ETH zürich

IT'IS FOUNDATION

EM-Neuro Modeling Across Scales for Bioelectronic Medicine

Lecture 2: Ion Channels and Membranes

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[*]IT'IS Foundation for Research on Information Technologies in Society

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Outline for today

- Lecture Overview
- The Hodgkin- Huxley Equation
- Phase Plane Analysis
- Temporal Discretization & Numerical Solving
- NEURON
- Summary of Today's Lecture & Outlook

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- **Lecture Overview**
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Course Outline

DATE	LECTURE THEME
19.02	Motivation, logistics & tooling (EN, TNE)
26.02	Ion channels & membranes (EN)
05.03	Axon models, activating functions & electrical stimulation (EN)
12.03	EM field simulation fundamentals & coupled EM-neuro workflows (EN)
19.03	Peripheral nerves & interfaces for bioelectronic medicine (EN)
26.03	Spinal cord stimulation for neuroprosthetics and pain management & low-frequency exposure safety (TNE)
02.04	Morphology, synapses, microcircuits; point vs spiking networks (TNE)
09.04	No class: Easter break
16.04	Neural mass & whole brain models; hybridization (TNE)
23.04	Recording modalities, signal content & the reciprocity theorem (TNE)
30.04	Non invasive brain stimulation & temporal interference (TNE)
07.05	Image based/personalized treatment planning and optimization (EN)
14.05	No class: Ascension Day
21.05	Verification, validation, UQ, and reproducibility (EN)
28.05	Project presentations & synthesis (EN, TNE)

Room: ETZ E7
13:15-14:00 Lecture
14:00-14:15 Break
14:15-15:00 Lecture
14:00-14:15 Break
15:15-16:00 Exercise

Lecture Recordings & Slides

Provided Here
(will successively appear)

Exercise Outline

DATE	EXERCISE THEME
19.02	"Hello Neuron": integrate-and-fire in Python/NEURON
26.02	Point neuron phase portrait; basic time integration numerics
05.03	Recruitment prediction for myelinated axon using AF/GAF
12.03	EM (FEM) modeling of transcranial brain stimulation
19.03	Stimulation selectivity and signal content modeling for nerve interfaces
26.03	Guest (SCS – NeuroRestore)
02.04	Mini project work
09.04	No class: Easter break
16.04	Guest (Neuromodulation Spin-Off – Z43)
23.04	Mini project work
30.04	Guest (NIBS – Kinderspital)
07.05	Mini project work
14.05	No class: Ascension Day
21.05	Mini project work
28.05	Project presentations

Room: ETZ E7

13:15-14:00 Lecture

14:00-14:15 Break

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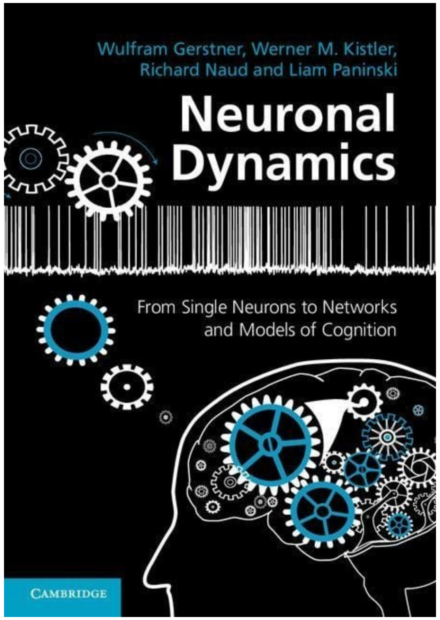
14:00-14:15 Break

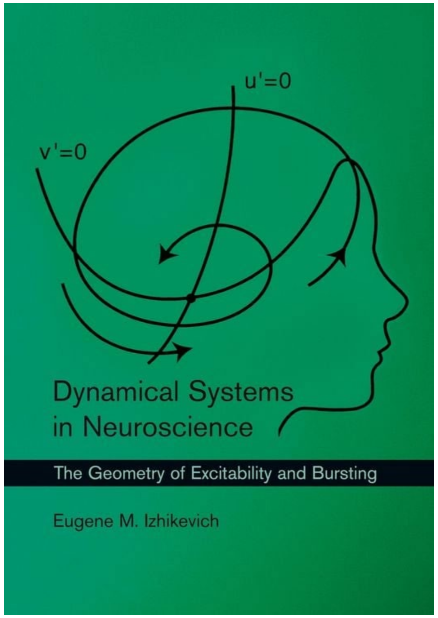
15:15-16:00 Exercise

Recommended Reading

- Gerstner, Wulfram, et al. *Neuronal dynamics: From single neurons to networks and models of cognition.* Cambridge University Press, 2014.
  - free online version: https://neuronaldynamics.epfl.ch/online/



- Izhikevich, Eugene M. *Dynamical systems in neuroscience*. MIT press, 2007.
  - free online version: https://www.izhikevich.org/publications/dsn.pdf



Course objectives

At the end of this lecture, you will have

- refreshed your knowledge about how Hodgkin-Huxley modelled neuron dynamics
- an intuitive understanding for non-linear neural dynamics and transitions between behavioural regimes
- started on your road to understand the numerics of neural dynamics simulations and associated challenges
- met the widely applied NEURON software from Yale

- The exercise project will revolve around implementing a simplified Hodgkin-Huxley-type simulator, studying time integration schemes, and performing a phase-plane analysis

Question To Think About Today

What matters more for model behavior: model form or model parameters?

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Hodgkin-Huxley Model

- *Who has met this model before?*
- example of a conductance-based model
- set of differential equations for ion-channel and transmembrane voltage dynamics
- famously proposed by Hodgkin and Huxley based on experiments with giant axons (squid)
- awarded with Nobel Prize in 1963
- many simplified or more sophisticated variants were later introduced
- extended with spatial dimension in the next lecture

J. Physiol. (1952) 117, 500–544

A QUANTITATIVE DESCRIPTION OF MEMBRANE CURRENT AND ITS APPLICATION TO CONDUCTION AND EXCITATION IN NERVE

By A. L. HODGKIN AND A. F. HUXLEY
From the Physiological Laboratory, University of Cambridge

