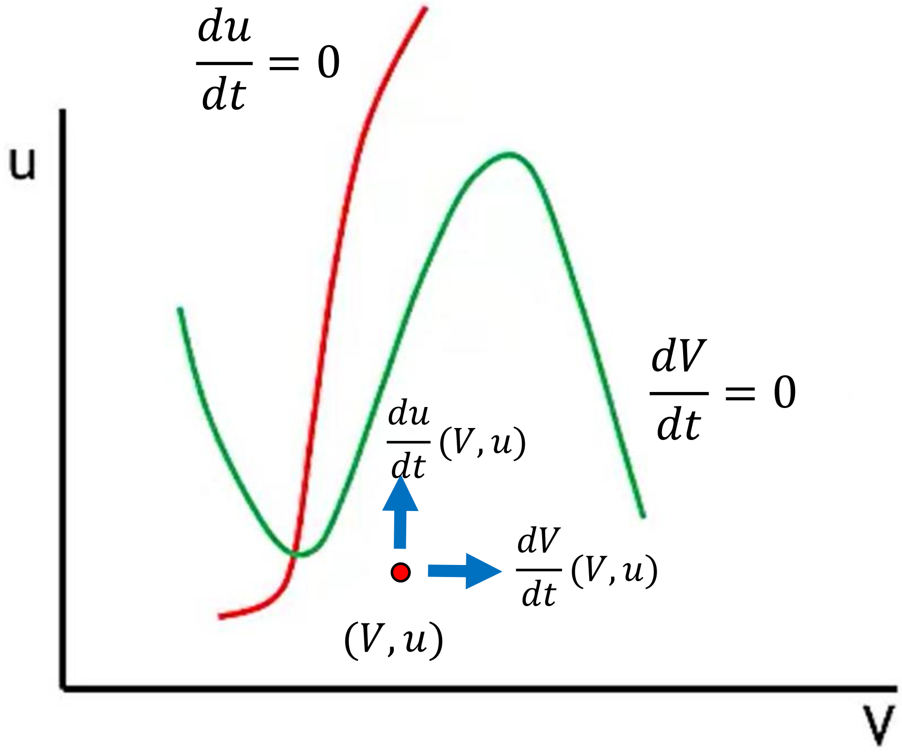
  - On one side of $\frac{dV}{dt} = 0$ the variable V is increasing ($\frac{dV}{dt} > 0$) and on the other side it is decreasing ($\frac{dV}{dt} < 0$)
  - On one side of $\frac{du}{dt} = 0$ the variable u is increasing ($\frac{du}{dt} > 0$) and on the other side it is decreasing ($\frac{du}{dt} < 0$)



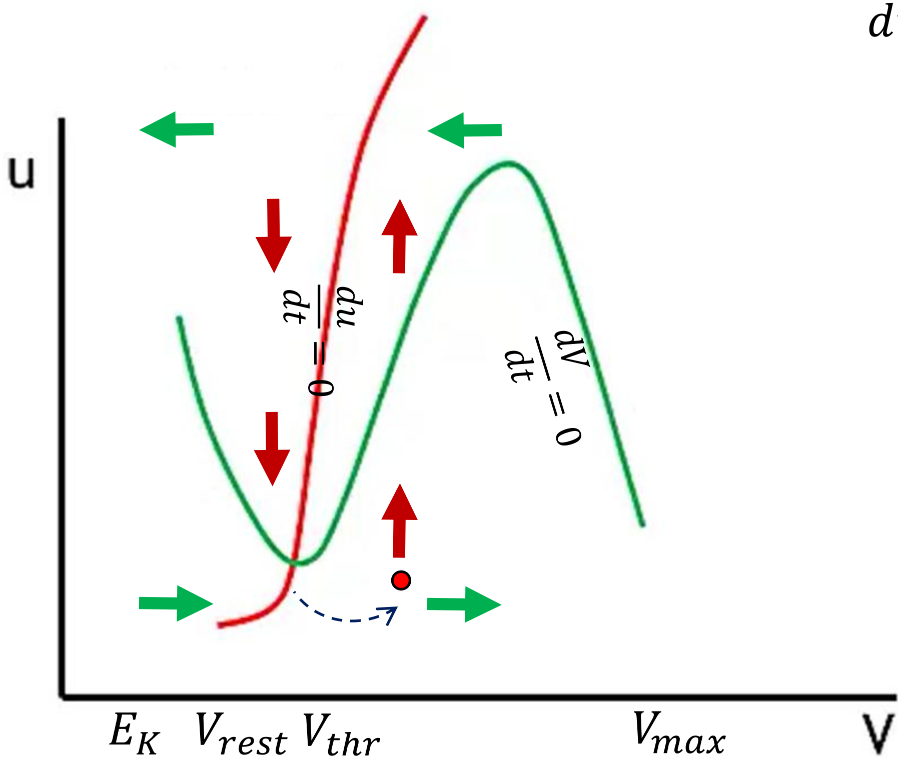
Two-Dimensional Models

- If we start out at a point (V, u) our movement will have:
  - Velocity in the V direction as $\frac{dV}{dt}$ (evaluated at (V, u))
  - Velocity in the u direction as $\frac{du}{dt}$ (evaluated at (V, u))



Two-Dimensional Models

- Let's now start at near rest and consider an input which takes us to some larger voltage range:

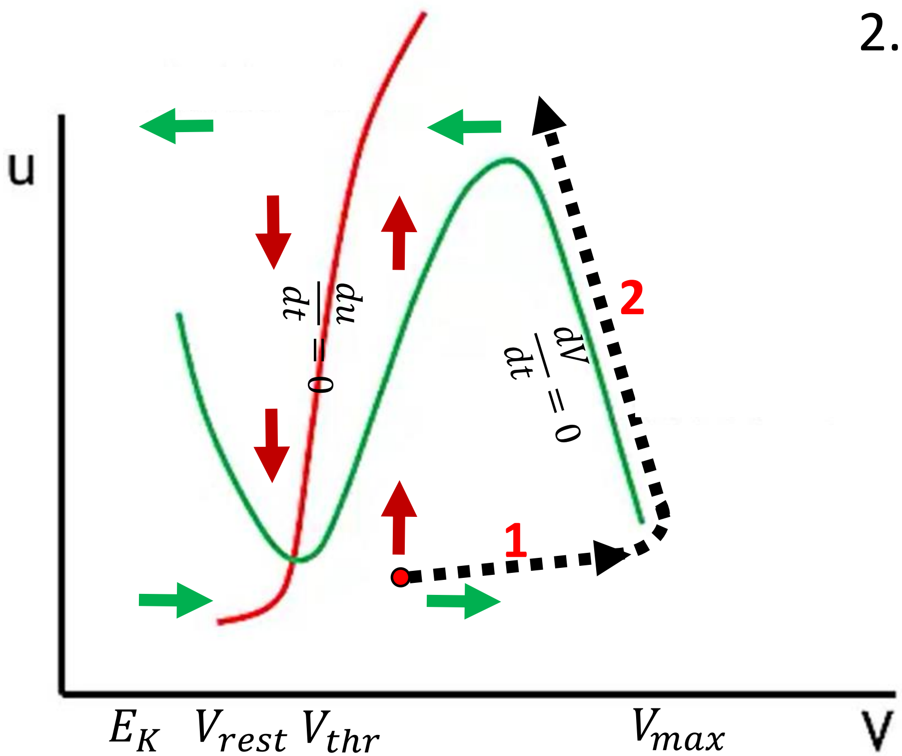


$$\frac{dV}{dt} = f(V) + G(u) + I(t)$$

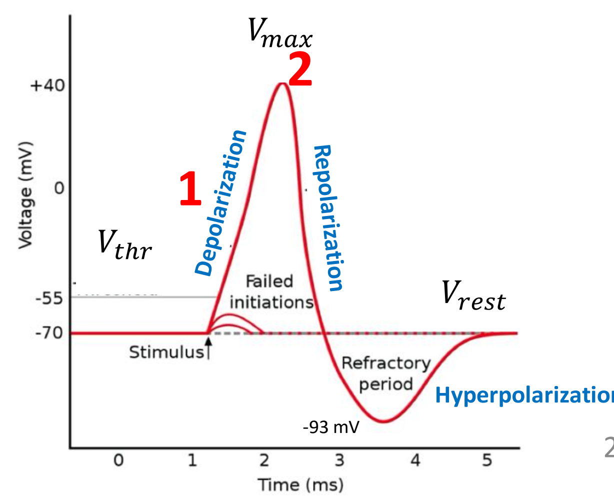
$$\frac{du}{dt} = -u + H(V)$$

Two-Dimensional Models

- Let's now start at near rest and consider an input which takes us to some larger voltage range:

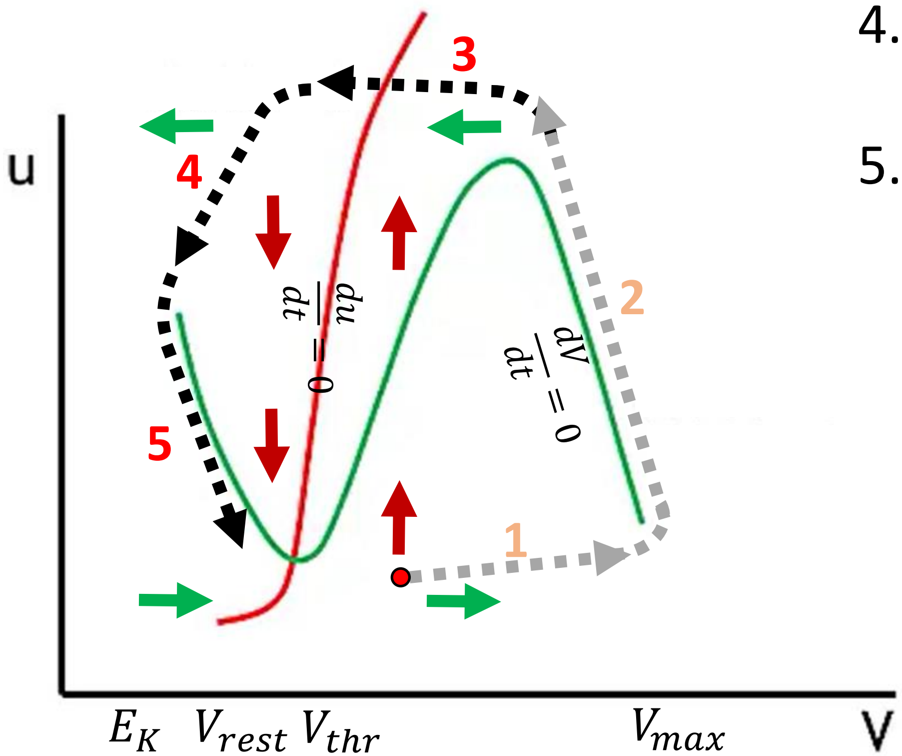


1. The nonlinearity $f(V)$ in voltage quickly increases V (causing a spike)
2. After crossing the V nullcline, the value of V decreases while we still increase in the value of u

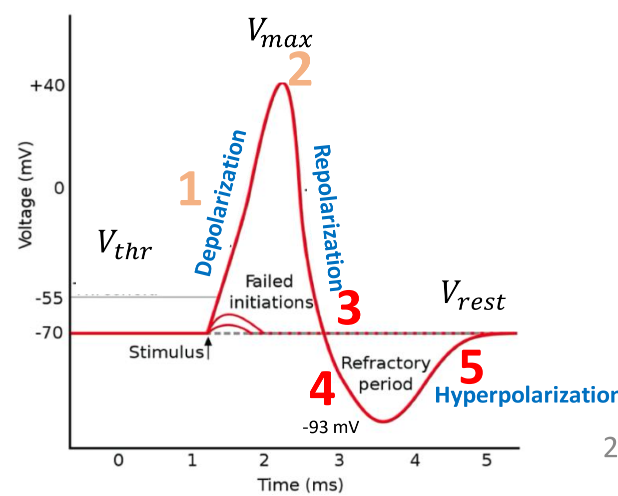


Two-Dimensional Models

- Let's now start at near rest and consider an input which takes us to some larger voltage range:

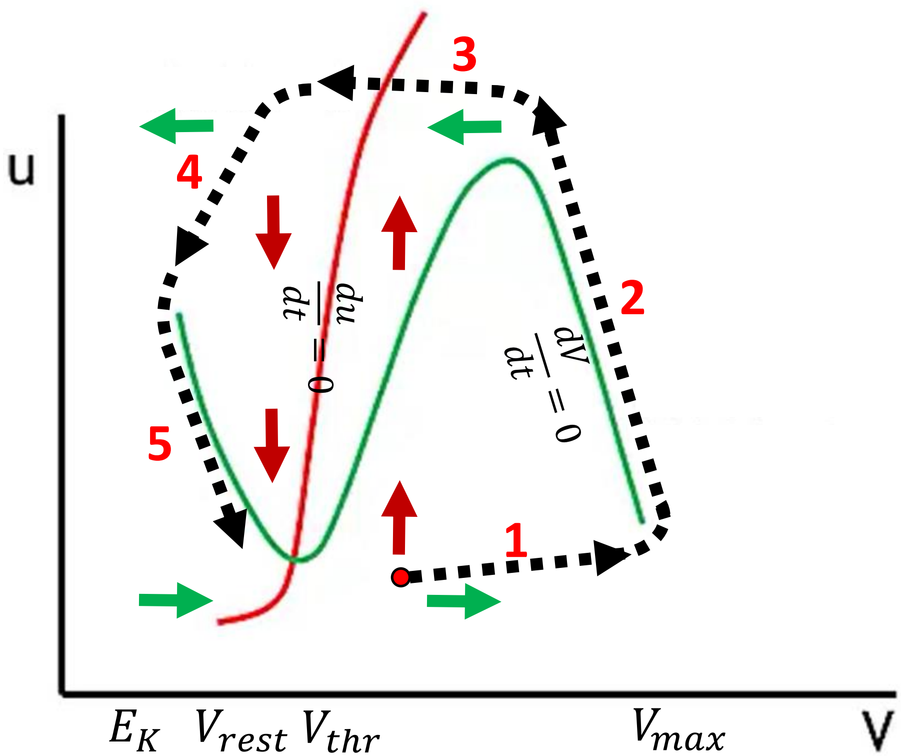


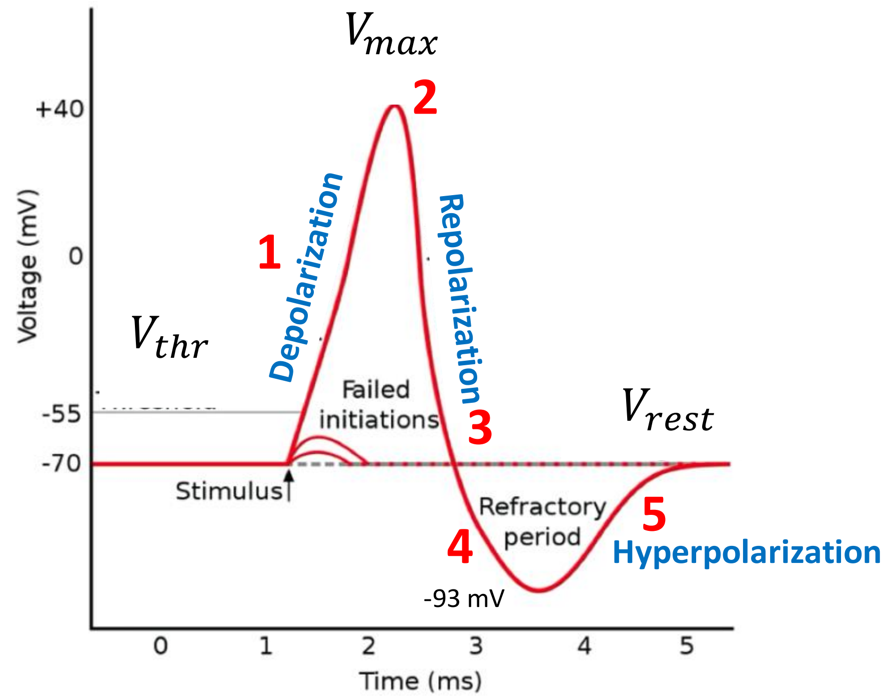
3. After crossing the u nullcline, the value of u decreases
4. The value of V further decreases towards E_K
5. Finally, V slightly increases towards V_{rest}



Two-Dimensional Models

- This process causes the membrane voltage to follow the model of an action potential (spike):





Phase Plane

- 2D dynamical system with state variable $(x(t), y(t))$:

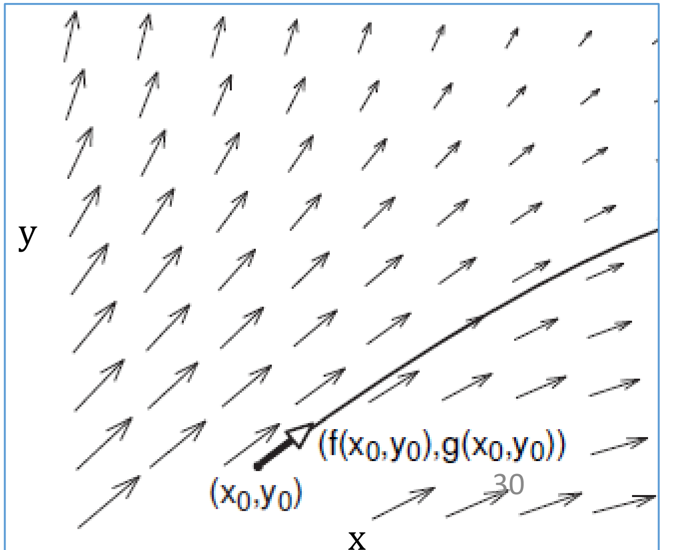
$$\dot{x} = f(x, y)$$
$$\dot{y} = g(x, y)$$

- For any point (x_0, y_0) on the phase plane:
  - The vector $(f(x_0,y_0), g(x_0,y_0))$ indicates the direction of change $(\dot{x}, \dot{y})$ of the state variable (x, y)

- Example:

  $f(x_0,y_0)$ and $g(x_0,y_0)$ both positive:

  → Both $x(t)$ and $y(t)$ increase at point (x_0,y_0)

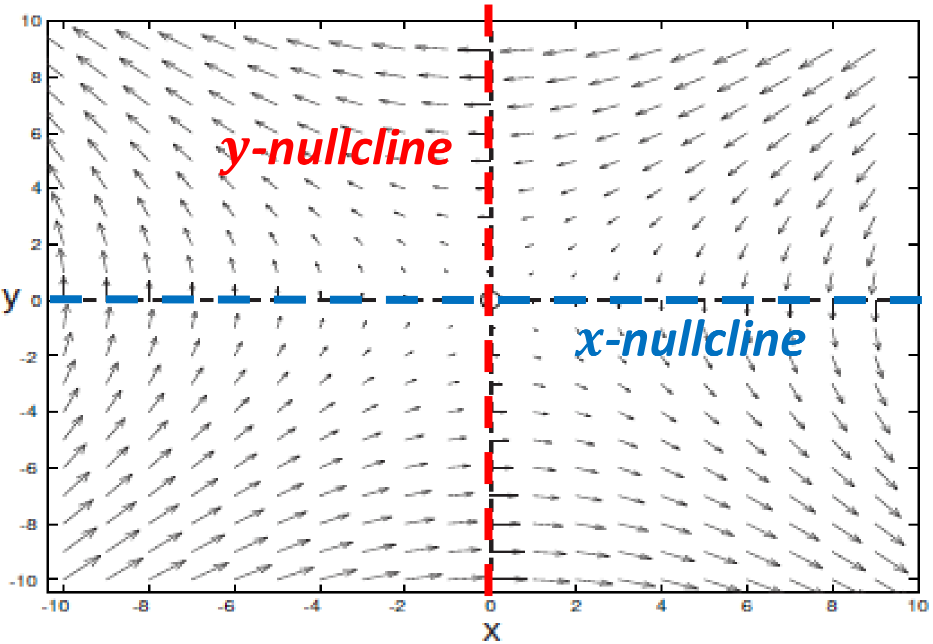


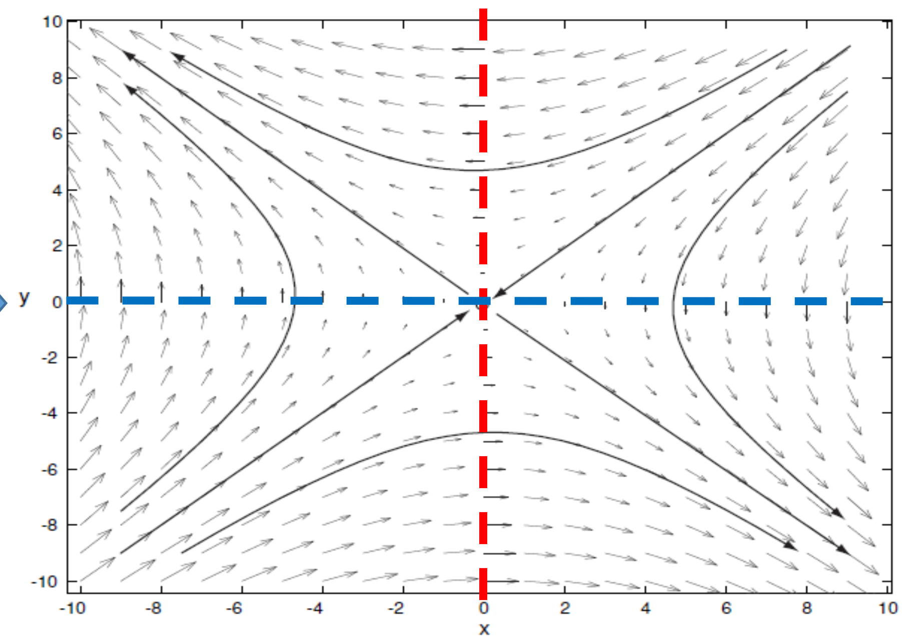
Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Trajectories