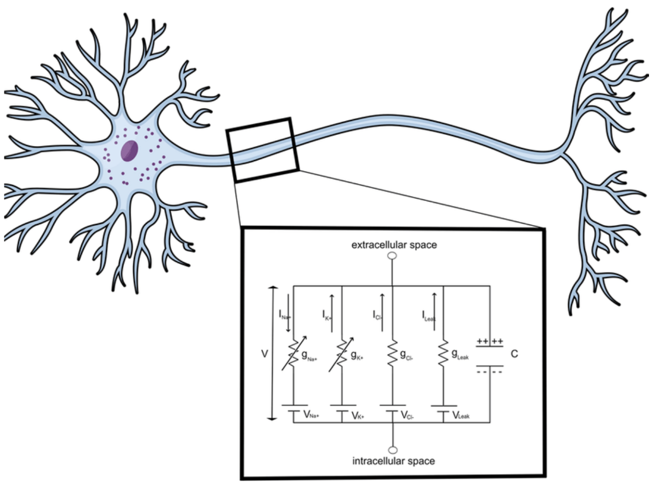
(*Received* 10 *March* 1952)

This article concludes a series of papers concerned with the flow of electric current through the surface membrane of a giant nerve fibre (Hodgkin, Huxley & Katz, 1952; Hodgkin & Huxley, 1952 *a–c*). Its general object is to discuss the results of the preceding papers (Part I), to put them into mathematical form (Part II) and to show that they will account for conduction and excitation in quantitative terms (Part III).

Hodgkin-Huxley Model

$$I = C_m \frac{dV_m}{dt} + g_K(V_m - V_K) + g_{Na}(V_m - V_{Na}) + g_l(V_m - V_l)$$

- explain ionic mechanisms underlying action potential initiation and propagation
- current conservation:
  - capacitive current (C)
  - leakage current (passive)
  - sodium & potassium currents (active)
    - channel gating dynamics



Potassium current

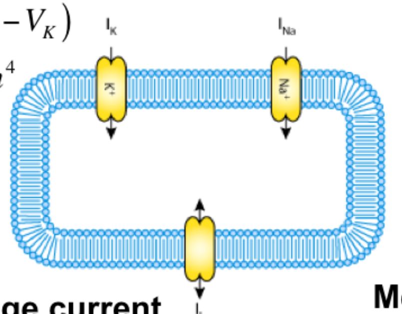
$$I_K = g_K(V - V_K)$$

$$g_K = g_{K_{max}} n^4$$

Sodium current

$$I_{Na} = g_{Na}(V - V_{Na})$$

$$g_{Na} = g_{Na_{max}} m^3 h$$



Gates (n,m,h)

$$\frac{dX}{dt} = \alpha_X(1 - X) - \beta_X X$$

Leakage current

$$I_{leak} = g_{leak_{max}}(V - V_{leak})$$

Membrane potential

$$\frac{dV}{dt} = \frac{I_{stim} - (I_K + I_{Na} + I_{leak})}{C_m}$$

https://www.researchgate.net/figure/Hodgkin-Huxley-Model-circuit-representation-of-the-neuronal-membrane-The-circuit_fig1_327250904

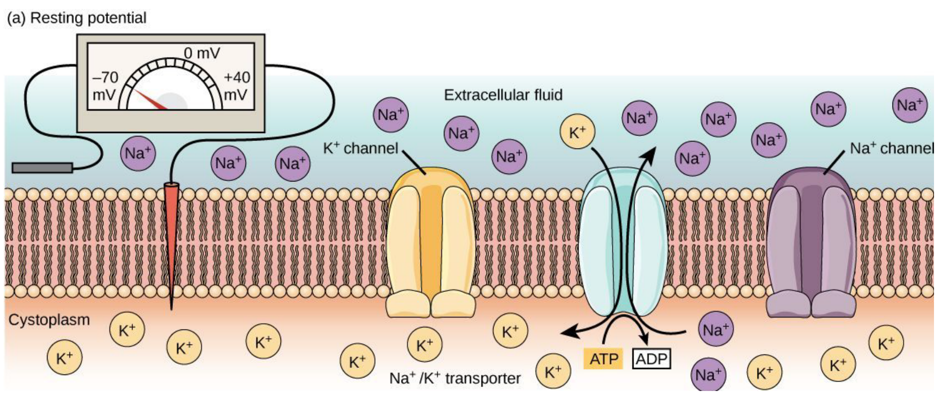
https://models.cellml.org/e/e1/tutorial

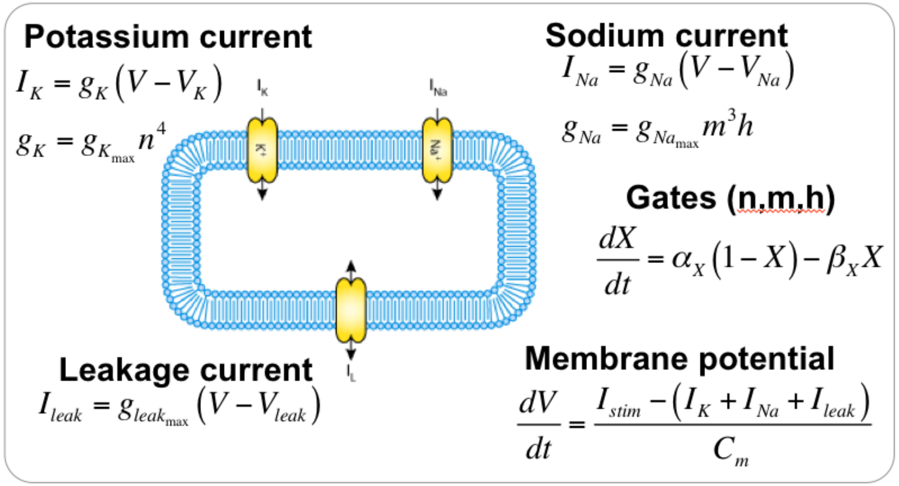
Hodgkin-Huxley Model

$$I = C_m \frac{dV_m}{dt} + g_K(V_m - V_K) + g_{Na}(V_m - V_{Na}) + g_l(V_m - V_l)$$

- ion-specific equilibrium potentials
- ion pumps maintain concentration differences
- results in Nernst potential
  - $V_{na} = 67mV$
  - ➢ reverse potential

$$V_{Eq.} = \frac{RT}{zF} \ln\left(\frac{[X]_{out}}{[X]_{in}}\right)$$





https://books.lib.uoguelph.ca/human-physiology/chapter/bioelectricity https://models.cellml.org/e/e1/tutorial

Hodgkin-Huxley Model

$$I = C_m \frac{\mathrm{d}V_m}{\mathrm{d}t} + \bar{g}_{\mathrm{K}} n^4 (V_m - V_K) + \bar{g}_{\mathrm{Na}} m^3 h (V_m - V_{Na}) + \bar{g}_l (V_m - V_l)$$

- probabilities of potassium channel subunit activation (*n*), sodium channel subunit activation (*m*), and sodium channel subunit inactivation (*h*)
- voltage-dependent rates
- stochastic

$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$

$$\frac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m$$

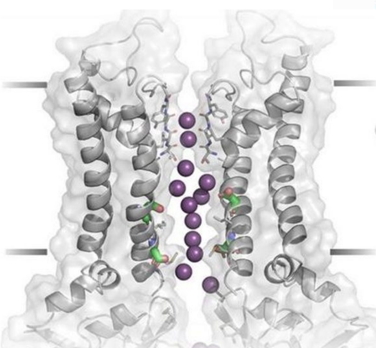
$$\frac{dh}{dt} = \alpha_h(V_m)(1-h) - \beta_h(V_m)h$$

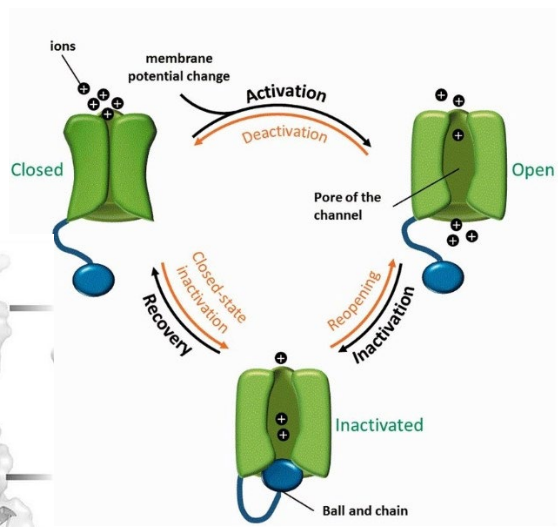
$$\alpha_p(V_m) = p_\infty(V_m)/\tau_p$$

$$\beta_p(V_m) = (1 - p_\infty(V_m))/\tau_p$$

$$\alpha_n(V_m) = \frac{0.01(10-V)}{\exp\left(\frac{10-V}{10}\right)-1} \qquad \alpha_m(V_m) = \frac{0.1(25-V)}{\exp\left(\frac{25-V}{10}\right)-1} \qquad \alpha_h(V_m) = 0.07\exp\left(-\frac{V}{20}\right)$$

$$\beta_n(V_m) = 0.125\exp\left(-\frac{V}{80}\right) \qquad \beta_m(V_m) = 4\exp\left(-\frac{V}{18}\right) \qquad \beta_h(V_m) = \frac{1}{\exp\left(\frac{30-V}{10}\right)+1}$$



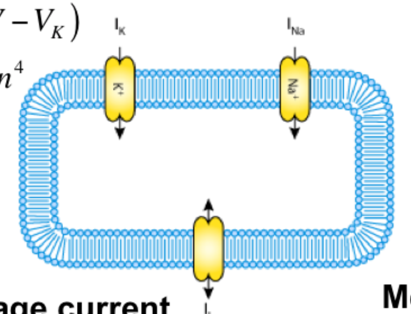


V, Hinard.; et al, 2016

Potassium current

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

$$g_K = g_{K_{max}} n^4$$



Sodium current

$$I_{Na} = g_{Na}(V - V_{Na})$$

$$g_{Na} = g_{Na_{max}} m^3 h$$

Gates (n,m,h)

$$\frac{dX}{dt} = \alpha_X(1-X) - \beta_X X$$

Leakage current

$$I_{leak} = g_{leak_{max}}(V - V_{leak})$$

Membrane potential

$$\frac{dV}{dt} = \frac{I_{stim} - (I_K + I_{Na} + I_{leak})}{C_m}$$

https://models.cellml.org/e/e1/tutorial

Hodgkin-Huxley Model

$$I = C_m \frac{\mathrm{d}V_m}{\mathrm{d}t} + \bar{g}_\mathrm{K} n^4 (V_m - V_K) + \bar{g}_\mathrm{Na} m^3 h (V_m - V_{Na}) + \bar{g}_l (V_m - V_l)$$