- Sample trajectories for different initial points:

$$\dot{x} = f(x, y) = -y$$
$$\dot{y} = g(x, y) = -x$$





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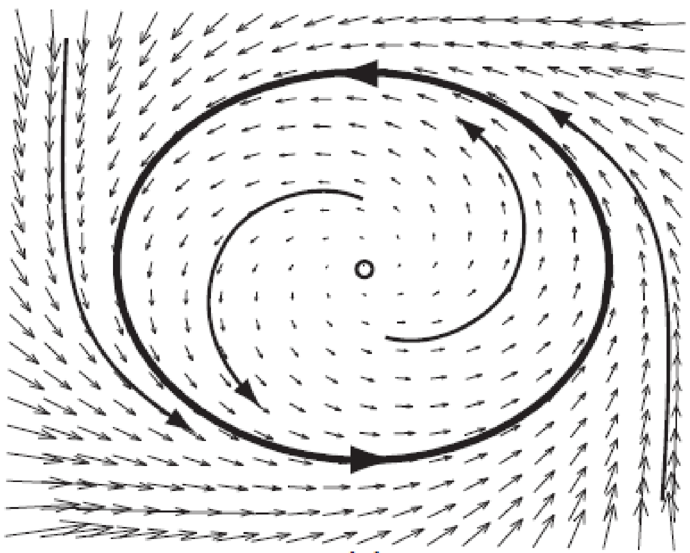
Limit Cycles

- A trajectory that forms a closed loop is called a ***limit cycle***
  - If the initial point of the system is on a limit cycle, then the state $(x(t), y(t))$ stays on the cycle forever

    → The system exhibits periodic behavior:

    $x(t) = x(t+T),\ \ y(t) = y(t+T)$ for some period $T > 0$



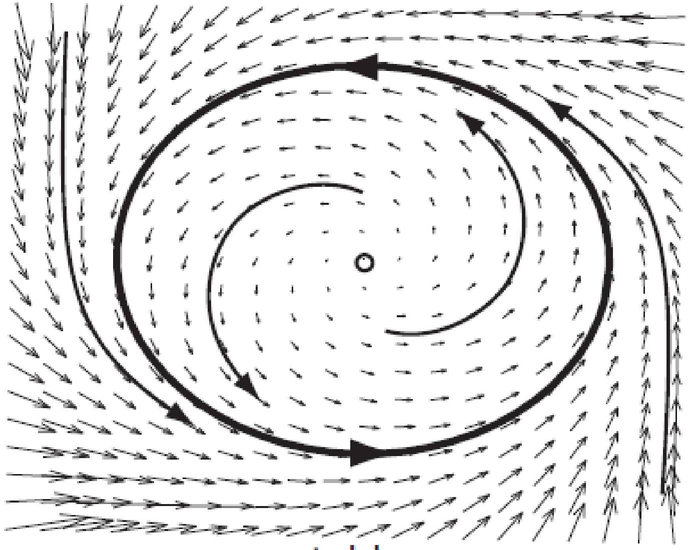
Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

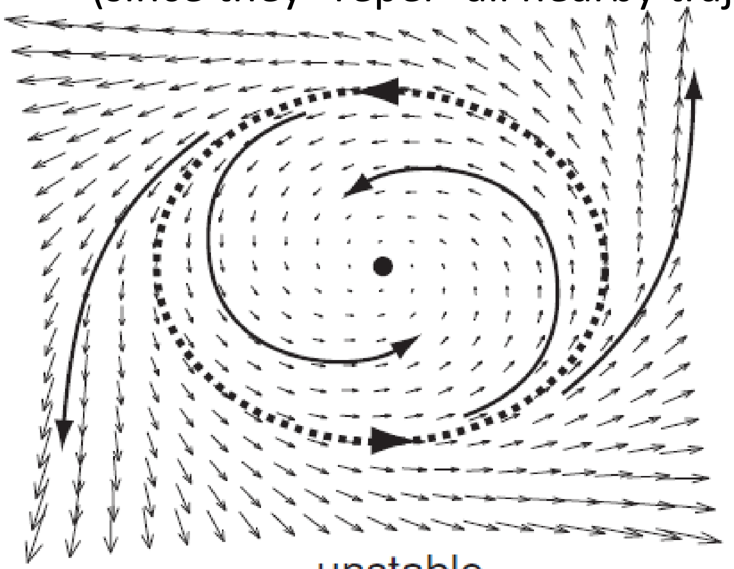
Limit Cycles

- ***Asymptotically stable*** limit cycle:
  Any trajectory with the initial point sufficiently near the cycle approaches the cycle as $t \to \infty$

Also called ***limit cycle attractors***
(since they “attract” all nearby trajectories)

Unstable limit cycles are called ***repellers***
(since they “repel” all nearby trajectories)





Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Back to Our Neural Dynamics – Nullclines and Fixed Points

- Let's consider a particular neural example of the (V, u) model:

$$\frac{dV}{dt} = f(V) + G(u) + I(t)$$

$$\frac{du}{dt} = -u + H(V)$$

$$C_m \frac{dV}{dt} = I_e - g_L(V - E_L) - g_{Na}m^3h\,.(V - E_{Na}) - g_K n^4\,.(V - E_K)$$

- General form of the Hudgkin-Huxley gate model:

$$I = \bar{g}m^a h^b (V - E)$$

See Izhikevich Sec. 5.1 and 5.1.2

- A variant of the Hudgkin-Huxley equation:

$$C_m \frac{dV}{dt} = I_e - \underbrace{g_L(V - E_L)}_{\text{Leak } I_L} - \underbrace{g_{Na}m_\infty(V)\,.\,(V - E_{Na})}_{\textbf{Instantaneous } I_{Na,p}} - \underbrace{g_K n\,.(V - E_K)}_{\text{Slower } I_K}$$

with a second equation modeling the slower potassium channel dynamics:

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

- This is called the $I_{Na,p} + I_K$ (**Persistent *Na* plus *K***) model
  - **Persistent current**: No inactivation gate involved (no h gate) for *Na* channel
  - **Instantaneous current**: Small time constant τ_m (i.e. $m_\infty(V)$ is reached instantly)

Back to Our Neural Dynamics – Nullclines and Fixed Points

Variant of HH equations: Persistent *Na* plus *K* model

$$C_m \frac{dV}{dt} = I_e - g_L(V - E_L) - g_{Na} m_\infty(V) . (V - E_{Na}) - g_K n . (V - E_K)$$
$$\tau(V) \frac{dn}{dt} = -n + n_\infty(V)$$

- The V-nullcline is defined by $\frac{dV}{dt} = 0$:

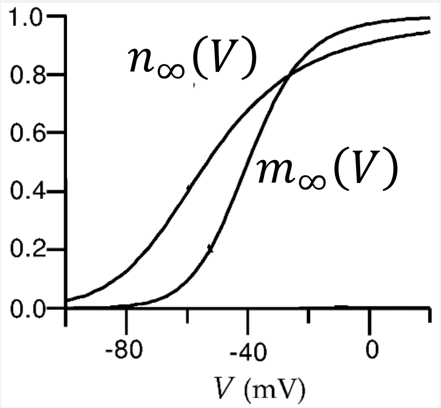
$$n = \frac{I_e - g_L(V - E_L) - g_{Na} m_\infty(V)(V - E_{Na})}{g_K(V - E_K)}$$

- The n-nullcline is defined by $\frac{dn}{dt} = 0$:

$$n = n_\infty(V)$$

➢ ***Let's draw these nullclines and create a phase plane diagram for the neural dynamics***

Recall the K^+ steady-state activation function $n_\infty(V)$ and the Na^+ activation function $m_\infty(V)$

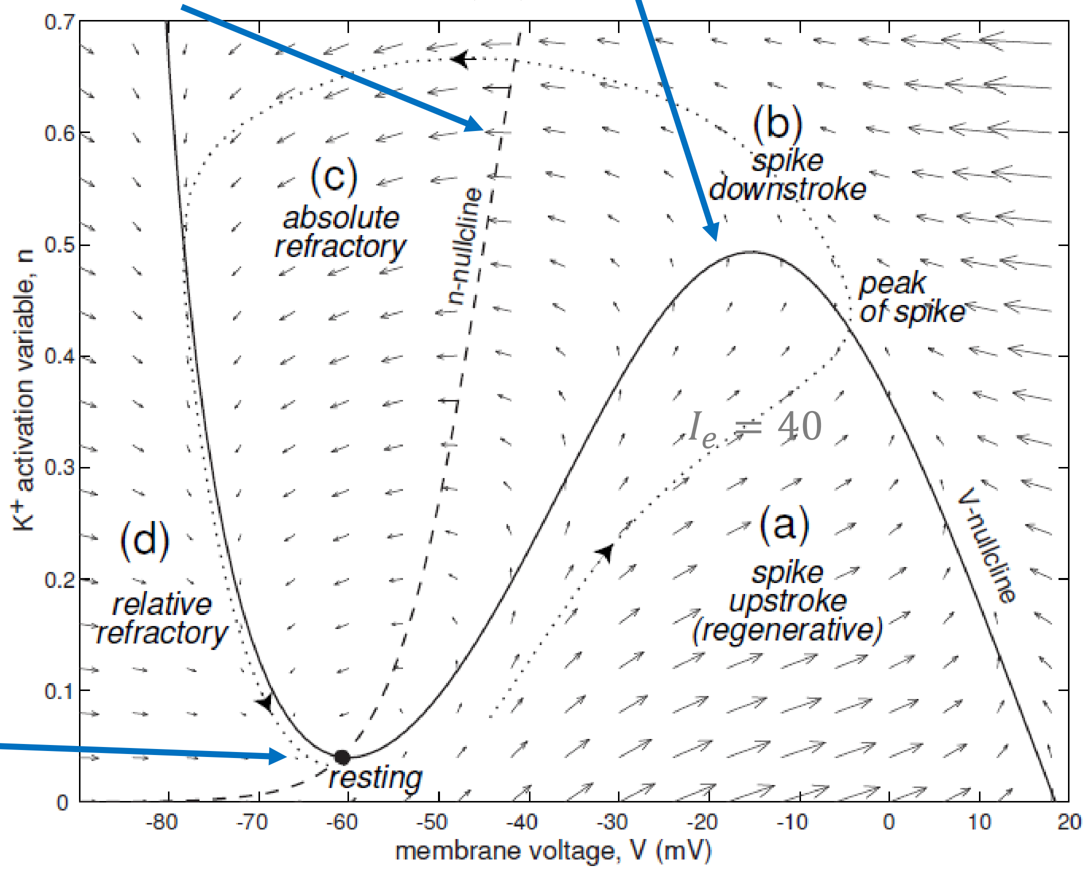


Back to Our Neural Dynamics – Nullclines and Fixed Points

- The V-nullcline: $n = \frac{I_e - g_L(V-E_L) - g_{Na} m_\infty(V)(V-E_{Na})}{g_K(V-E_K)}$

(This typically has the form of a cubic parabola)

- The n-nullcline: $n = n_\infty(V)$



The ***fixed point*** corresponds to the neuron's resting state

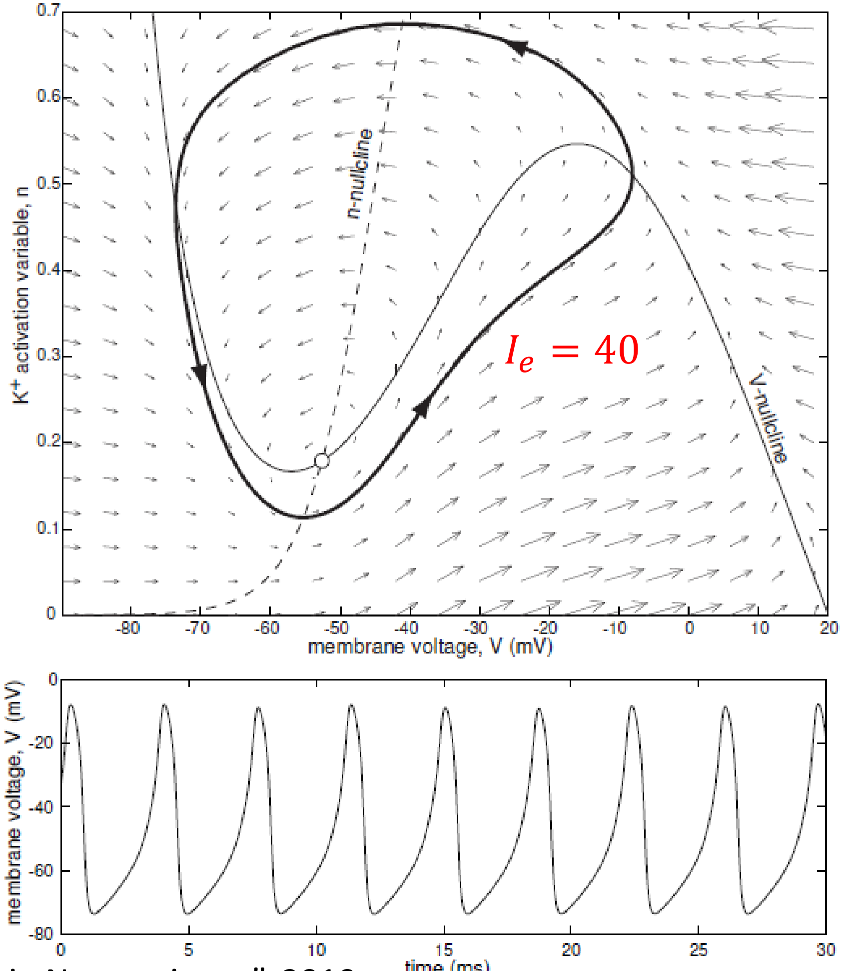
At neuron's resting potential:

- Both $m_\infty(V)$ and $n_\infty(V)$ are very small
- With $m_\infty(V) \approx 0$ and $n = n_\infty(V) \approx 0$ and without input current I_e, the voltage V is close to E_L

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Neural Dynamics – Limit Cycle

- A strong input current changes the trajectory to a limit cycle and causes periodic spiking of the neuron



Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability

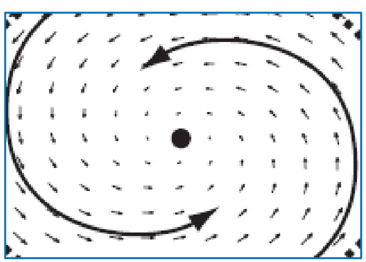
Fixed Points and Their Stability

$$\dot{x} = f(x,y)$$
$$\dot{y} = g(x,y)$$

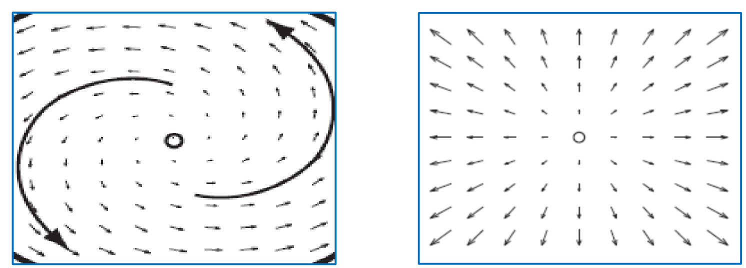
Fixed points:

- Points where $\dot{x} = \dot{y} = 0 \rightarrow$ $\left.\begin{aligned} f(x,y) &= 0 \\ g(x,y) &= 0 \end{aligned}\right\}$ Intersection of nullclines

- If the initial point (x_0, y_0) is near the fixed point:
  - The trajectory may converge to / diverge from the fixed point (depending on its stability)



Asymptotically stable fixed point



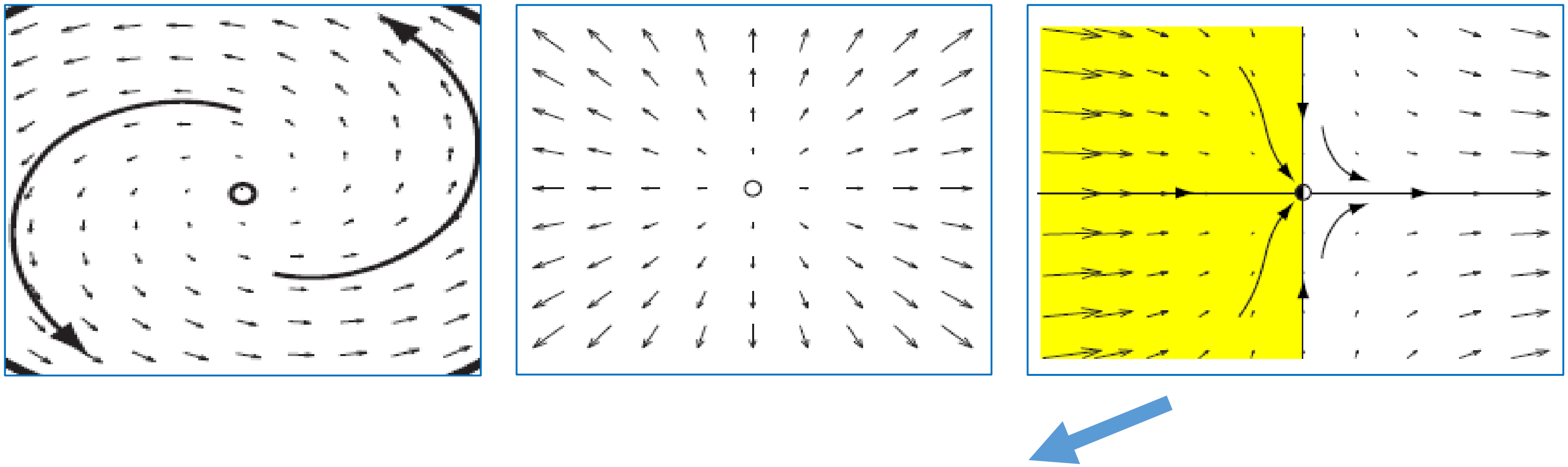
Unstable fixed points

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability

Unstable fixed point:

- At least one trajectory diverges from the fixed point
  (This should happen no matter how close the initial condition is to the fixed point)



- Any trajectory starting in the yellow area ***(attraction domain)*** converges to the fixed point
- But any trajectory starting in the white area diverges from it
  (regardless of how close the initial point is to the fixed point)

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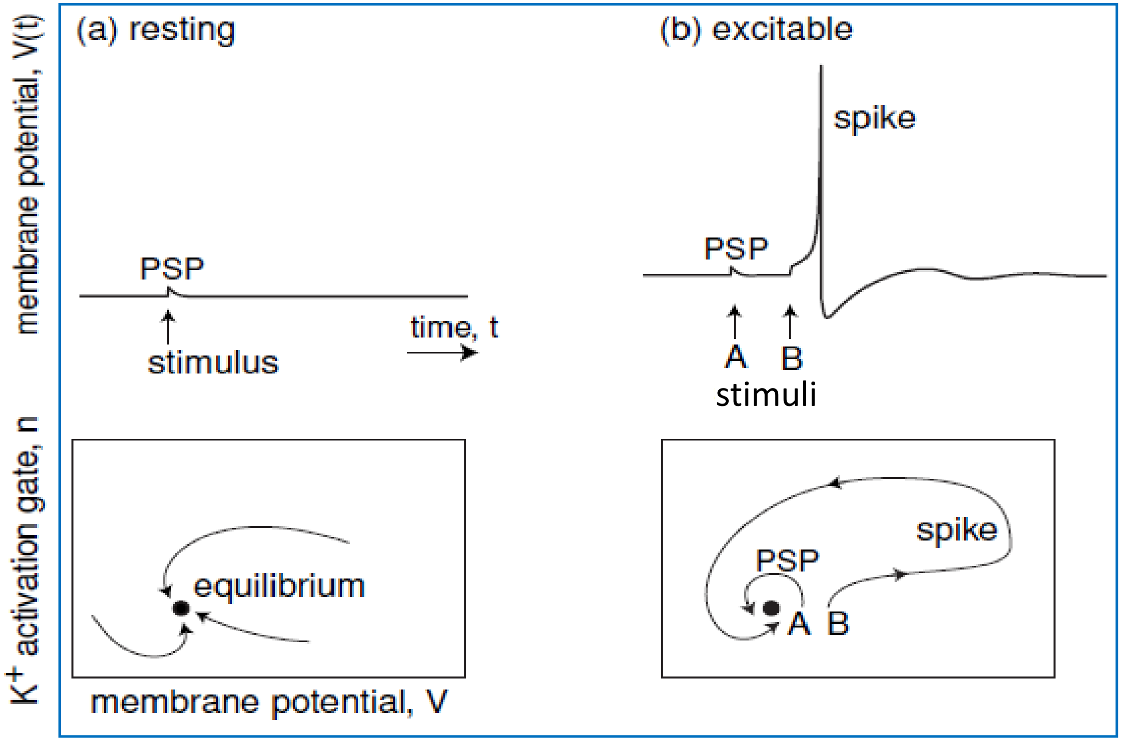
Neuronal States – Resting → Excitable & Periodic Spiking