- probabilities of potassium
  cha
  soc
  (*m*)
  ina
- vol
- sto

dn

$n) - \beta_n(V_m)n$

$m) - \beta_m(V_m)m$

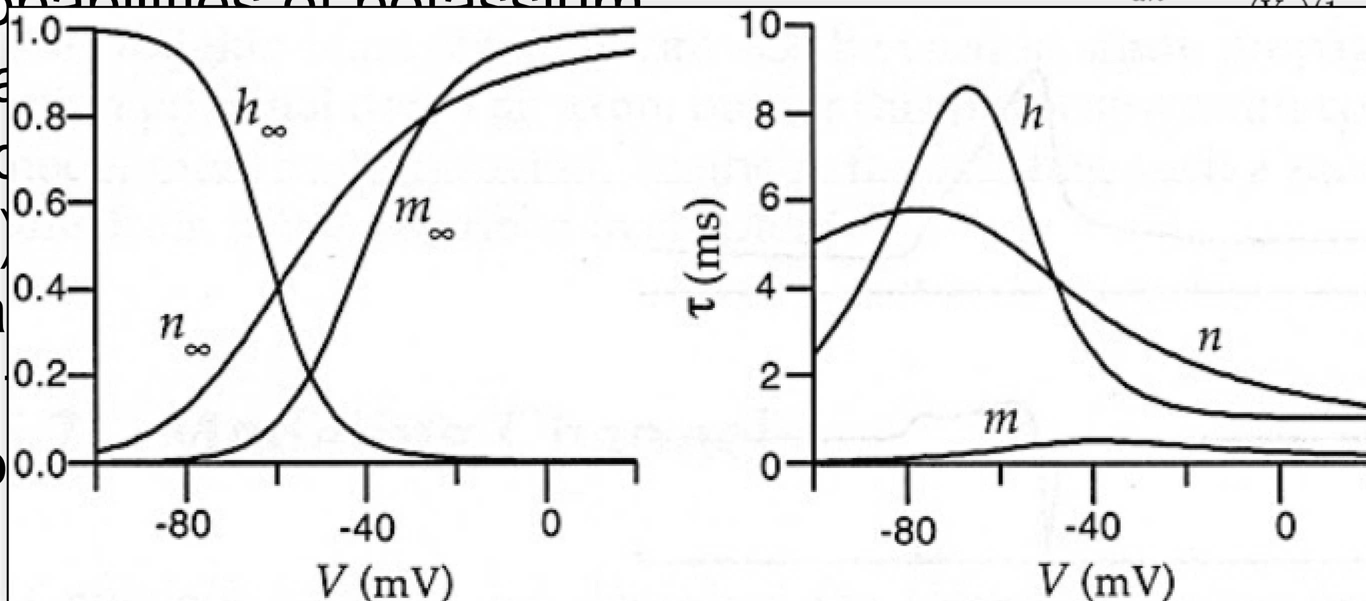
$h) - \beta_h(V_m)h$

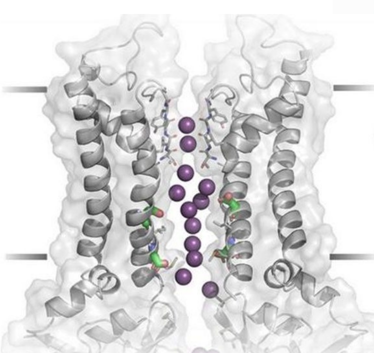
$= p_\infty(V_m)/\tau_p$

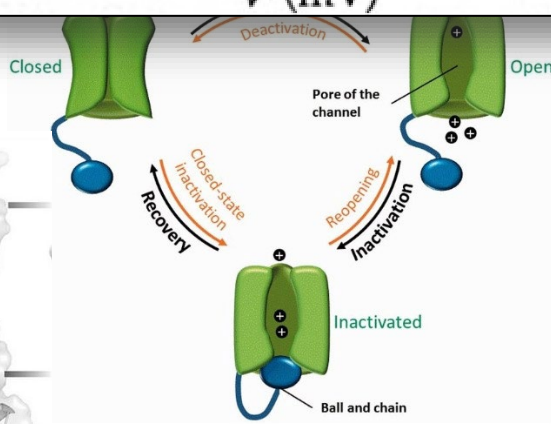
$(1 - p_\infty(V_m))/\tau_p$

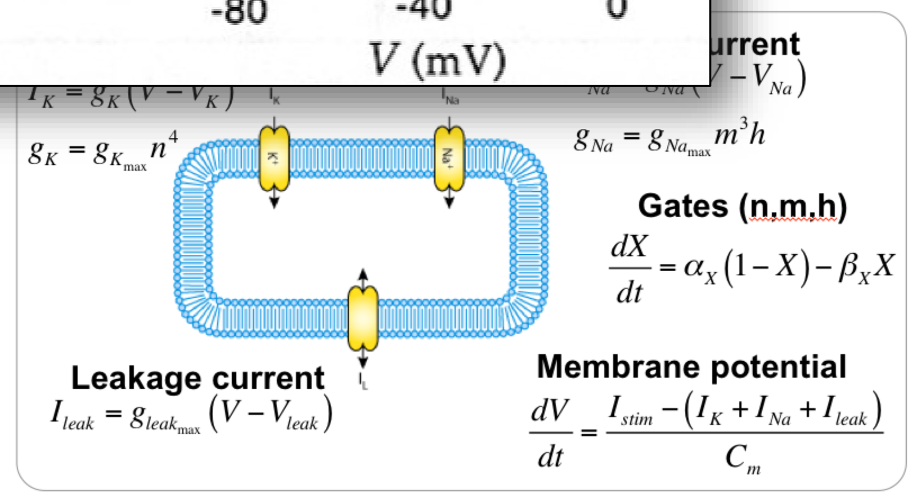
$) = 0.07 \exp\left(-\frac{V}{20}\right)$

$) = \frac{1}{\exp\left(\frac{30-V}{10}\right)+1}$









V, Hinard.; et al, 2016

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- probabilities of potassium channel subunit activation (n), sodium char[...] (m), and soc[...] inactivation ([...]
- voltage-depe[...]
- stochastic

Inherent time constants:
- channel dynamics
- ratio of conductances and membrane capacitance

$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$

$$\frac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m$$

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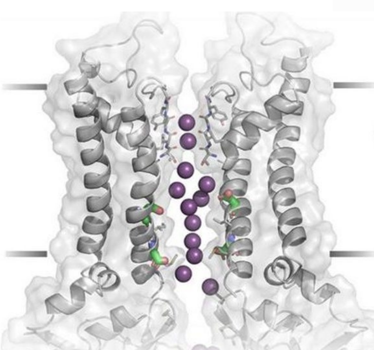

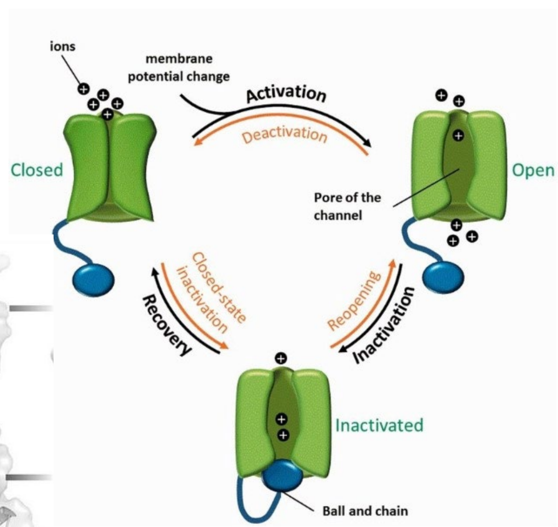

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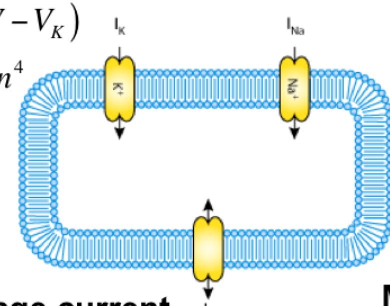

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- probabilities of potassium ch... (n)... so...ct... (m... su... ina...
- vo...
- st...