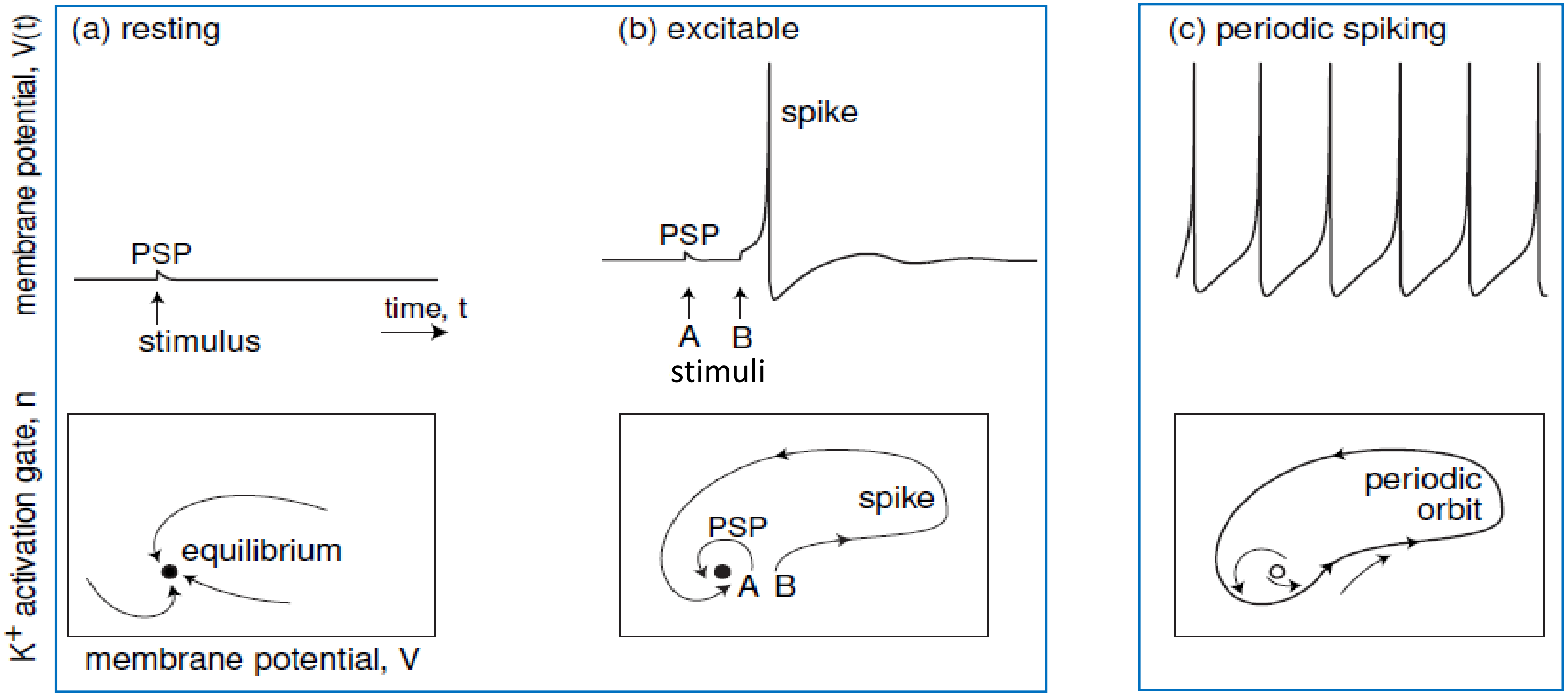


- The neuron remains quiet with small stimuli
  (Stable equilibrium)

- Small stimulus (A) → Small excursion from equilibrium (no spike)
- Large stimulus (B) → Amplified by neuron's dynamics → Spike
  (Stable equilibrium)

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

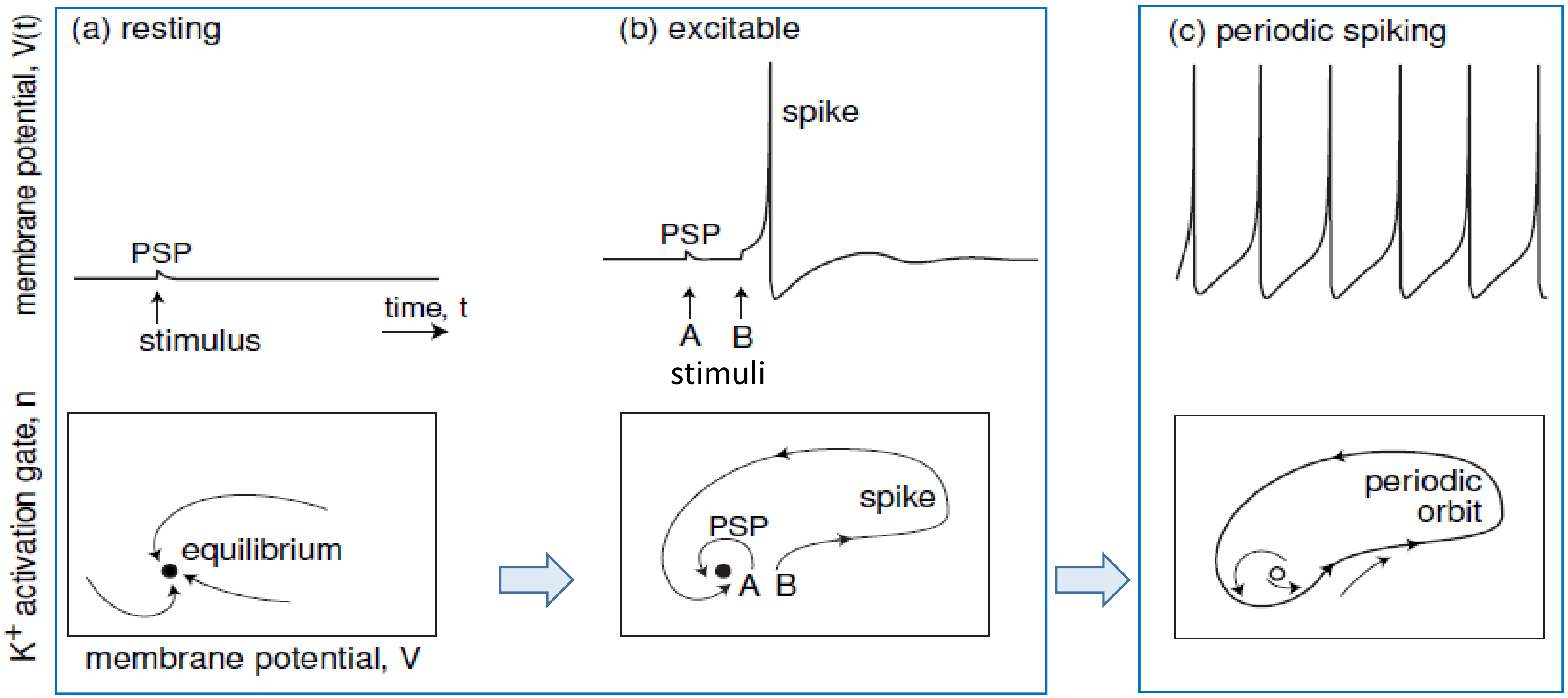
Neuronal States –
Resting → Excitable & Periodic Spiking



- Sufficiently strong input → Periodic spiking activity **(Stable limit cycle)**

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Neuronal States –
Resting → Excitable & Periodic Spiking



Only quantitative change of behavior

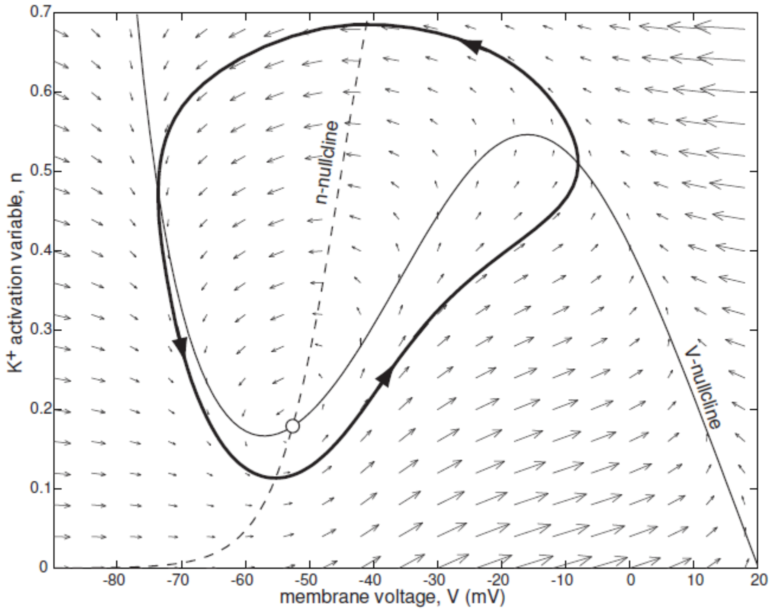
A qualitative change of behavior

- ***We will study how a neuron changes its behavior to repeated and periodic spiking***

This change of behavior is called bifurcation

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability



- How to determine the stability of a fixed point?
  - We need to look at the ***behavior of the 2D vector field*** in a local neighborhood of the fixed point
    - Often visual inspection of the vector field does not give conclusive information about stability
  - ➢ ***This can be done using analytical tools which we discuss next***

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Fixed Points and Their Stability

Practice in HW

- Consider a 2D dynamical system:

$$\dot{x} = f(x, y)$$
$$\dot{y} = g(x, y)$$

with a fixed point (x_0, y_0)

- The nonlinear functions f and g can be linearized near the fixed point:

$$f(x, y) = a(x - x_0) + b(y - y_0) + \text{higher order terms}$$

$$g(x, y) = c(x - x_0) + d(y - y_0) + \text{higher order terms}$$

where:

$$a = \left.\frac{\partial f}{\partial x}\right|_{(x_0, y_0)}, \qquad b = \left.\frac{\partial f}{\partial y}\right|_{(x_0, y_0)}$$

$$c = \left.\frac{\partial g}{\partial x}\right|_{(x_0, y_0)}, \qquad d = \left.\frac{\partial g}{\partial y}\right|_{(x_0, y_0)}$$

Fixed Points and Their Stability

Practice in HW

- Define:

$$u = x - x_0$$
$$w = y - y_0$$

as deviations from the fixed point

- We will have:

$$\dot{u} = \dot{x} = f(x, y) \approx a(x - x_0) + b(y - y_0) = au + bw$$
$$\dot{w} = \dot{y} = g(x, y) \approx c(x - x_0) + d(y - y_0) = cu + dw$$

- The linearized system:

$$\dot{u} = au + bw$$
$$\dot{w} = cu + dw$$

or in matrix form:

$$\begin{bmatrix} \dot{u} \\ \dot{w} \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{bmatrix} u \\ w \end{bmatrix}$$

Fixed Points and Their Stability

Practice in HW

$$\begin{bmatrix} \dot{u} \\ \dot{w} \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{bmatrix} u \\ w \end{bmatrix}$$

- The Jacobian matrix corresponding to fixed point (x_0, y_0):

$$L = \begin{bmatrix} a & b \\ c & d \end{bmatrix} = \begin{bmatrix} \left.\frac{\partial f}{\partial x}\right|_{(x_0,y_0)} & \left.\frac{\partial f}{\partial y}\right|_{(x_0,y_0)} \\ \left.\frac{\partial g}{\partial x}\right|_{(x_0,y_0)} & \left.\frac{\partial g}{\partial y}\right|_{(x_0,y_0)} \end{bmatrix}$$

Fixed Points and Their Stability

Practice in HW

- ***Eigenvalues*** and ***eigenvectors*** of L:

$$\boxed{L = \begin{bmatrix} a & b \\ c & d \end{bmatrix}}$$

$$Lv_1 = \lambda_1 v_1$$
$$Lv_2 = \lambda_2 v_2$$

- We can solve for the eigenvalues by setting:

$$(L - \lambda I)v = 0$$

→ This equation states that the vector v is in the null space of the matrix $(L - \lambda I)$

- In other words, the matrix $(L - \lambda I)$ has a rank deficiency

→ Its determinant is zero:

Refer to linear algebra for details

$$det(L - \lambda I) = 0$$

Characteristic equation of matrix L

Fixed Points and Their Stability

Practice in HW

- Solution of the characteristic equation yields eigenvalues of L:

$$det(L - \lambda I) = det\begin{bmatrix} a-\lambda & b \\ c & d-\lambda \end{bmatrix} = 0$$

- In polynomial form:

$$\lambda^2 - (a+d)\lambda + ad - bc = 0$$

or:

$$\lambda^2 - \tau\lambda + \Delta = 0$$

with:

$$\tau = \mathrm{trace}(L) = a + d$$

$$\Delta = \det(L) = ad - bc$$

$$L = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

- Eigenvalues:

$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}, \qquad \lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$

  - Both real when: $\tau^2 - 4\Delta \geq 0$

Fixed Points and Their Stability

Practice in HW

- General form of the solution to:

$$\begin{bmatrix}\dot{u}\\ \dot{w}\end{bmatrix} = \begin{bmatrix}a & b\\ c & d\end{bmatrix}\begin{bmatrix}u\\ w\end{bmatrix}$$

(for distinct eigenvalues) is:

$$\begin{bmatrix}u(t)\\ w(t)\end{bmatrix} = c_1 e^{\lambda_1 t} v_1 + c_2 e^{\lambda_2 t} v_2$$

c_1 and c_2 depend on the initial conditions

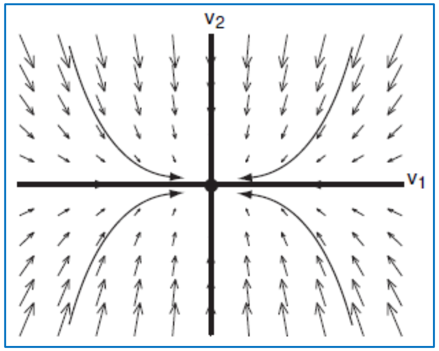
- Stability:
  - If both eigenvalues have negative real parts: $e^{\lambda_1 t}, e^{\lambda_1 t} \to 0$

$$\big(u(t), w(t)\big) \to (0, 0)$$

Thus:

$$\big(x(t), y(t)\big) \to (x_0, y_0)$$

→ The fixed point (x_0, y_0) is exponentially (asymptotically) stable



  - If either eigenvalue has a positive real part, the fixed point is unstable

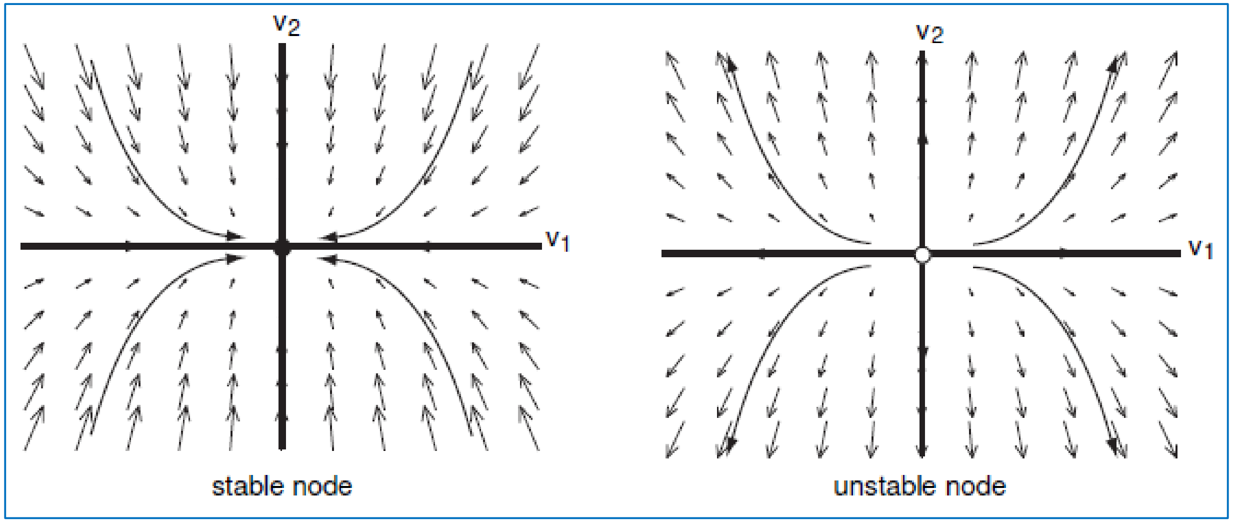
Fixed Points and Their Stability

$$\begin{bmatrix} u(t) \\ w(t) \end{bmatrix} = c_1 e^{\lambda_1 t} v_1 + c_2 e^{\lambda_2 t} v_2$$

Classification of fixed points:

1. Node:

- **Real eigenvalues, both the same sign** $|\lambda_1| < |\lambda_2|$
- Stable if both negative: $\lambda_2 < \lambda_1 < 0$
- Unstable if both positive: $\lambda_2 > \lambda_1 > 0$
- Trajectories converge to or diverge from the node along eigenvector v_1 (corresponding to the eigenvalue having smallest absolute value)



Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

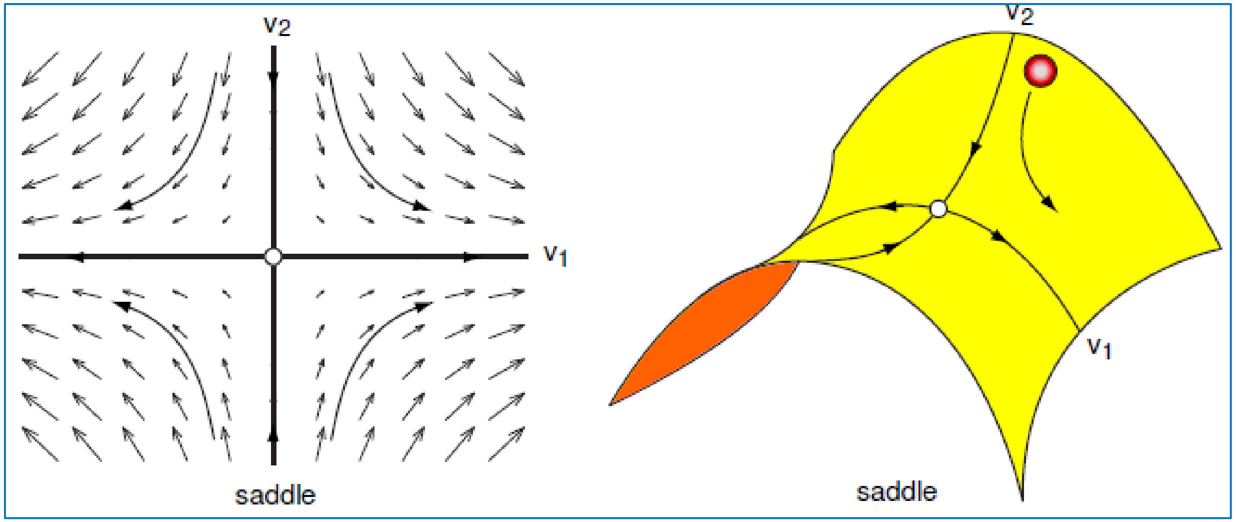
Fixed Points and Their Stability

Classification of fixed points:

$$\begin{bmatrix} u(t) \\ w(t) \end{bmatrix} = c_1 e^{\lambda_1 t} v_1 + c_2 e^{\lambda_2 t} v_2$$

2. *Saddle:*

- **Real eigenvalues, opposite signs:** $\lambda_2 < 0 < \lambda_1$
- Always unstable
- Trajectories approach saddle along eigenvector v_2 (corresponding to negative (stable) eigenvalue) and diverge from the saddle along eigenvector v_1 (corresponding to positive (unstable) eigenvalue)



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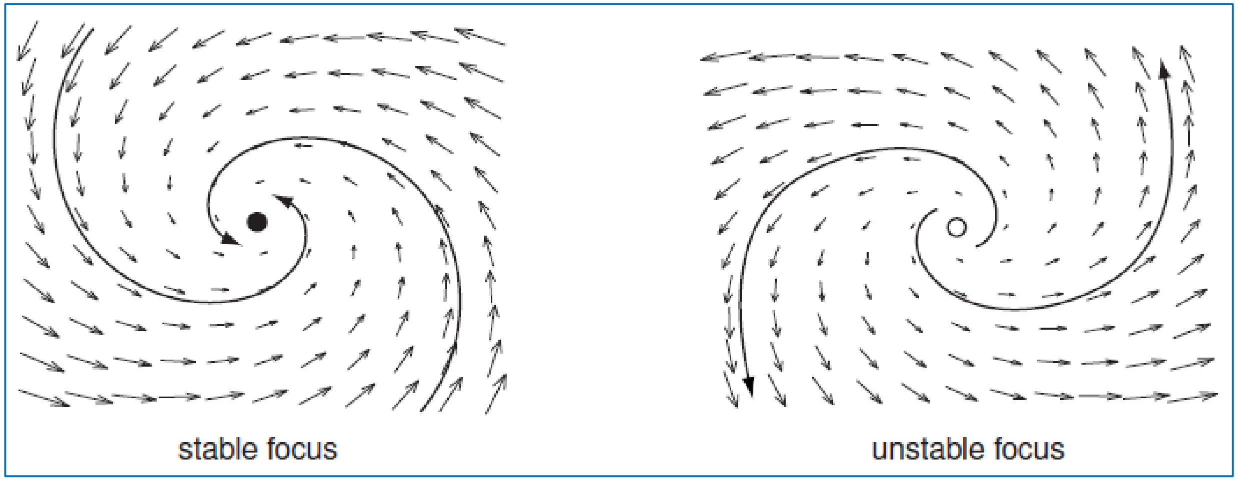
Fixed Points and Their Stability

Classification of fixed points:

$$\begin{bmatrix} u(t) \\ w(t) \end{bmatrix} = c_1 e^{\lambda_1 t} v_1 + c_2 e^{\lambda_2 t} v_2$$

3. Focus:

- **Complex conjugate eigenvalues:** $\lambda_1 = \sigma + j\omega,\ \lambda_2 = \sigma - j\omega$
- Stable when real parts negative: $\sigma < 0$
- Unstable when real parts positive: $\sigma > 0$
- Imaginary part ω determines the frequency of rotation of trajectories around the focus



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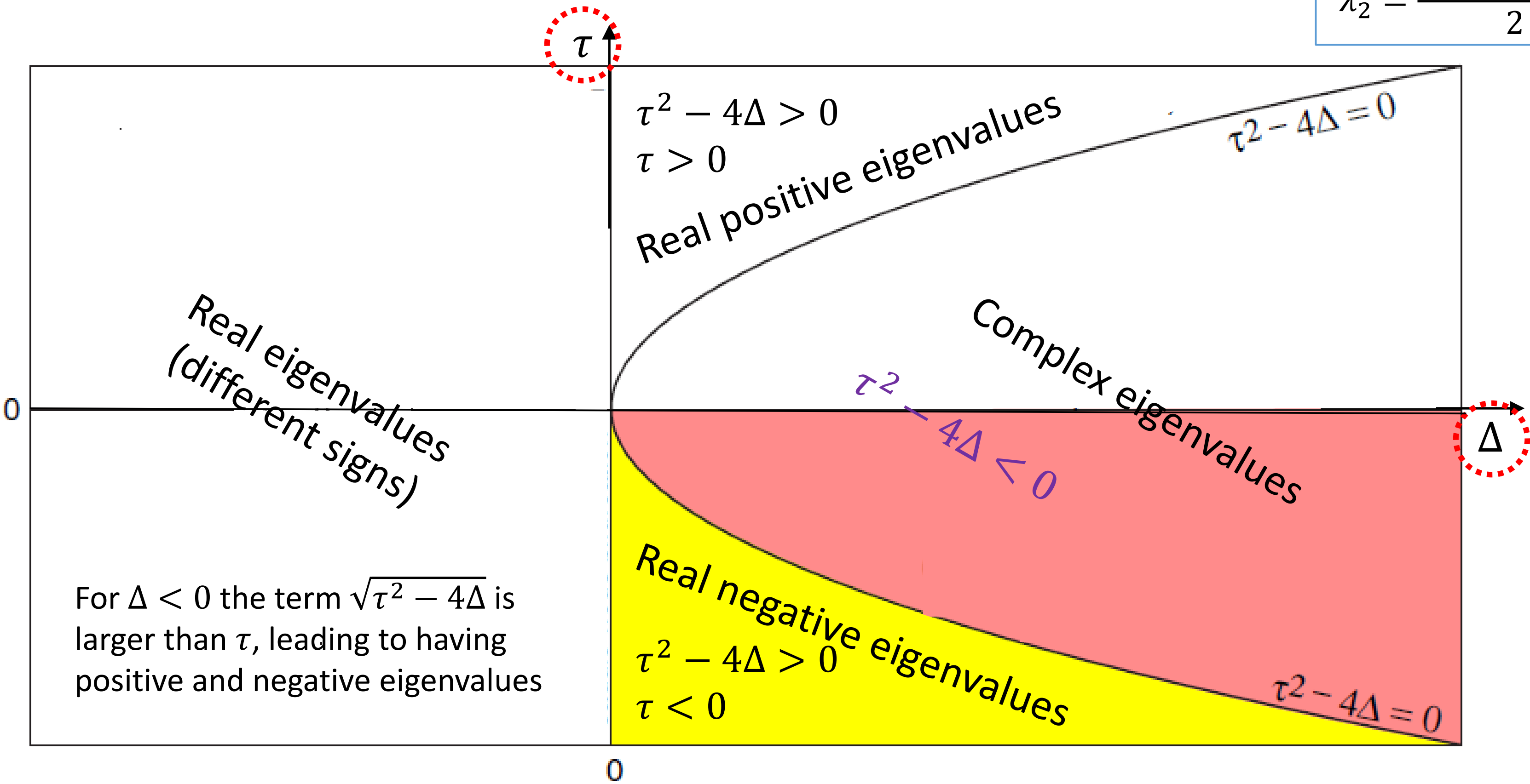
Fixed Points and Their Stability

Classification of fixed points according to the trace (τ) and the determinant (Δ) of the Jacobian matrix L

$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}$$
$$\lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$



Colored regions correspond to stable fixed points

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability

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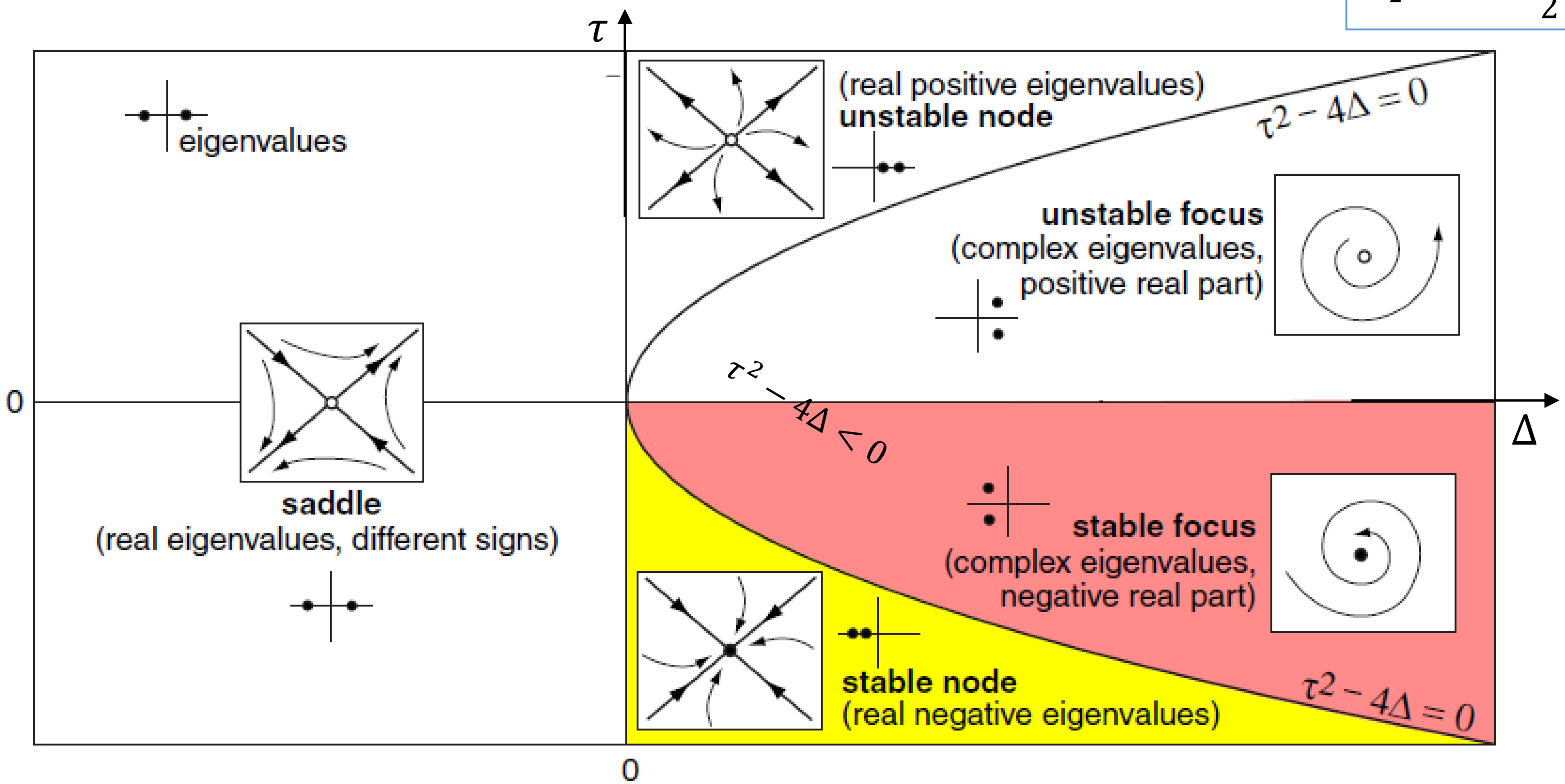


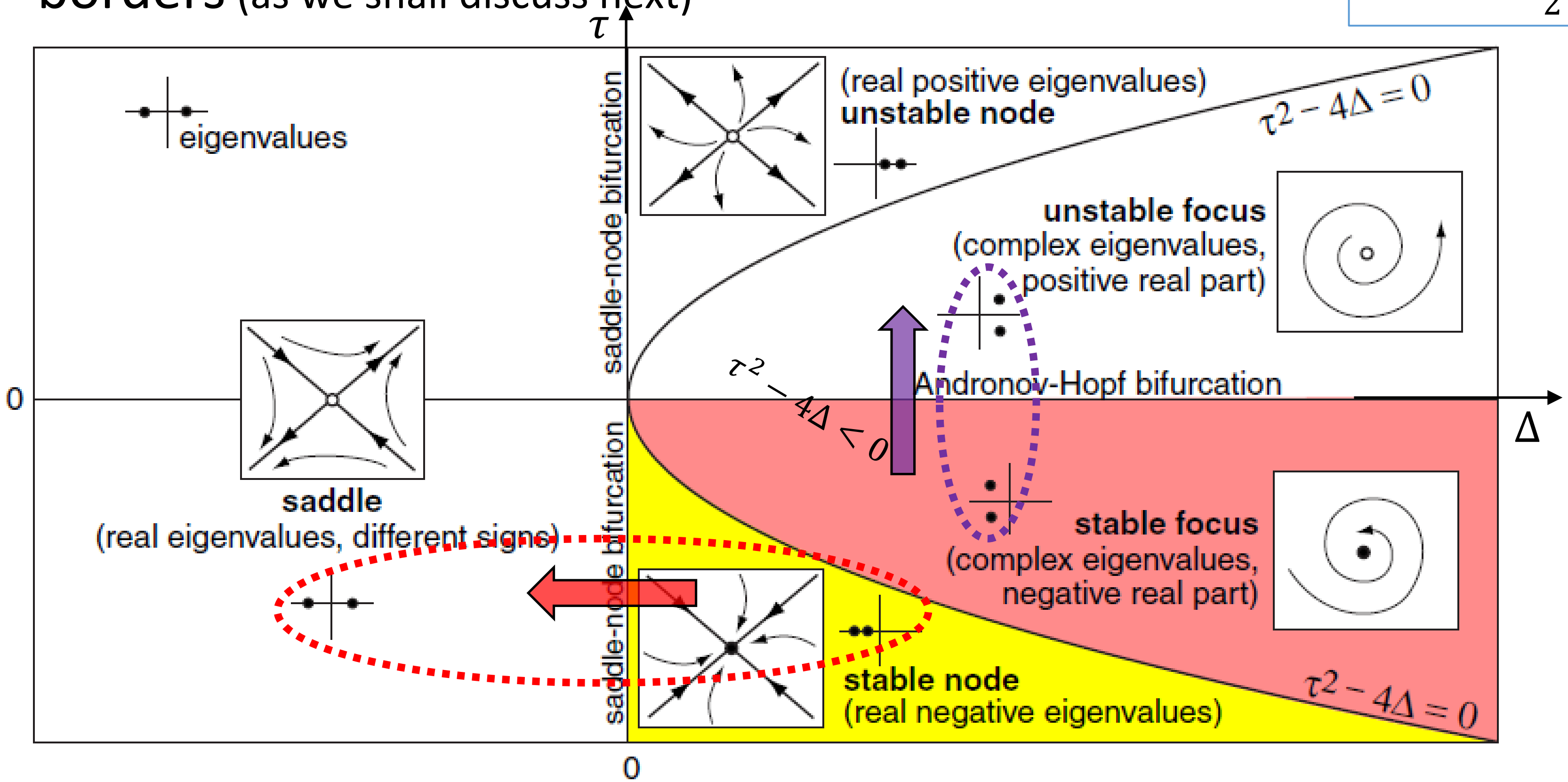
Colored regions correspond to stable fixed points

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability

- Interesting change of behavior occurs when the eigenvalues corresponding to a fixed point cross the borders (as we shall discuss next)

$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}$$
$$\lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$



Colored regions correspond to stable fixed points

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Fixed Points and Their Stability

We have studied so far:

- Fixed points with eigenvalues with <u>non-zero real-parts</u>
  (called ***hyperbolic***)
  which can be stable or unstable

Fixed Points and Their Stability

Extra Info

We have studied so far:

- Fixed points with eigenvalues with non-zero real-parts (called ***hyperbolic***)
  which can be stable or unstable
  - The Hartman-Grobman theorem:
    The vector-field and the dynamic of a nonlinear system near such a hyperbolic equilibrium is topologically equivalent to its linearization
    (i.e. the higher-order terms can be ignored)

$$\dot{x} = f(x, y)$$
$$\dot{y} = g(x, y)$$

The nonlinear functions f and g can be linearized near the fixed point (x_0, y_0):

$$f(x, y) = a(x - x_0) + b(y - y_0) + \text{higher order terms}$$
$$g(x, y) = c(x - x_0) + d(y - y_0) + \text{higher order terms}$$

Remark: The term *hyperbolic* refers to the shape of the saddle trajectories (and is hence not an inclusive term for the behavior of all fixed points with non-zero real parts for their eigenvalues)

Fixed Points and Their Stability

What about zero eigenvalues (or eigenvalues with zero real parts)?

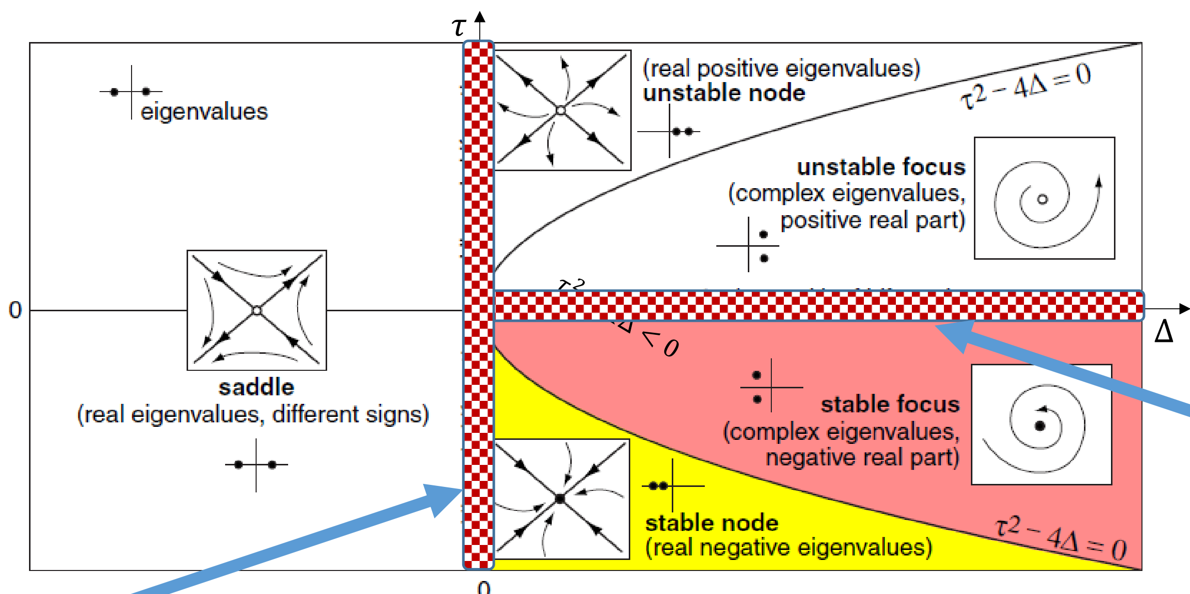
- A fixed point with an eigenvalue with zero real-part is called ***non-hyperbolic***
- A zero eigenvalue (or a pair of eigenvalues with zero real parts) arises when the fixed point undergoes a ***bifurcation*** *(change of behavior)*

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Fixed Points and Their Stability

What about zero eigenvalues (or eigenvalues with zero real parts)?