$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$

... $- \beta_m(V_m)m$

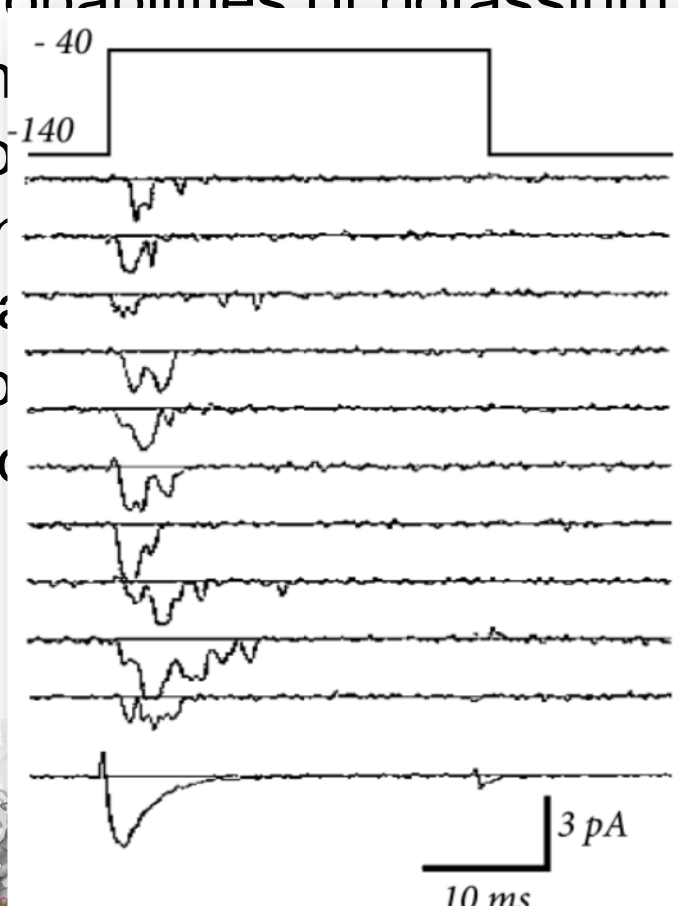
... $\beta_h(V_m)h$

... $(V_m)/\tau_p$

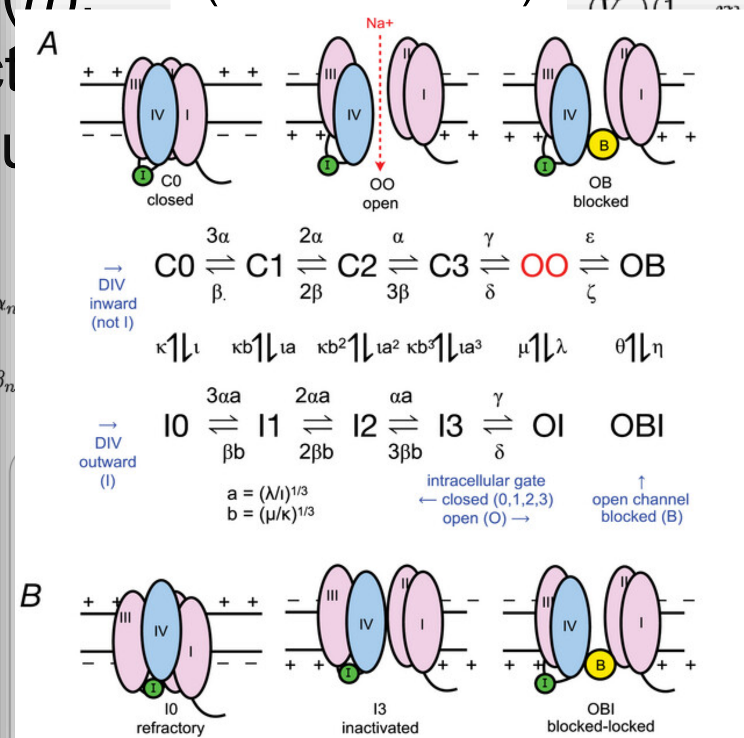
... $p_\infty(V_m))/\tau_p$

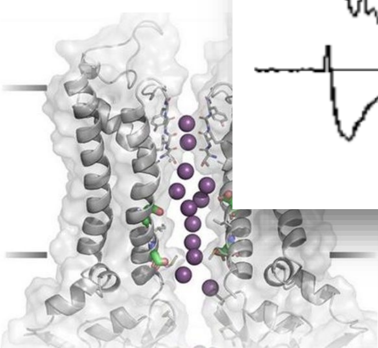
α_n ... $.07 \exp\left(-\frac{V}{20}\right)$

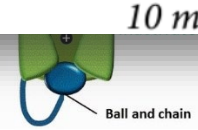
β_n ... $\frac{1}{\exp\left(\frac{30-V}{10}\right)+1}$

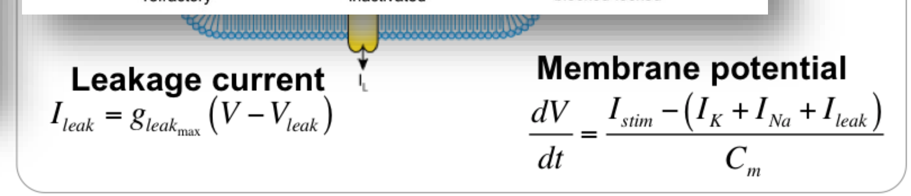


(Markov model)









V, Hinard.; et al, 2016

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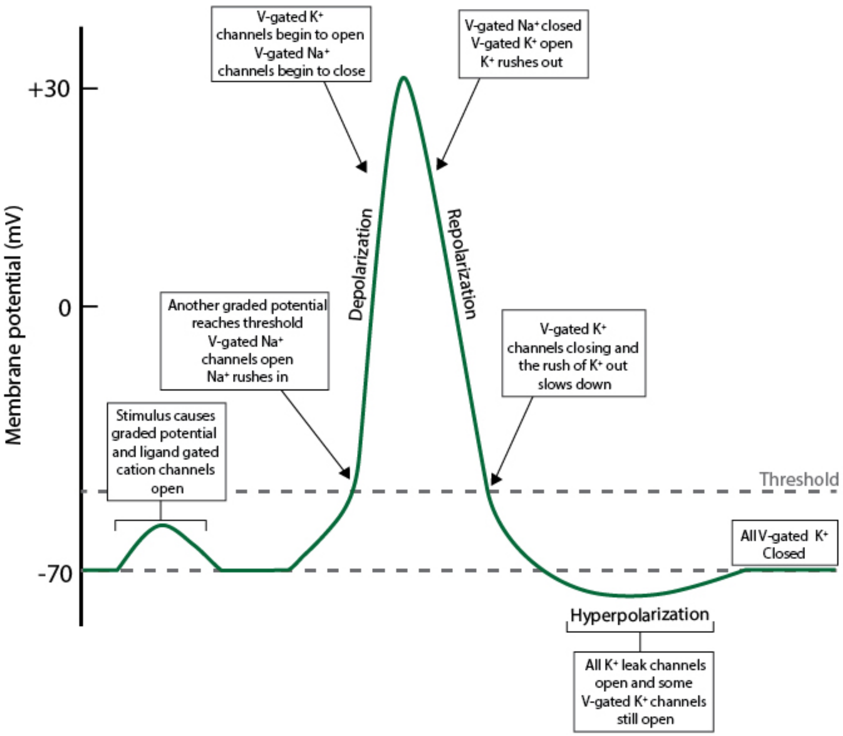