- A fixed point with an eigenvalue with <u>zero real-part</u> is called ***non-hyperbolic***



$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}$$
$$\lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$

$$\tau = 0, \qquad \Delta > 0 \rightarrow$$
$$Re\{\lambda_1\} = Re\{\lambda_2\} = 0$$

Pure imaginary eigenvalues

$$\Delta = 0 \rightarrow$$
$$\lambda_1 = \tau, \qquad \lambda_2 = 0$$

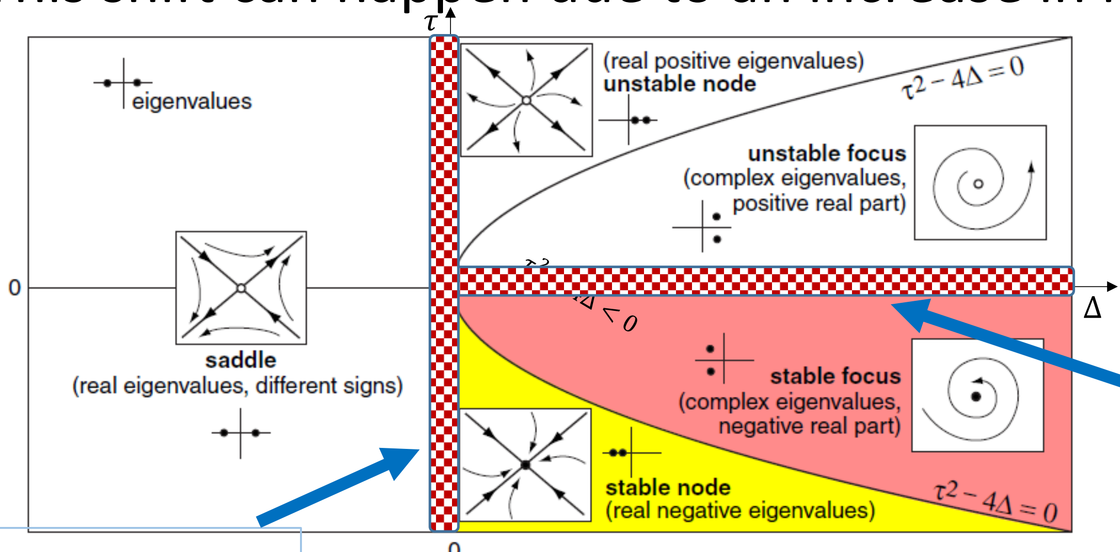
Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Bifurcation
(Saddle-Node / Hopf)

Two Types of Bifurcation –
(Transition from resting state to repetitive spiking)

Starting from a stable fixed point (the yellow or pink regions in the diagram):

- Both eigenvalues have negative real values
  - **Saddle-Node Bifurcation:** When Δ becomes zero, one eigenvalue (λ_2) turns zero
  - **Andronov – Hopf Bifurcation:** When τ becomes zero (for $\Delta > 0$), the real part of both eigenvalues become zero
- This shift can happen due to an increase in input current



$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}$$
$$\lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$

Andronov – Hopf Bifurcation

$$\tau = 0, \qquad \Delta > 0 \;\rightarrow$$
$$Re\{\lambda_1\} = Re\{\lambda_2\} = 0$$

$$\Delta = 0 \;\rightarrow$$
$$\lambda_1 = \tau, \qquad \lambda_2 = 0$$

Saddle-Node Bifurcation

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Saddle-Node Bifurcation

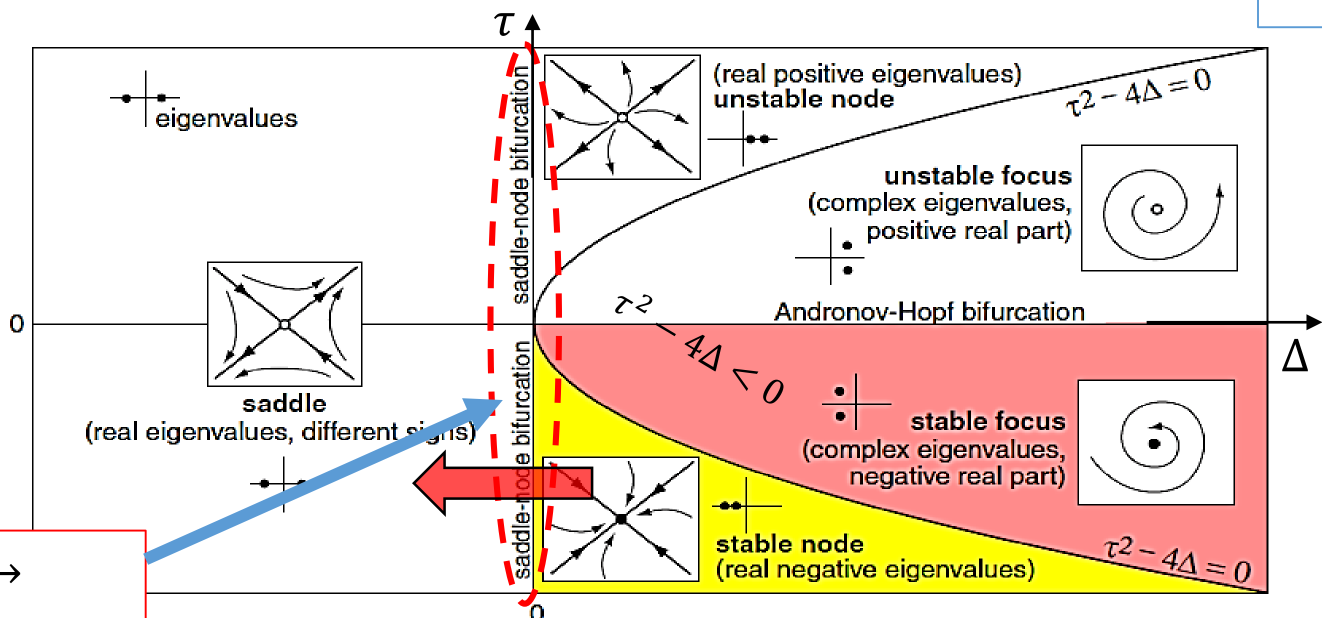
Starting from a stable node (the yellow region in the diagram):

- Both eigenvalues are real and negative
- When Δ becomes zero, one eigenvalue (λ_2) turns zero

→ Saddle-Node Bifurcation

$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}$$

$$\lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$



$$\Delta = 0 \rightarrow$$

$$\lambda_1 = \tau, \qquad \lambda_2 = 0$$

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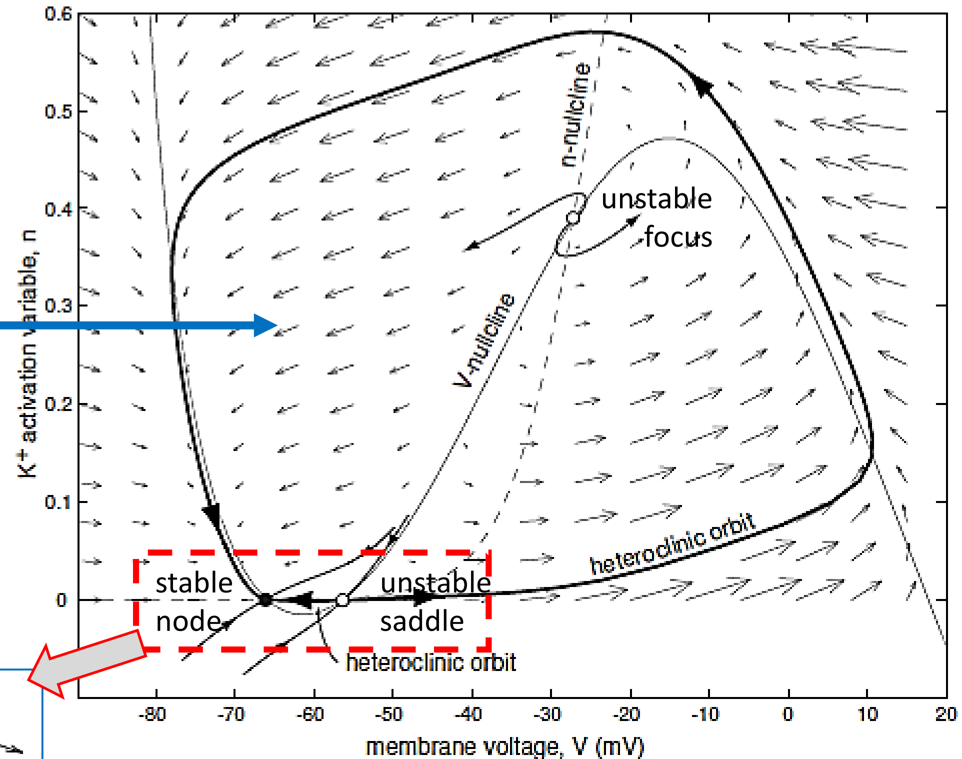
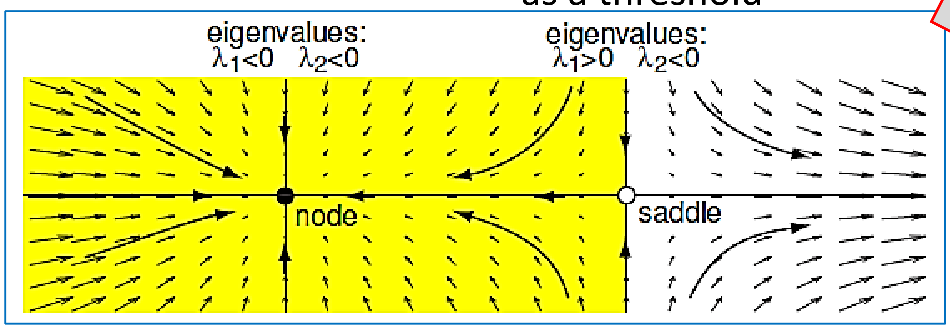
Saddle-Node Bifurcation

- Phase portrait for a zero value of the input current: $I = 0$
  - A stable node: Resting state
  - A saddle (which is always unstable)
  - An unstable focus

- Trajectories inside the loop (including those originating at the unstable focus) terminate at the stable node



The saddle serves as a threshold



The two nullclines collide at 3 fixed points in this case

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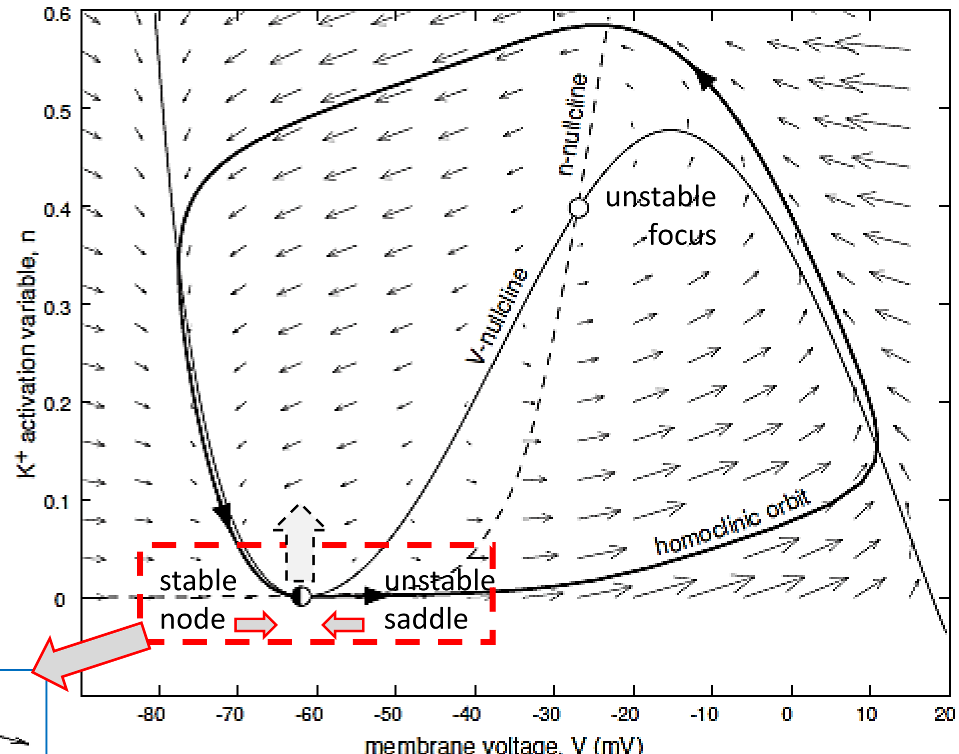
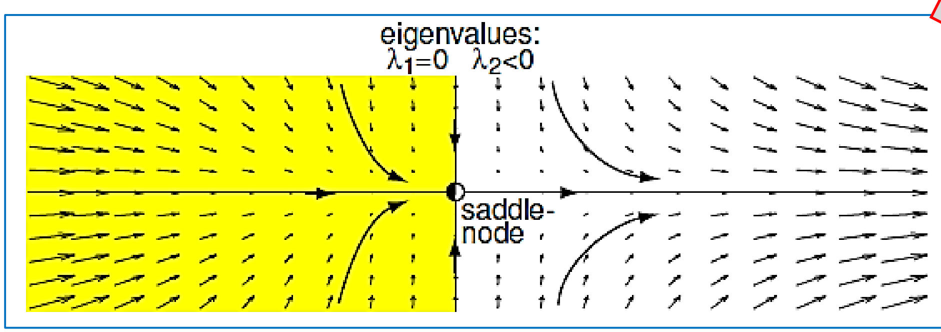
Saddle-Node Bifurcation

- Increasing the input current:
  - Shifts the cubic V-nullcline upward

  → Distance between the node and saddle decreases until they merge → One eigenvalue is zero
  - The nullclines only touch each other in this case:
    - ***Saddle-node bifurcation*** occurs

$I = 4.5$





Stable on one side (left),
unstable on the other side (right)

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

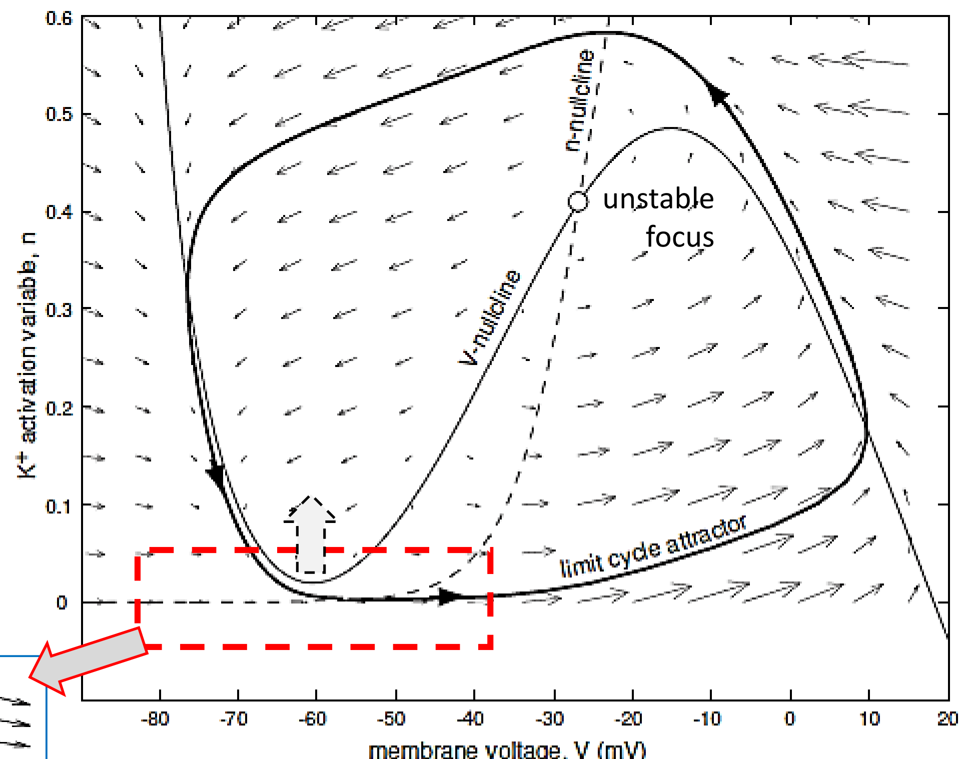
Saddle-Node Bifurcation

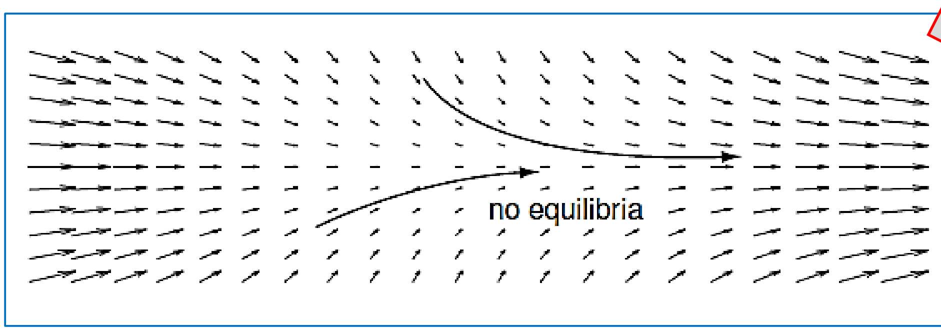
- Further increasing the input current:
  - Shifts the cubic V-nullcline more upward

  → The node and the saddle disappear

  - The new phase portrait has only a limit cycle attractor
    - It corresponds to repetitive firing

$I = 10$





A limit cycle is created, causing repeated spiking by the neuron

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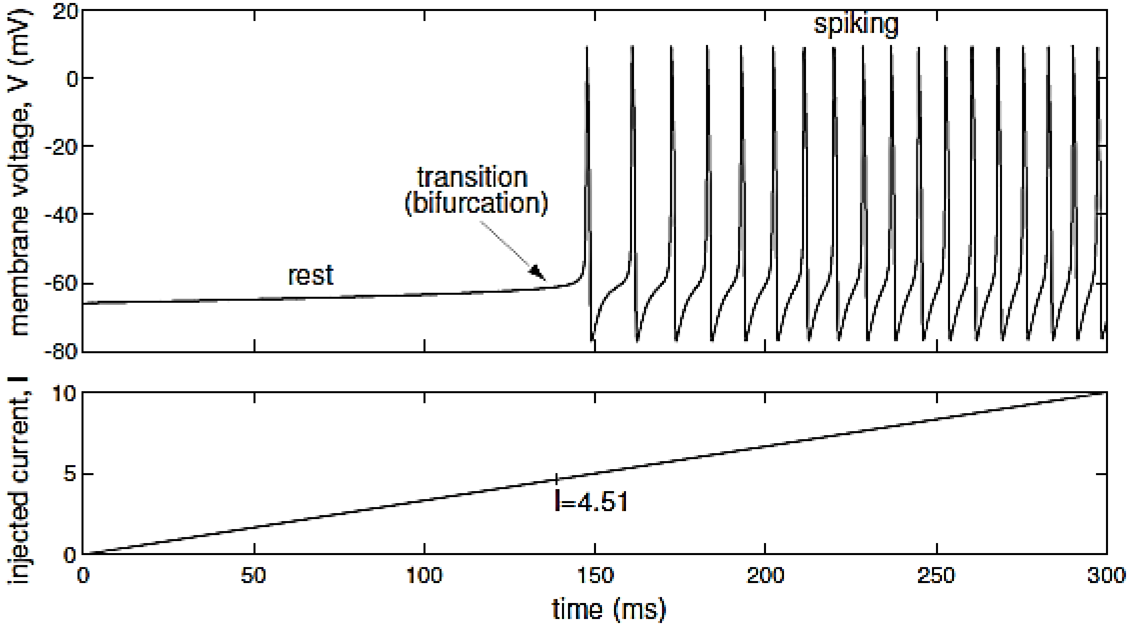
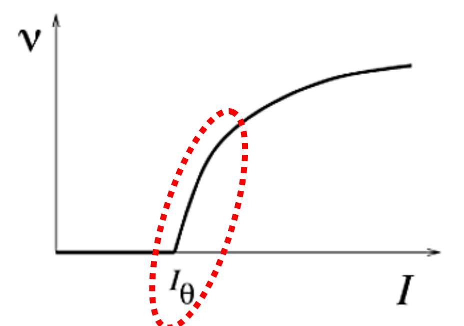
Saddle-Node Bifurcation

- Transition from resting state to repetitive spiking
  - With injected ramp current I





Spiking frequency ν during a limit cycle oscillation:

- is subject to a threshold on the input current
- is a continuous function of the applied current

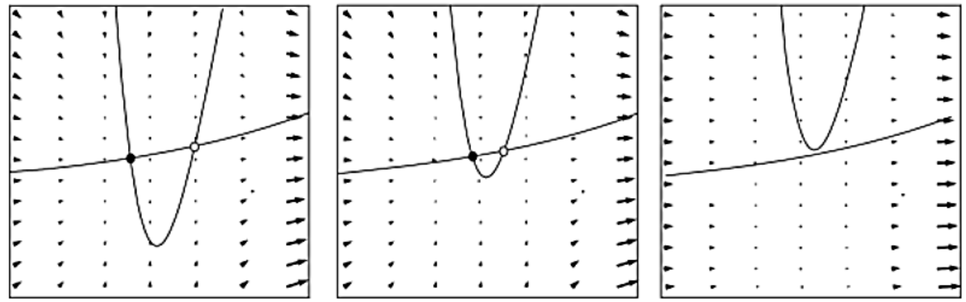
➢ Spiking rate increases with increasing I while the voltage amplitude remains fixed

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Wulfram Gerstner “Neuronal Dynamics”, 2014

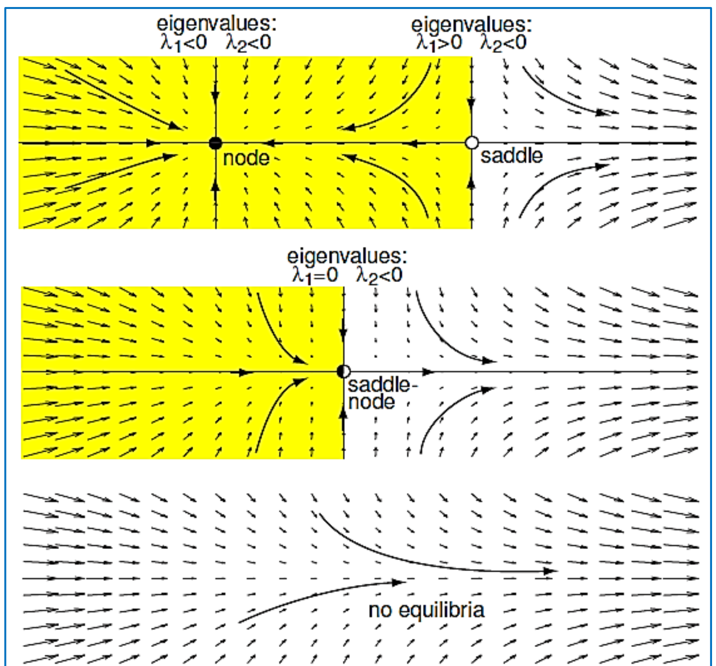
Saddle-Node Bifurcation – Summary

- The V-nullcline moves upward as the current is increased

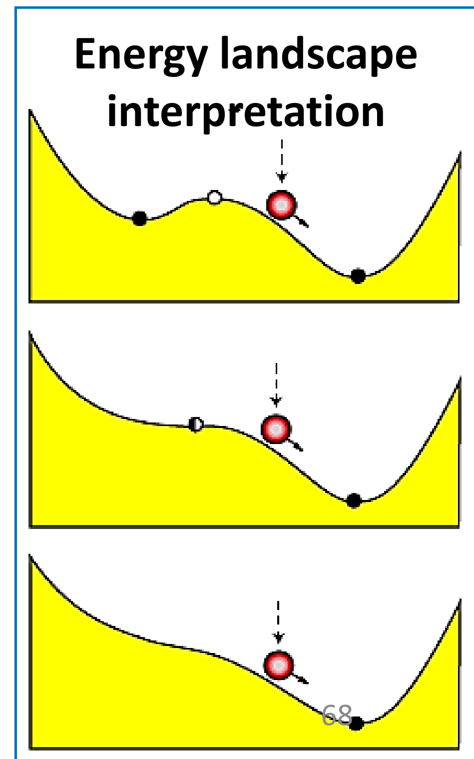


Wulfram Gerstner "Neuronal Dynamics", 2014

- The saddle and node fixed points approach each other, merge, and annihilate each other



Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010



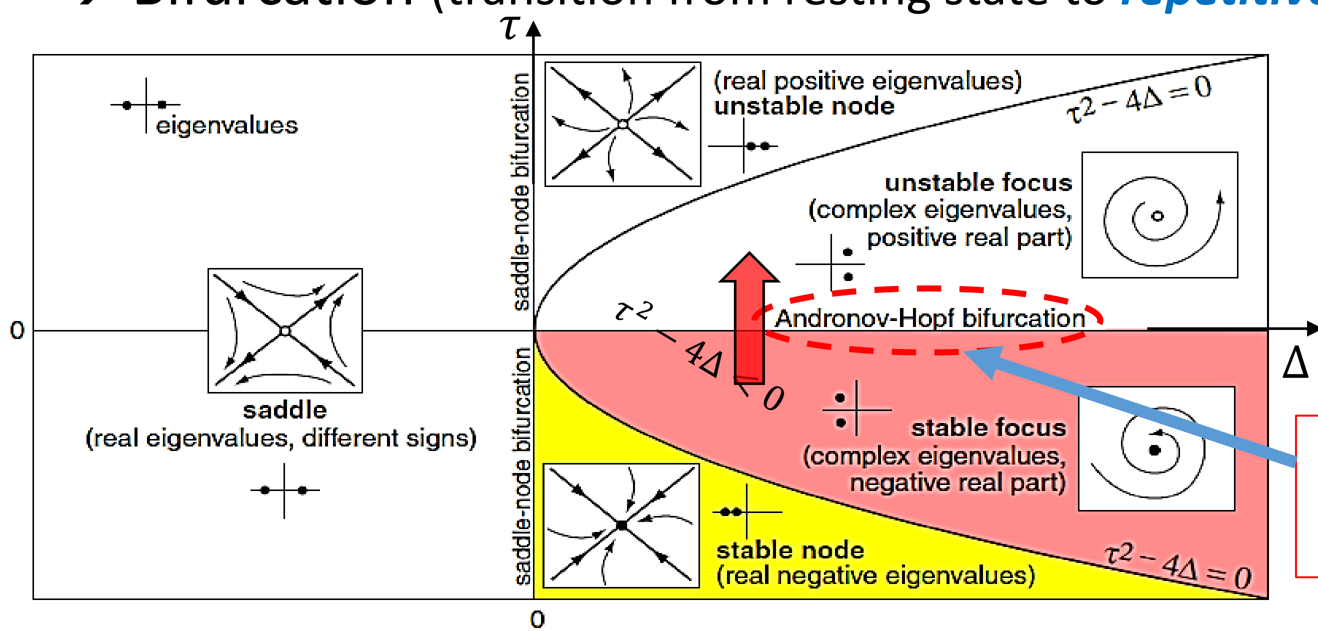
Andronov – Hopf Bifurcation

This is also called *Poincare-Andronov-Hopf* bifurcation, or *Hopf* bifurcation in different books on dynamical systems

Starting from a stable focus (the pink region in the diagram):

- Both eigenvalues are complex with negative real parts
- When τ becomes zero, real parts of eigenvalues turn zero (pure imaginary eigenvalues)

→ Bifurcation (transition from resting state to ***repetitive spiking***)



$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}$$

$$\lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$

$$\tau = 0, \qquad \Delta > 0 \rightarrow$$

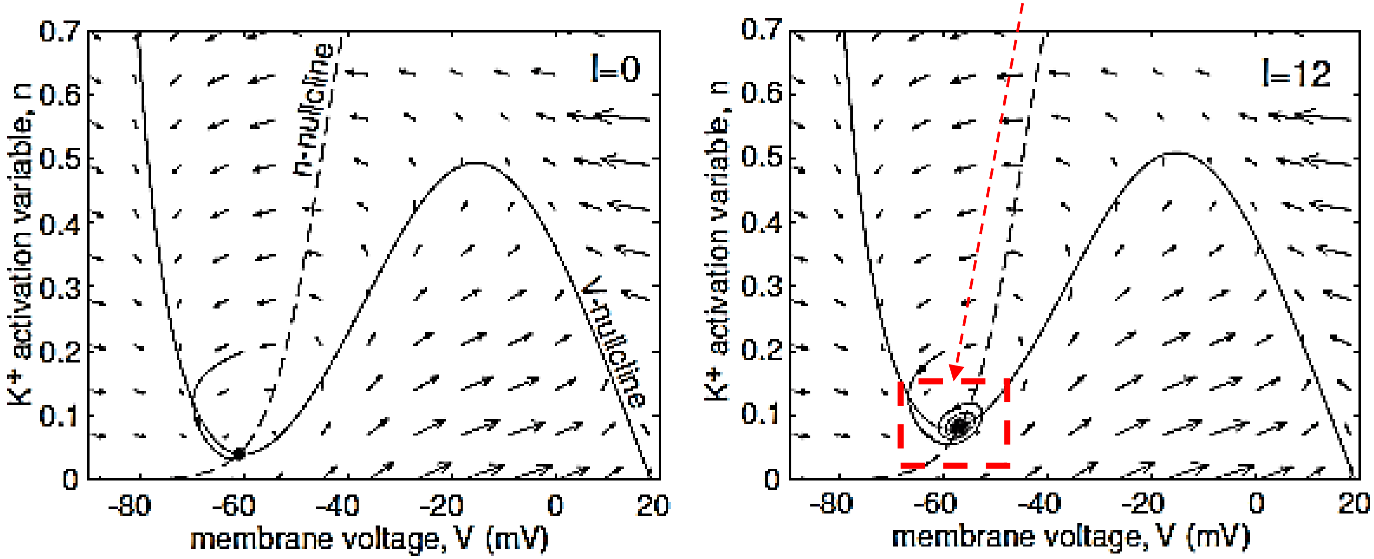
$$Re\{\lambda_1\} = Re\{\lambda_2\} = 0$$

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Andronov – Hopf Bifurcation

- Small I → The fixed point is a ***stable focus*** (rest state)
  (a pair of complex-conjugate eigenvalues with negative real part)
- When I increases past $I = 12$, the focus loses stability:
  - The real part of the eigenvalues increases as $0 < I < 12$
  - It becomes zero at *I* = 12 (purely imaginary eigenvalues)

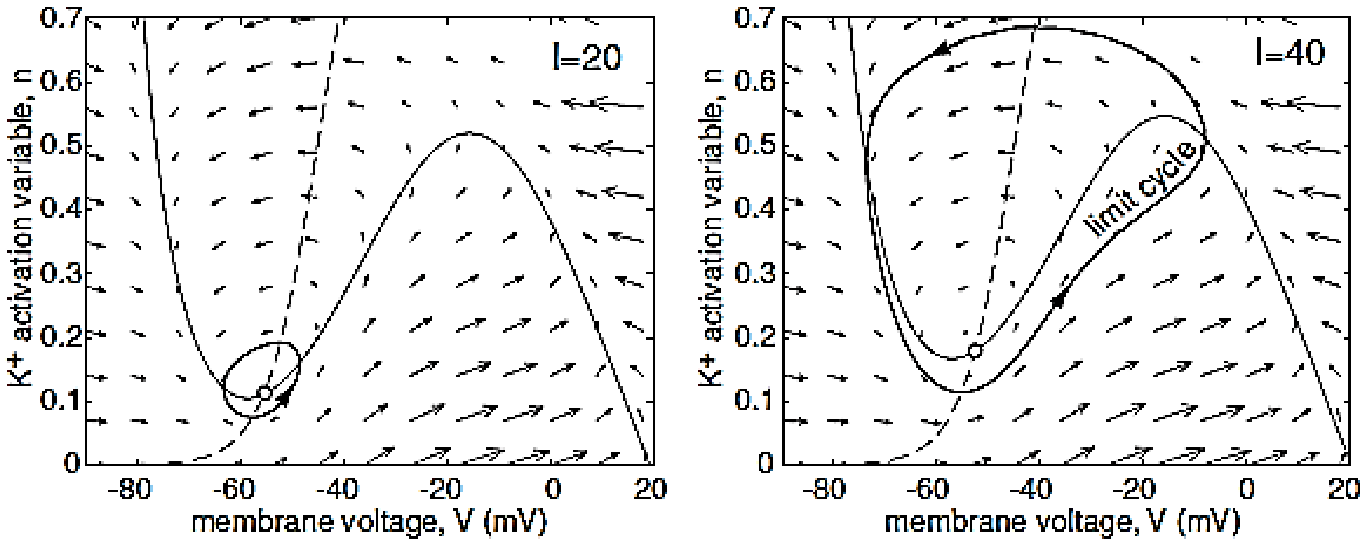
    → **A <u>small-amplitude</u> limit cycle attractor begins**
  - The real part becomes positive for $I > 12$



Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Andronov – Hopf Bifurcation

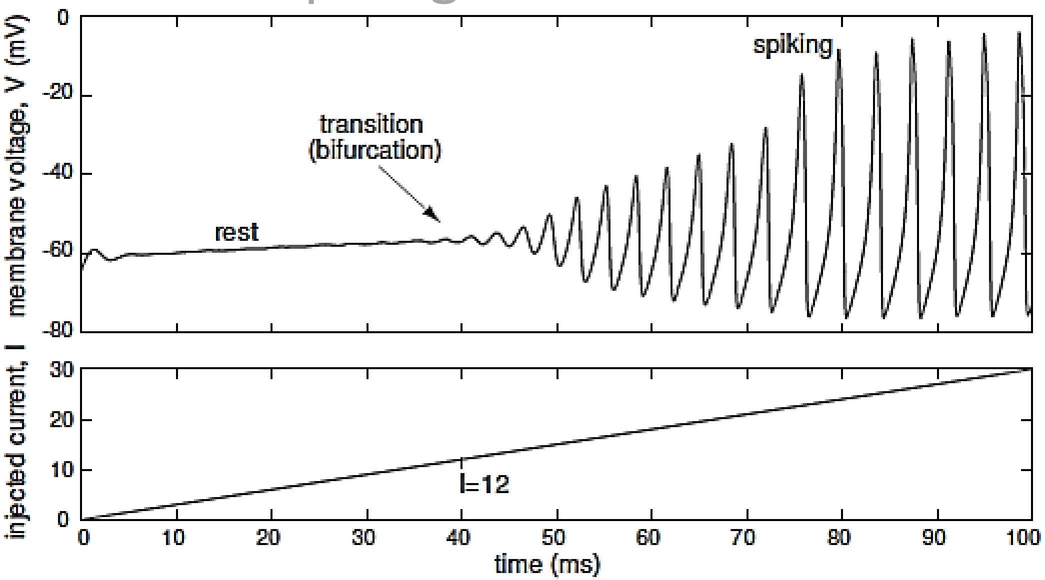
- The transition from stable to unstable focus described above is called ***Andronov-Hopf*** bifurcation
  - It occurs when the eigenvalues become purely imaginary, as it happens when *I* = 12
- Increasing I beyond $I = 12$ results in the transition from rest to spiking behavior
  - Note: The cycles can be small or large depending on the input current

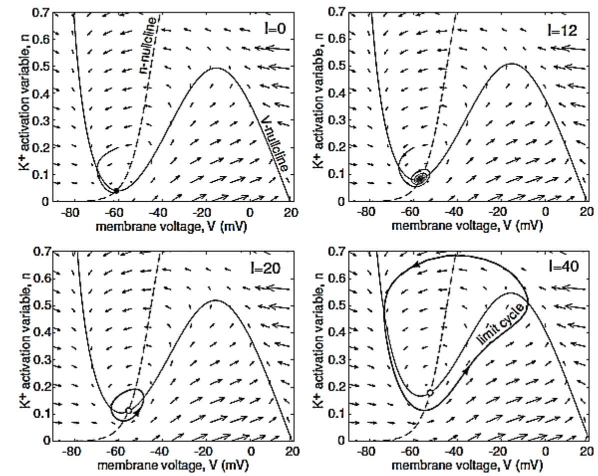


Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

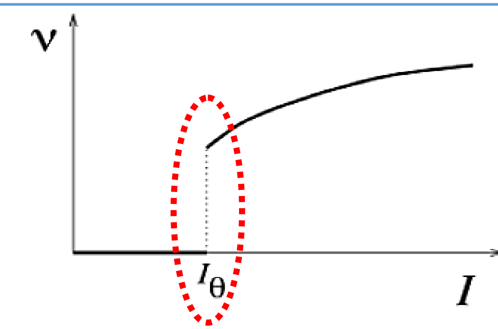
Andronov – Hopf Bifurcation

- Increasing I beyond $I = 12$ results in the transition from rest to spiking behavior





- Spiking rate remains fixed with increasing I but the amplitude of the voltage swing increases



- Spiking frequency ν has a discontinuity with the applied current (threshold)
- It starts and stays at a high value

Wulfram Gerstner "Neuronal Dynamics", 2014

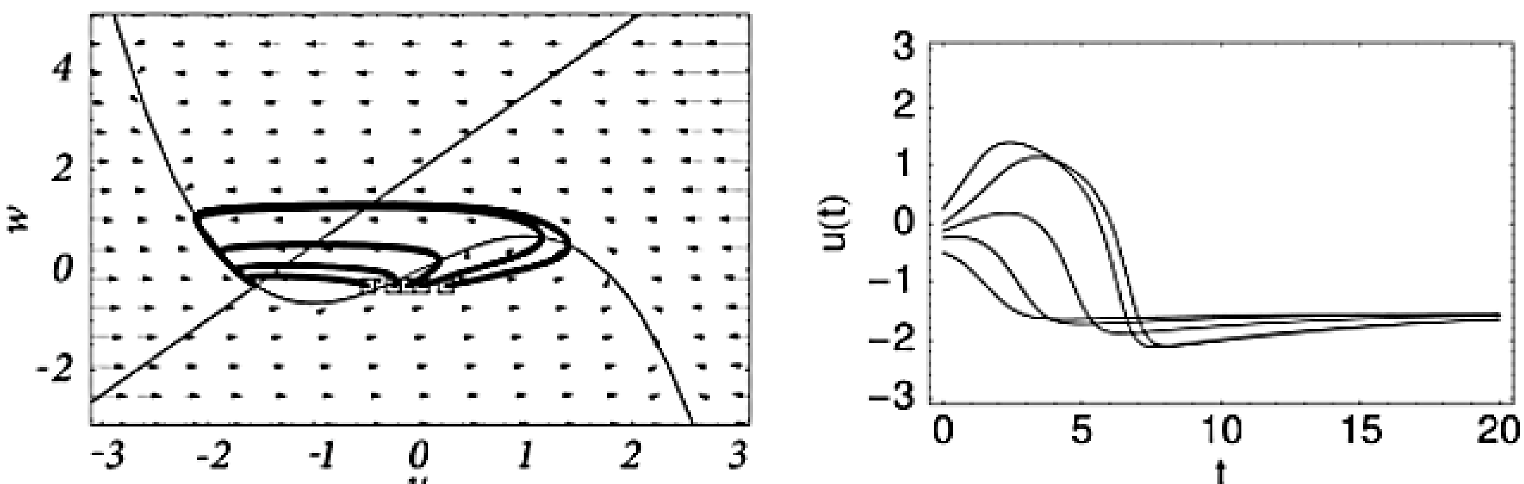
Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Andronov – Hopf Bifurcation

Extra Info

Unlike the saddle-node bifurcation:

- Slight increase of the amplitude of the input pulse → Large increase in the amplitude of the response
- Peak of the response is always reached with roughly the same delay (independently of the size of the input pulse)
  - Velocity of larger trajectories is larger → Similar time cycles for different trajectory sizes **(imaginary part of the eigenvalues determines the oscillation frequency)**
- Amplitude of the response increases continuously with the input

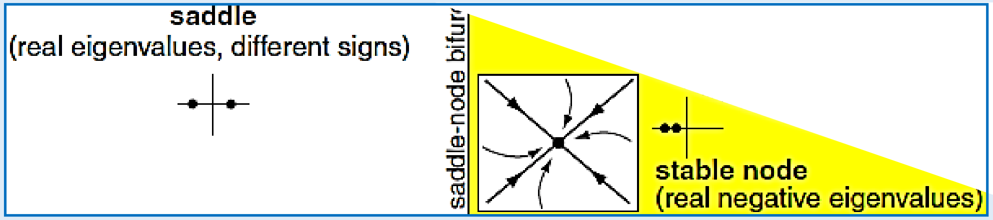


Wulfram Gerstner "Neuronal Dynamics", 2014

Saddle – Node versus Andronov – Hopf Bifurcation

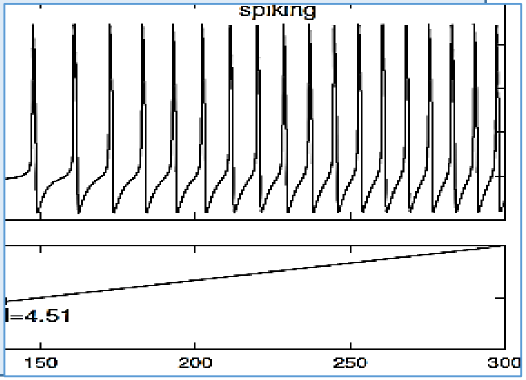
➢ The saddle-node and Andronov-Hopf bifurcations result in dramatically different neuro-computational properties:

- Neurons near saddle-node bifurcation act as ***integrators***



- These are filters with poles on the real axis:
  → They act like lowpass filters
  (***Integrator*** refers to the transfer function $\frac{1}{s}$ with its pole shifted on the real axis)

- They integrate over the input pulse trains of their neighbors
  - Higher input spike rates → Increased input current → Higher output spike rate



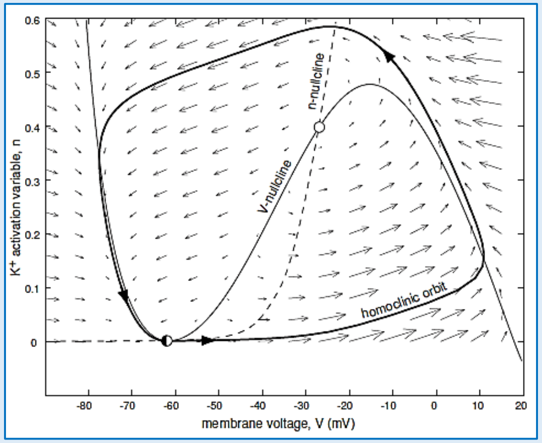
Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

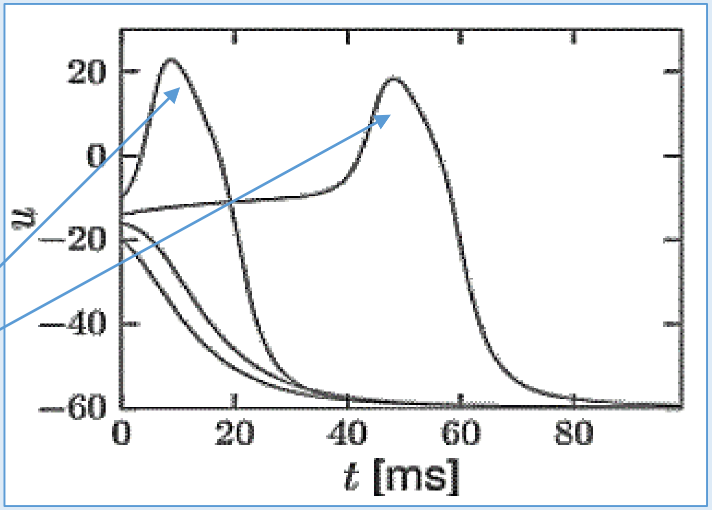
Saddle – Node versus Andronov – Hopf Bifurcation