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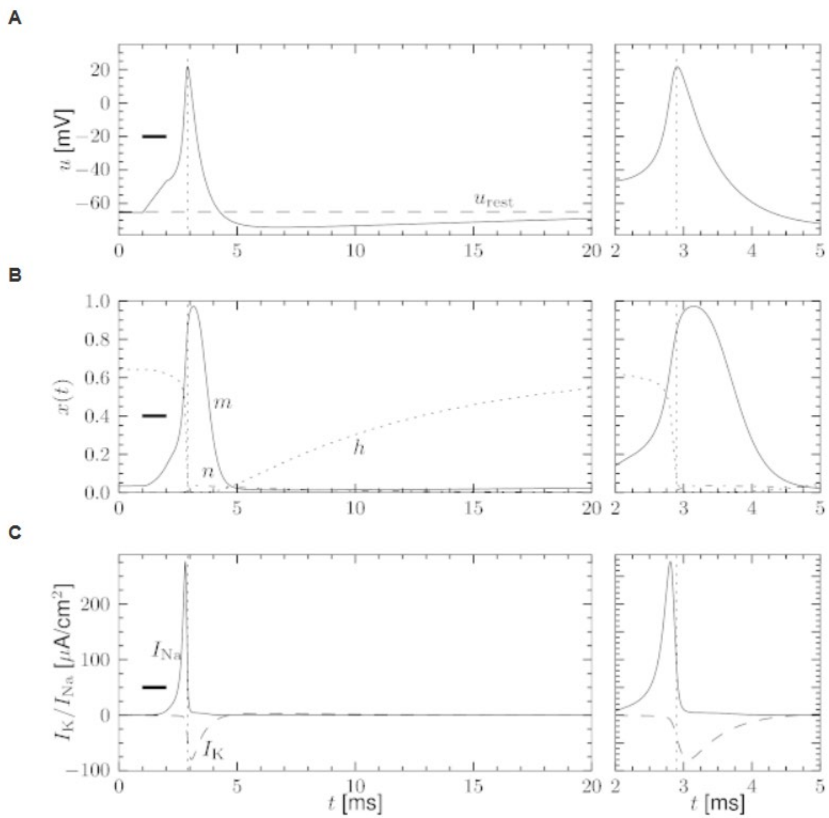
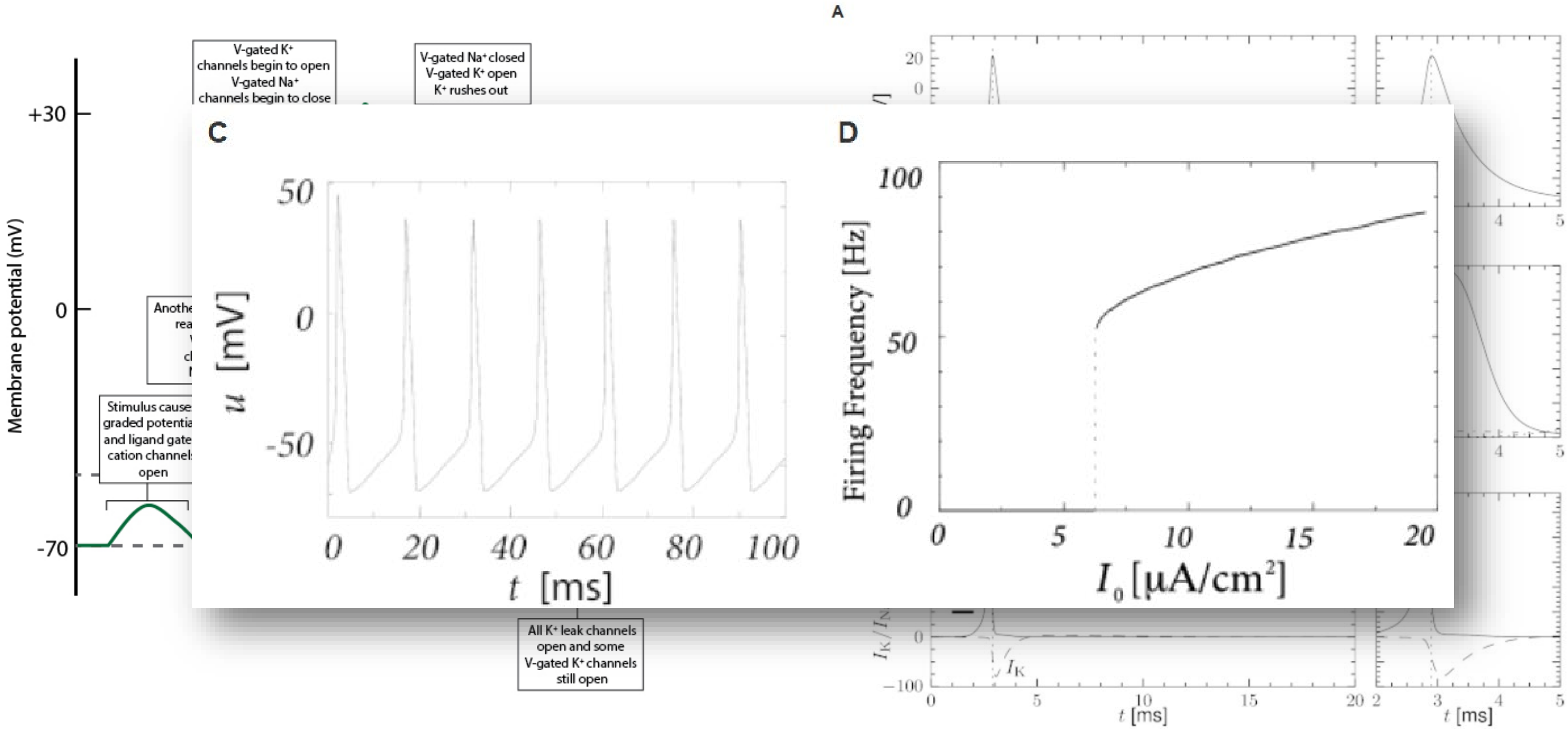


https://neuronaldynamics.epfl.ch/online/Ch2.S2.html

Hodgkin-Huxley Model

$$I = C_m \frac{dV_m}{dt} + \bar{g}_K n^4 (V_m - V_K) + \bar{g}_{Na} m^3 h (V_m - V_{Na}) + \bar{g}_l (V_m - V_l)$$



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https://neuronaldynamics.epfl.ch/online/Ch2.S2.html

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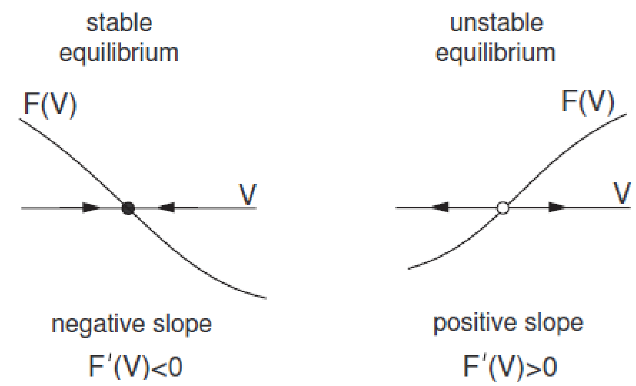
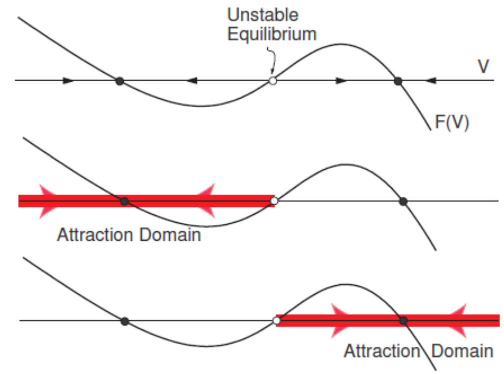
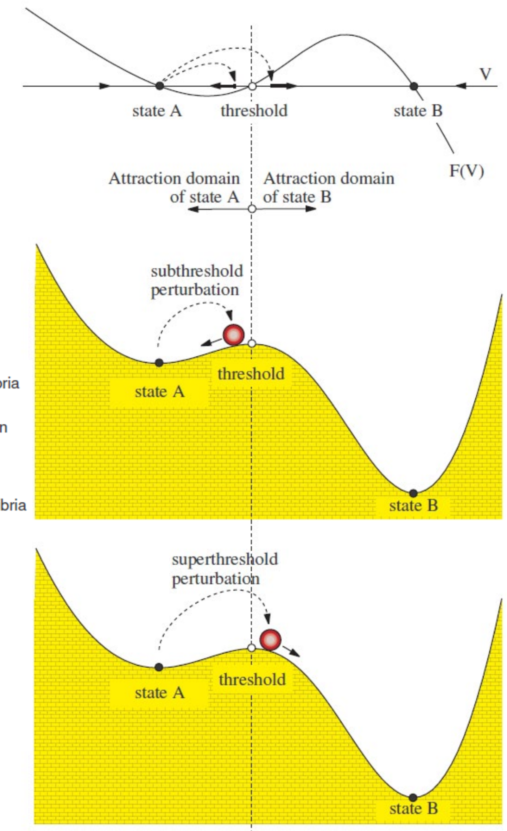
Nonlinear Dynamics in 1D

- $V' = F(V)$
- fixpoints
  - stability depends on sign of slope

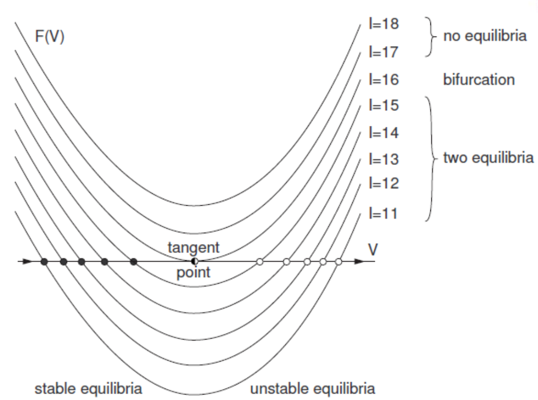


- attractors



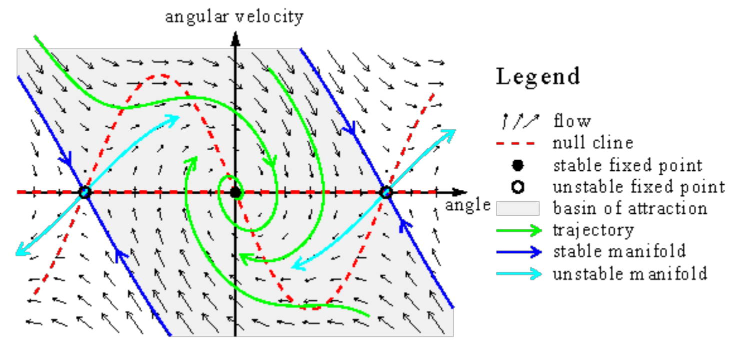


- bifurcation
  - $V' = F_I(V)$

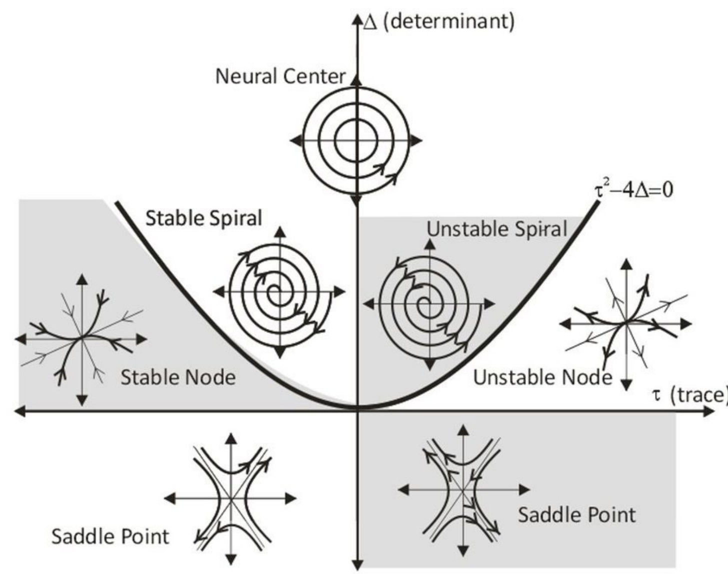


Nonlinear Dynamics in 2D

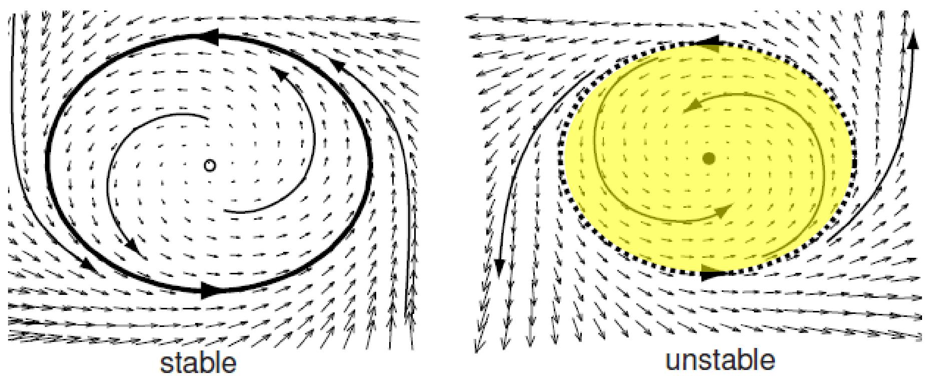
- $$\frac{\partial}{\partial t}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} F_u(u,v) \\ F_v(u,v) \end{pmatrix}$$
- fixpoints & nullclines
  - phase plot
  - nullcline intersection are fixpoints
  - stability depends on Eigenvalues of Jacobian
- attractors & limit cycles