Extra Info

- The saddle-node and Andronov-Hopf bifurcations result in dramatically different neuro-computational properties:

- Neurons near saddle-node bifurcation act as ***integrators***
  - They show a **threshold** (**all-or-nothing**) **behavior**
    - They either generate a significant pulse (for a large input pulse)
    - Or their state decays back to rest (for a small input pulse)





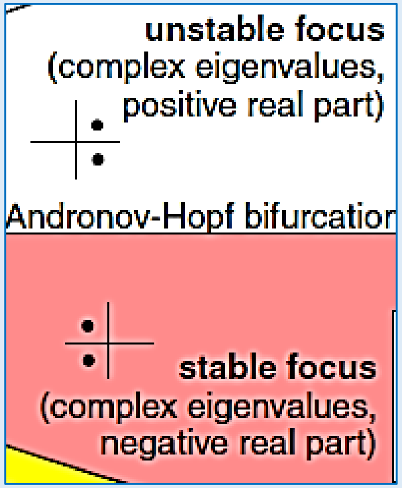
- **The shape of the output action potential is always the same**

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Saddle – Node versus
Andronov – Hopf Bifurcation

➢ The saddle-node and Andronov-Hopf bifurcations result in dramatically different neuro-computational properties:

- Neurons near Andronov-Hopf bifurcation show damped oscillatory potentials and act as ***resonators***
  - They prefer oscillatory input with the same frequency as that of their own damped oscillations **(resonant frequency)**
  - Increasing the input's frequency may delay or even terminate their response (they may filter out the input)



- These are filters with conjugate complex poles near the imaginary axis:
  → They act like bandpass filters
  (***Resonator*** refers to a bandpass filtering behavior tuned to a resonance frequency)

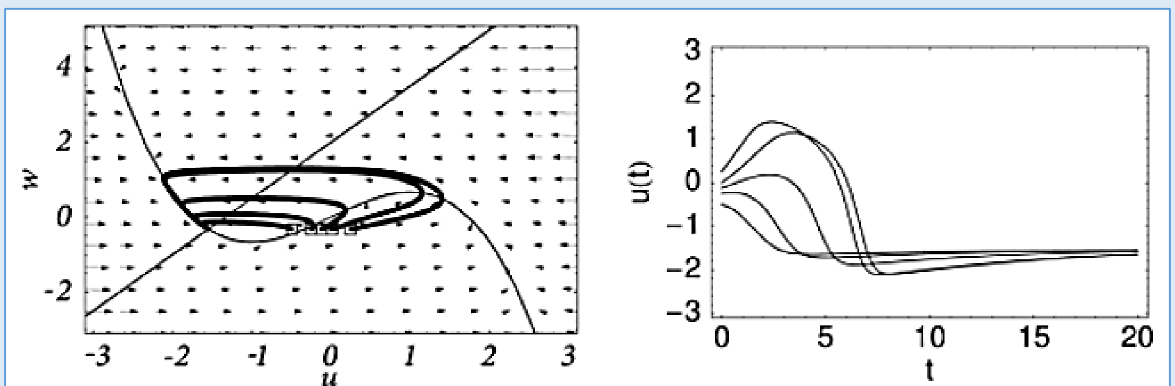
Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Saddle – Node versus Andronov – Hopf Bifurcation

Extra Info

➢ The saddle-node and Andronov-Hopf bifurcations result in dramatically different neuro-computational properties:

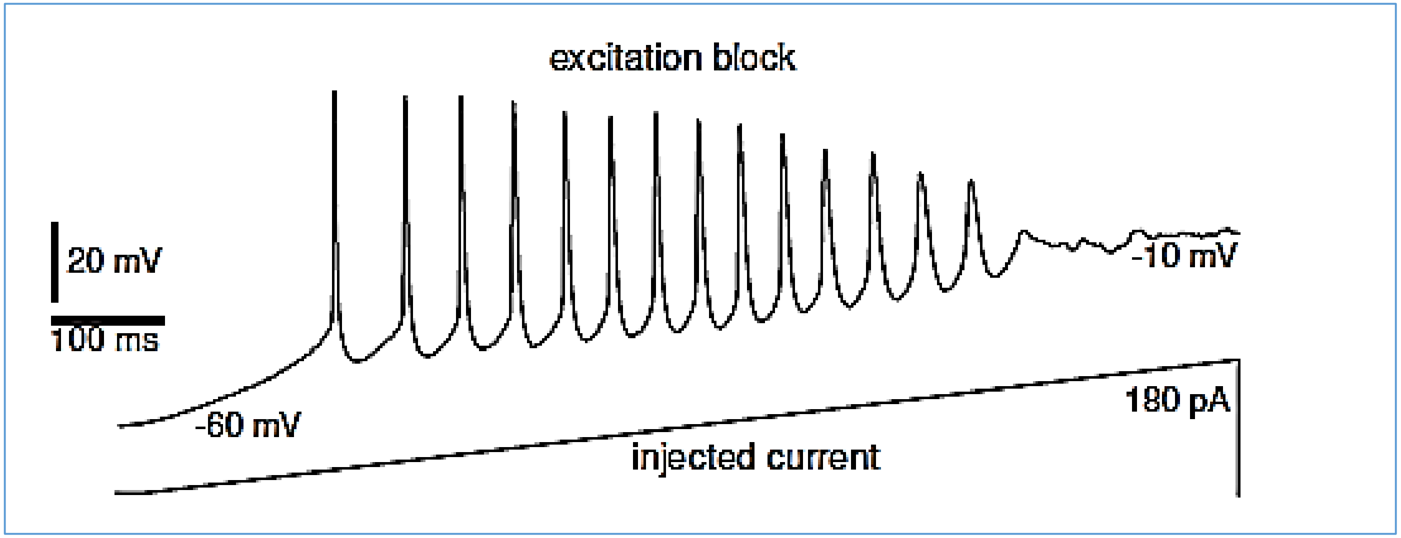
- Neurons near Andronov-Hopf bifurcation show damped oscillatory potentials and act as ***resonators***
  - Amplitude of response depends continuously on the amplitude of input pulse:
    - **The size of the limit cycle can grow with the input amplitude**



Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Andronov – Hopf Bifurcation – Excitation Block

- Spiking activity of a (layer 5 pyramidal) neuron of rat's visual cortex is ***blocked by strong excitation*** (i.e. injection of strong positive current)



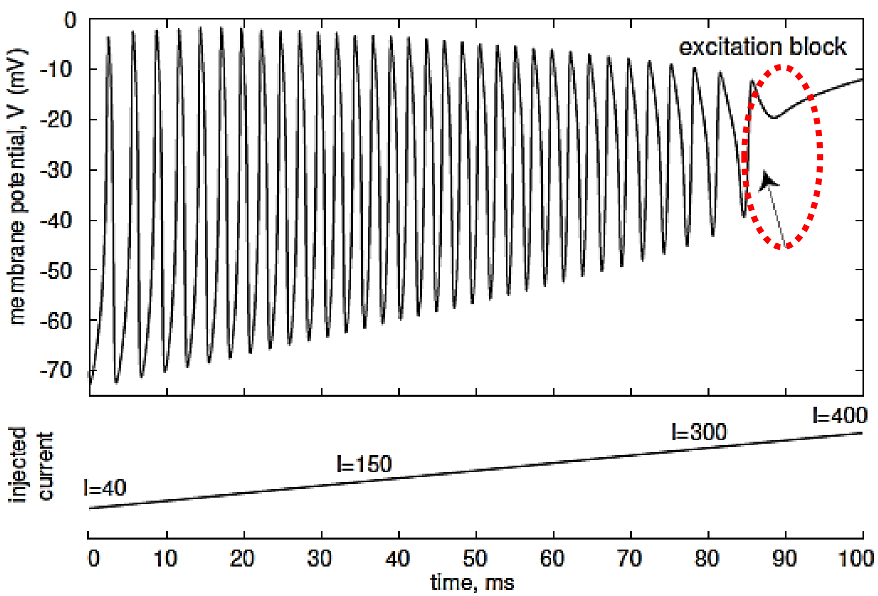
> ➢ ***Let's examine the phase plane to see why this happens***

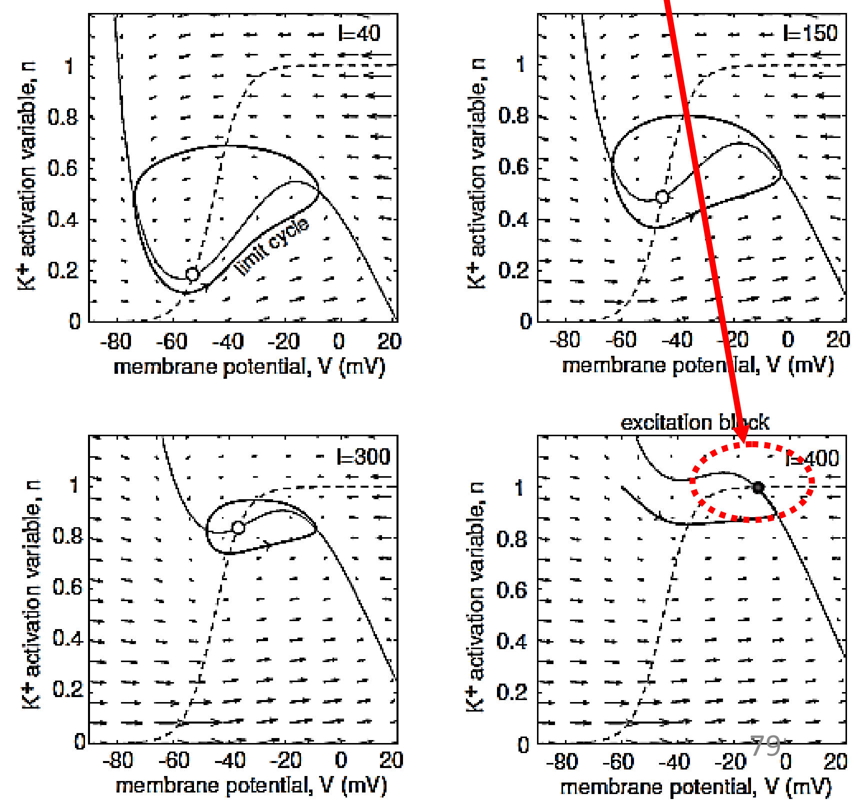
Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Andronov – Hopf Bifurcation – Excitation Block

- As the magnitude of the injected current increases:
  - The unstable fixed point moves to the right branch of the V-nullcline and becomes stable

  → The limit cycle shrinks and the spiking activity disappears



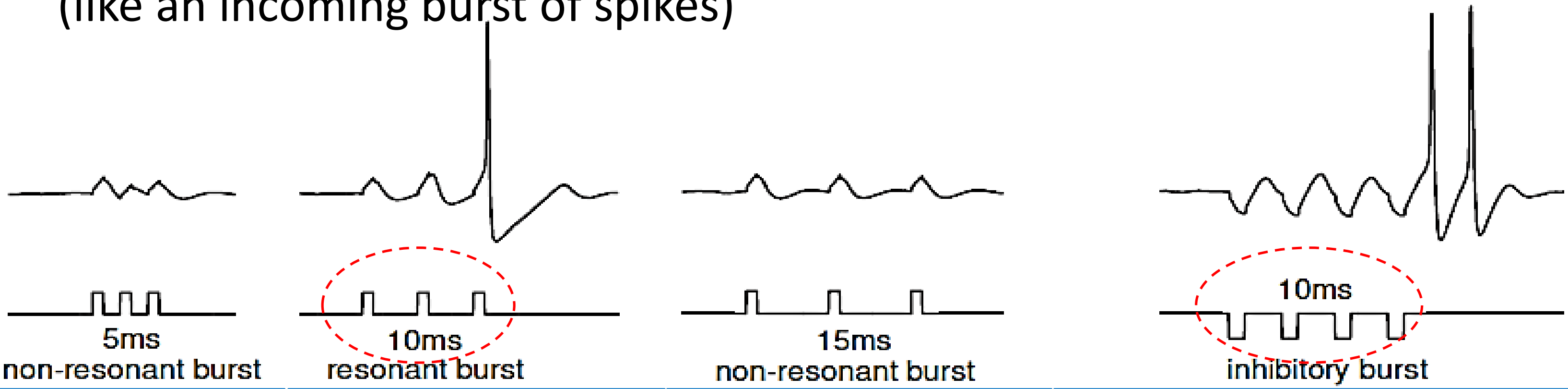


Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Andronov – Hopf Bifurcation –
Excitatory and Inhibitory Pulse Trains

A rat’s (brainstem mesencephalic V) neuron:

- Neuron is stimulated with **brief pulses of current**
  (like an incoming burst of spikes)



High stimulation rate (strong input) → No spikes	Slow (10 ms) stimulation rate → Spike	Slower stimulation rate → No spikes	Same slow (10 ms) stimulation rate with ***inhibitory*** input → Spikes

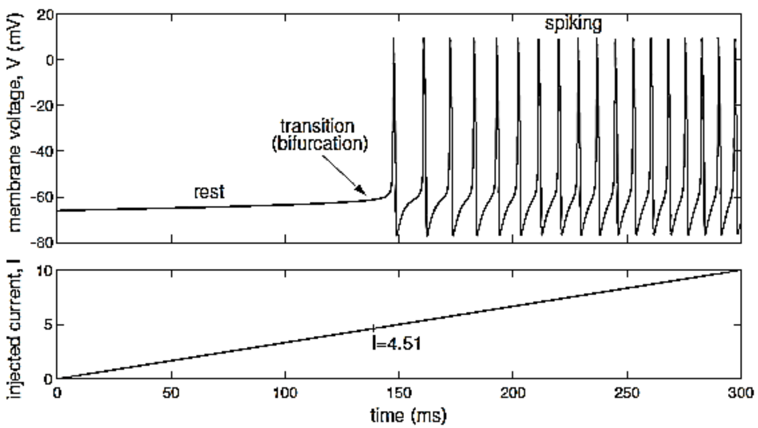
- Spiking occurs when the frequency of input current ***resonates*** with the frequency of ***subthreshold oscillation*** of the neuron
- If the same inputs are applied to a cortical pyramidal neuron (integrator type), only the first input (high stimulation rate) may cause spikes

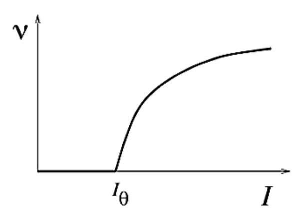
Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Saddle – Node versus Andronov – Hopf Bifurcation – Summary

Saddle-Node Bifurcation:

- Increase in input current → Higher spiking rate





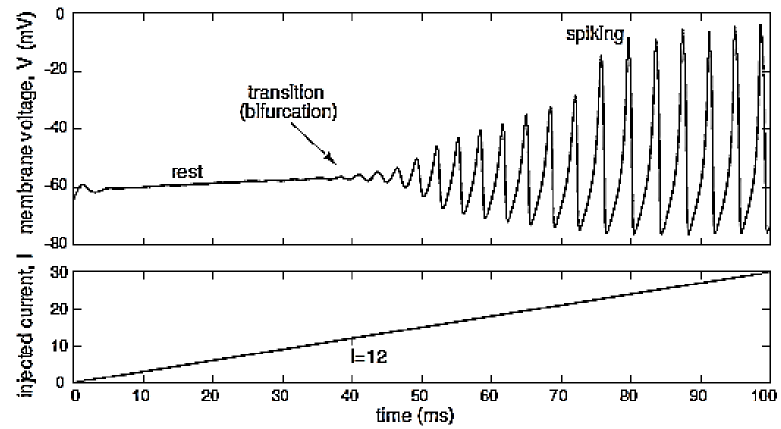
Spiking frequency ν during a limit cycle oscillation:

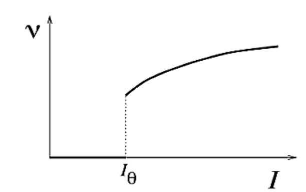
- is subject to a threshold on the input current
- is a continuous function of the applied current

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Andronov–Hopf Bifurcation:

- Increase in input current → Almost fixed spiking rate





- Spiking frequency ν has a discontinuity with the applied current (threshold)
- It starts and stays at a high value

Wulfram Gerstner “Neuronal Dynamics”, 2014

Practice in HW

Simplified 2D Models

FitzHugh – Nagumo Model

- Many neural spiking activities can be described by only considering the region of the phase plane around its fixed point:

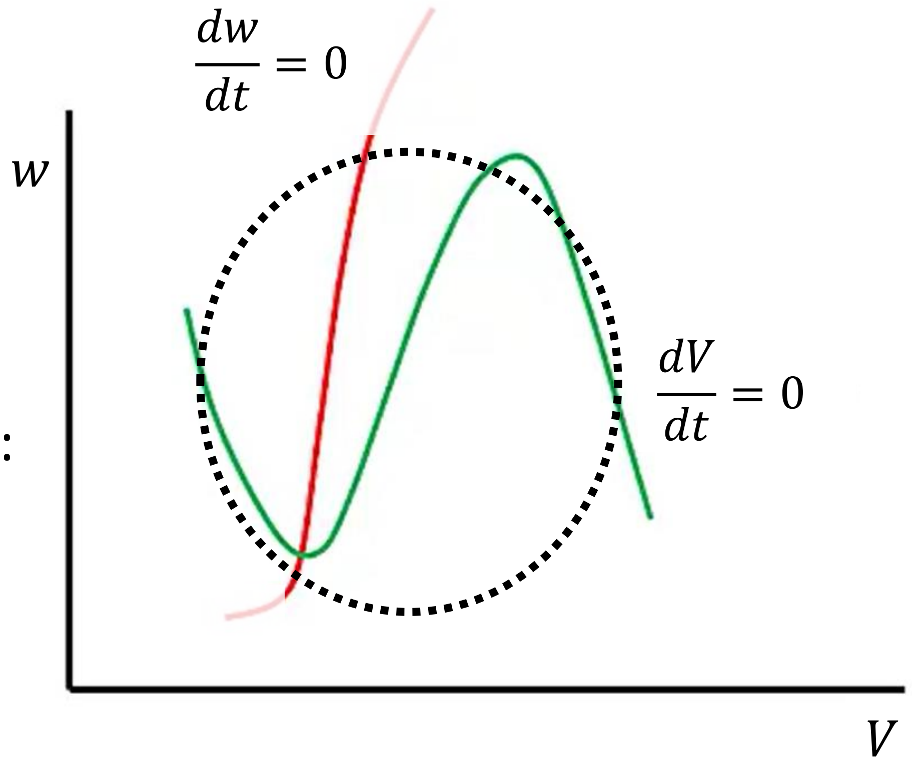
- Voltage dynamics can be approximated by a ***cubic*** function:

$$\frac{dV}{dt} = V(a-V)(V-1) - w + I$$

with a linear (negative) coupling to w

- Dynamics of w are ***linear*** in V and w:

$$\frac{dw}{dt} = -cw + bV$$



Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

FitzHugh – Nagumo Model

Assume $I = 0$ → Fixed point at $(0, 0)$

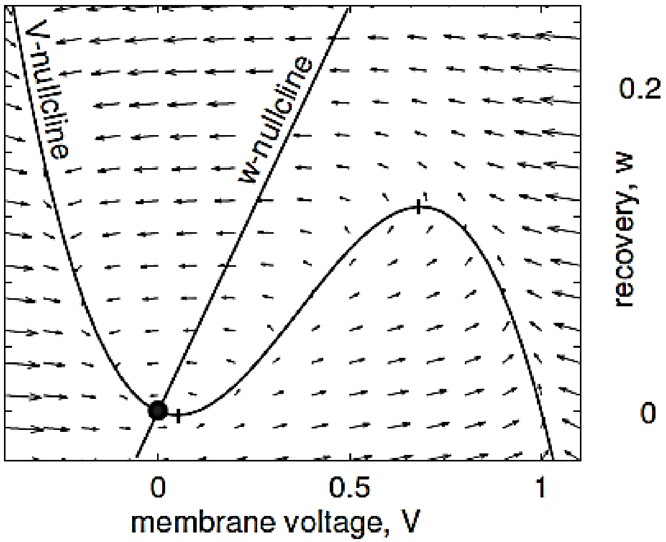
- V-nullcline:

$$f(V, w) = V(a - V)(V - 1) - w$$
$$= -V^3 + (a + 1)V^2 - aV - w = 0$$

- w-nullcline:

$$g(V, w) = -cw + bV = 0$$

Note: In order to calculate the derivatives for the Jacobian matrix, one needs to write the nullcline equations this way



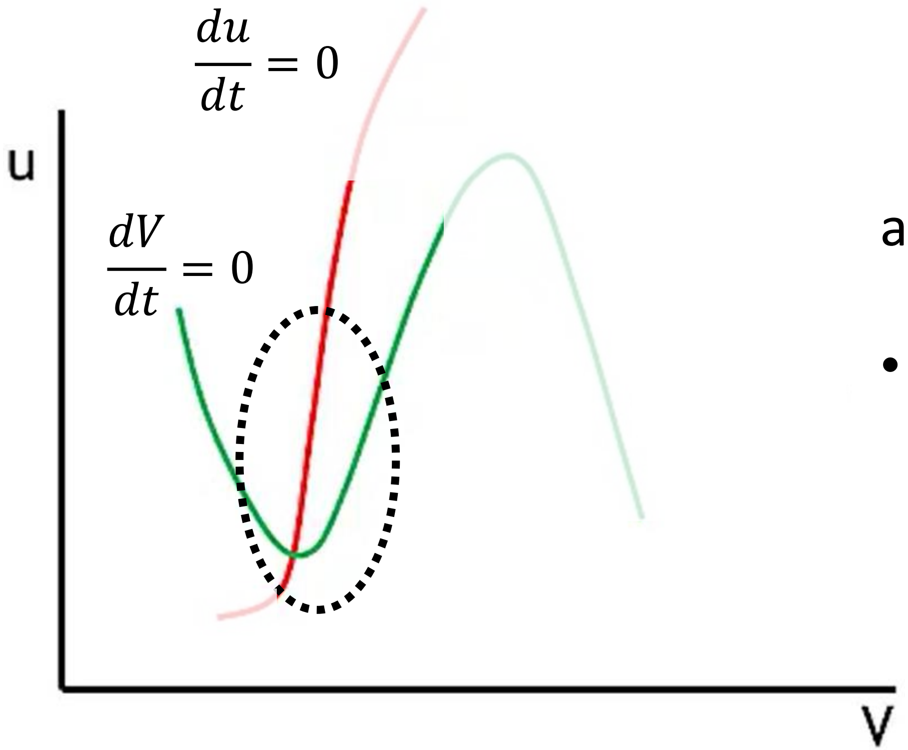
There can be 1, 2, or 3 fixed points

Eugene Izhikevich "Dynamical Systems in Neuroscience", 2010

Izhikevich "Simple" Model

Practice in HW

- Many neural spiking activities can be described by only considering the region of the phase plane around its fixed point:



- Voltage dynamics are approximated by a ***quadratic*** function:

$$\frac{dV}{dt} = -\alpha V + \beta V^2 + \gamma - u + I(t)$$

and a linear coupling to u

- Dynamics of u are ***linear*** in V and u:

$$\frac{du}{dt} = a(-u + bV)$$

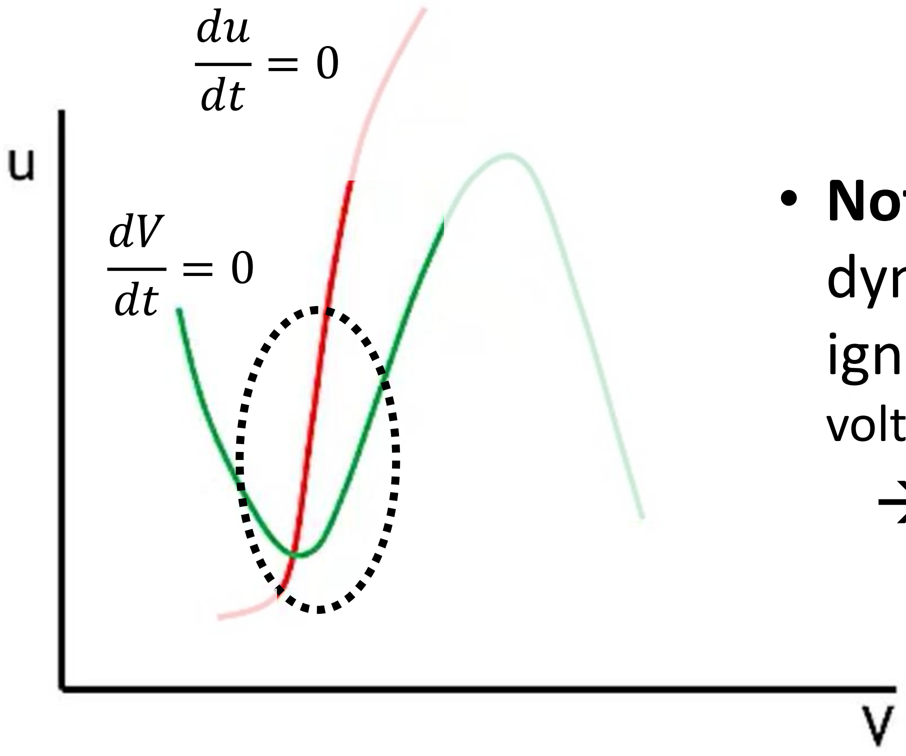
Izhikevich

Izhikevich "Simple" Model

Practice in HW

$$\frac{dV}{dt} = -\alpha V + \beta V^2 + \gamma - u + I(t)$$
$$\frac{du}{dt} = a(-u + bV)$$

- As V gets larger, so does u (2nd Eq.)
- Then the coupling of $-u$ to V in the 1st Eq. causes V to decrease



- **Note:** The role of higher order dynamics in variables has been ignored (they are needed to restore the voltage to reset after a spike)

  → We need to add in a maximum value and a reset value for the variables

  (see next page)

Izhikevich

Izhikevich “Simple” Model

Practice in HW

- The role of higher order dynamics in variables has been ignored (they are needed to restore the voltage after a spike)

→ We need to add in a maximum value and a reset value for the variables

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - u + I(t)$$

$$\frac{du}{dt} = a(-u + bV)$$

if $V = 30\ mV$

then $V \rightarrow c$ and $u \rightarrow u + d$

Izhikevich

Izhikevich “Simple” Model

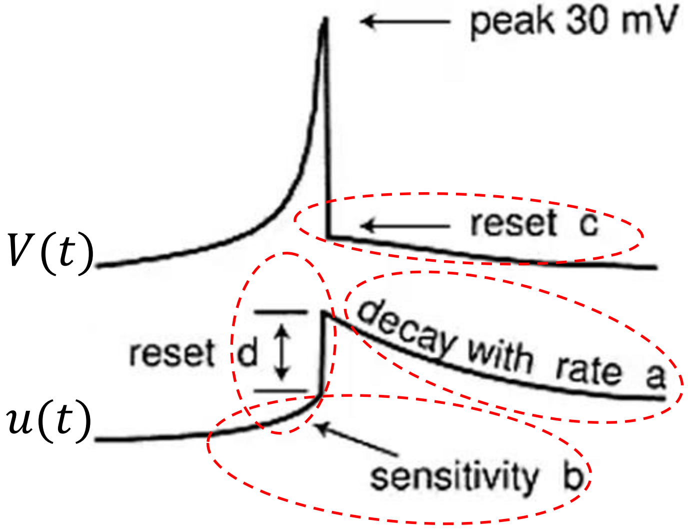
Practice in HW

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - u + I(t)$$

$$\frac{du}{dt} = a(-u + bV)$$

if $V = 30\ mV$

then $V \rightarrow c$ and $u \rightarrow u + d$



- a sets the time scale of the recovery variable ($\frac{1}{a}$ is the time constant, so low values of a correspond to slow recovery)
- b describes the sensitivity of the recovery variable to fluctuations of the membrane potential (large b causes more increase in u due to an increase in V)
- c is the voltage reset value
- d describes the reset of the recovery variable (high values delay repeated spiking)

Izhikevich

Izhikevich "Simple" Model

Practice in HW

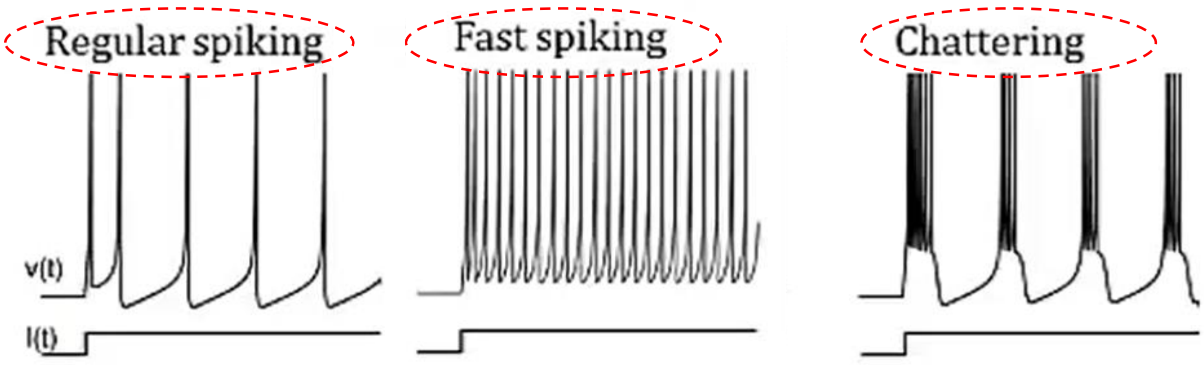
- Examples of neural spiking activity generated by the simplified model (using the 4 parameters):

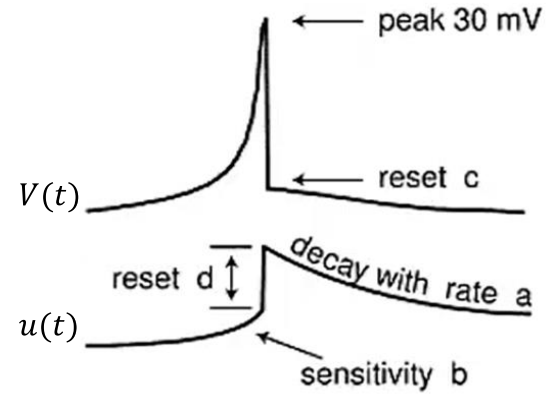
$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - u + I(t)$$

$$\frac{du}{dt} = a(-u + bV)$$

if $V = 30\ mV$

then $V \rightarrow c$ and $u \rightarrow u + d$





Izhikevich

Izhikevich "Simple" Model

Practice in HW

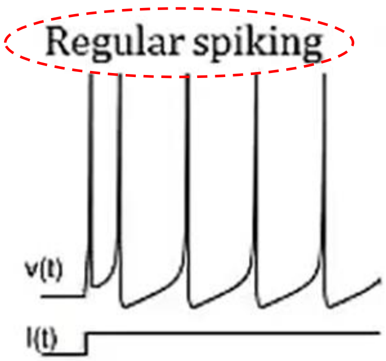
- Examples of neural spiking activity generated by the simplified model (using the 4 parameters):

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - u + I(t)$$

$$\frac{du}{dt} = a(-u + bV)$$

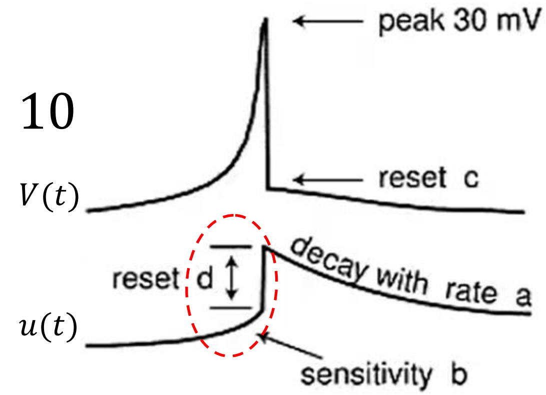
if $V = 30\ mV$

then $V \to c$ and $u \to u + d$



Base values for the model parameters:

$a = 0.02, \quad b = 0.2, \quad c = -65, \quad d = 2, \quad I = 10$



- A high value $d = 8$ (increased influence of the K+ channel)

  → **Regular spiking**

  (common for excitatory neurons – spiking with fatigue)

Izhikevich

Izhikevich "Simple" Model

Practice in HW

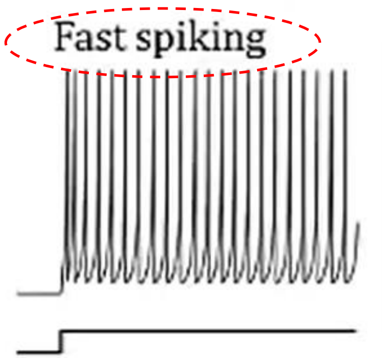
- Examples of neural spiking activity generated by the simplified model (using the 4 parameters):

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - u + I(t)$$

$$\frac{du}{dt} = a(-u + bV)$$

if $V = 30\ mV$

then $V \to c$ and $u \to u + d$



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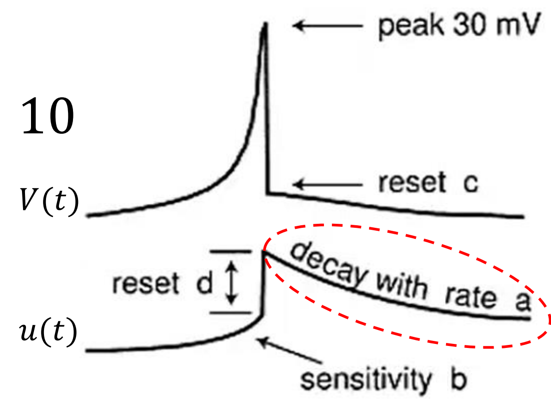


- A high value $a = 0.1$ (fast closing of the K+ channel)

  → **Fast spiking** (common in some inhibitory neurons)

Izhikevich

Izhikevich "Simple" Model

Practice in HW

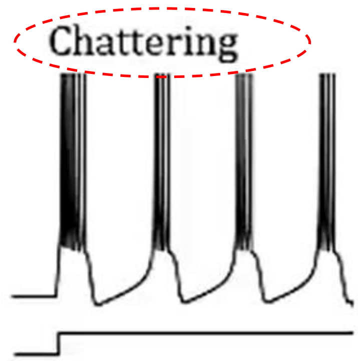
- Examples of neural spiking activity generated by the simplified model (using the 4 parameters):

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - u + I(t)$$

$$\frac{du}{dt} = a(-u + bV)$$

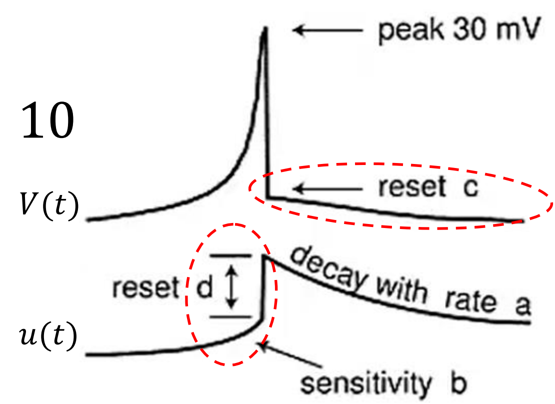
if $V = 30\ mV$

then $V \rightarrow c$ and $u \rightarrow u + d$



Base values for the model parameters:

$a = 0.02,\quad b = 0.2,\quad c = -65,\quad d = 2,\quad I = 10$

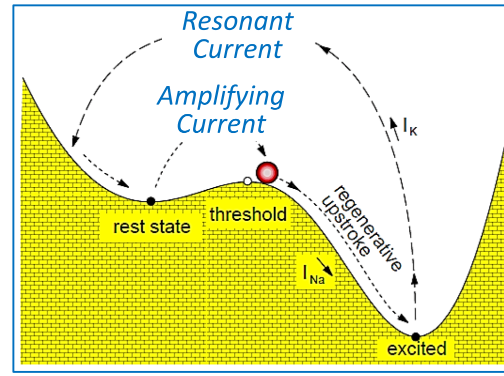


- A high value $c = -50$ (voltage is ready to rise again) and moderate value $d = 2$ (effect of K+ channel rapidly ends) → **Chattering**

Izhikevich

Summary

- The types of currents that flow into and out of the membrane determine neuronal dynamics
- All currents can be divided into two types:
  - ***Amplifying (integrating)***:
    E.g. persistent Na+ current $I_{Na,p}$
    (increase of membrane potential due to Na+ influx)
  - ***Resonant***:
    E.g. persistent K+ current I_K
    (fast closing of the K+ channel allows for repeated spiking)



- There are tens of known currents
  →Millions of electrophysiological mechanisms of spike generation
  →Any mechanism must have at least one amplifying and one resonant current

➢ Explore more: ***Izhikevich book***

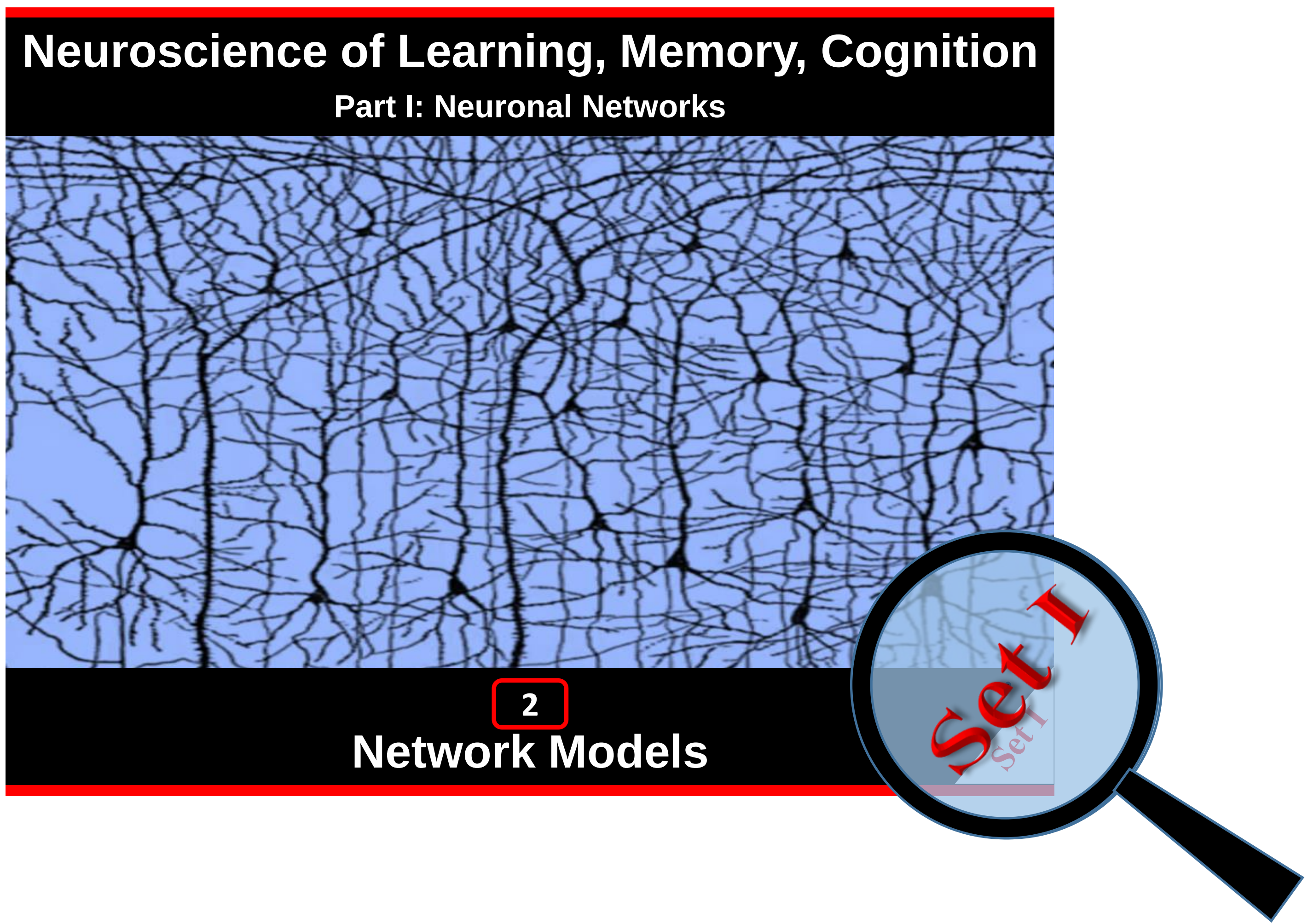
Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Outline

- Sensing & perception
  - Neurons in the brain
  - Visual cortex & receptive fields
  - Vision & perception
- Neurons & spikes
  - Electrical personality of a neuron
  - Ionic channels
  - Action potential
- The Hudgkin-Huxley equation
  - The passive membrane
  - Voltage-gated channels
  - Anatomy of a spike
- Neuronal dynamics
  - Phase portrait models
  - Fixed points and their stability
  - Bifurcation (saddle-node / Hopf)
  - Simplified 2D models

Next


Neuroscience of Learning, Memory, Cognition
Part I: Neuronal Networks
2
Network Models
Set I