https://elmer.unibas.ch/pendulum/bterm.htm



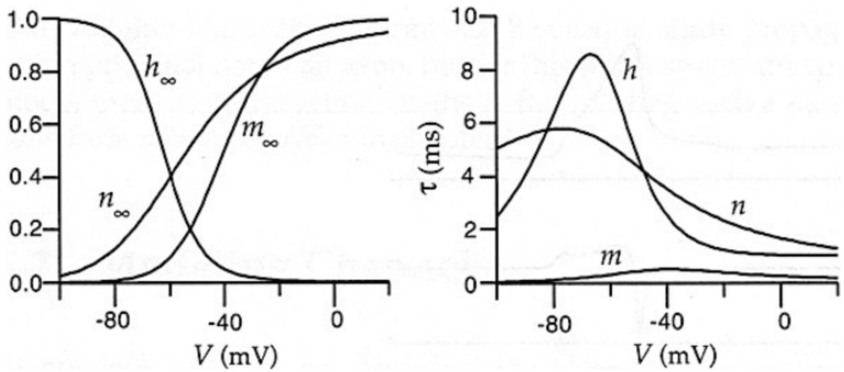
Erbaş, K. C. (2022) Chaos Theory and Applications, 4(1), 37-44



https://jdmonaco.com/files/monaco-2022-afrl-quest-slides.pdf

HH Dimensionality Reduction

- observations
  - time-scales of *n* and *h* dynamics are similar
  - voltage dependences of equilibrium functions can be approximated as linearly dependent
  - *m* dynamics is almost instantaneous
  - ➢ can reduce HH equations to 2D system (V_m=*u*, *w*)

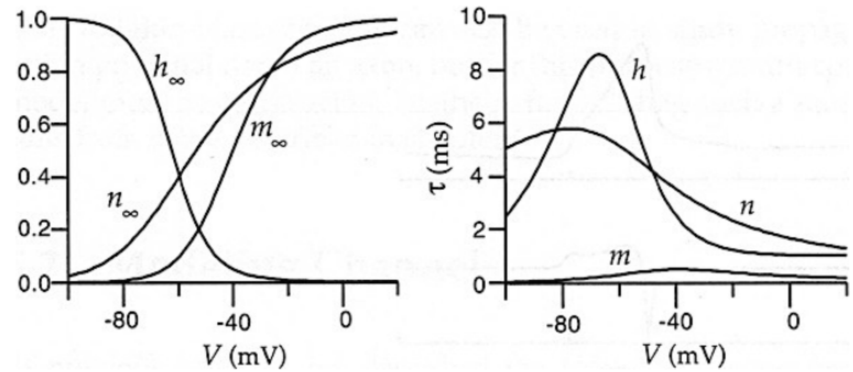


$$C\frac{\mathrm{d}u}{\mathrm{d}t} = -g_{\mathrm{Na}}[m_0(u)]^3\,(b-w)\,(u-E_{\mathrm{Na}}) - g_{\mathrm{K}}\left(\frac{w}{a}\right)^4(u-E_{\mathrm{K}}) - g_L\,(u-E_L) + I$$

$$\frac{\mathrm{d}u}{\mathrm{d}t} = \frac{1}{\tau}\left[F(u,w) + R\,I\right] \qquad \frac{\mathrm{d}w}{\mathrm{d}t} = \frac{1}{\tau_w}G(u,w) \qquad \text{with } R = g_L^{-1},\ \tau = R\,C$$

HH Dimensionality Reduction

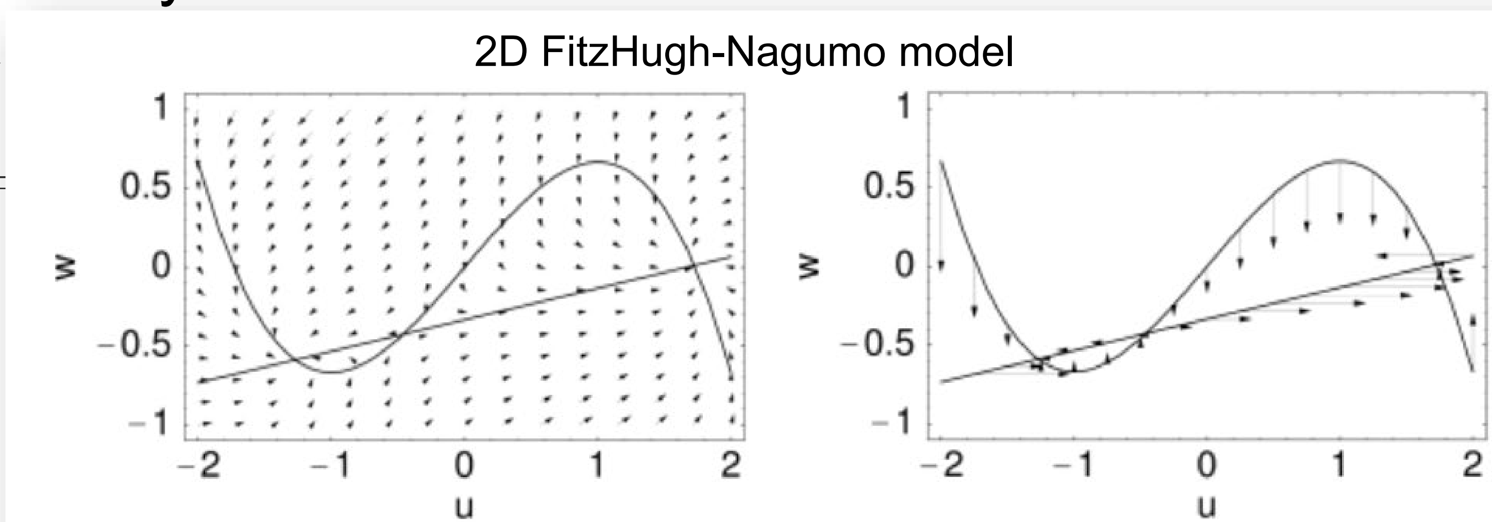
- observations
  - time-scales of *n* and *h* dynamics are similar
  - voltage dependences of equilibrium functions can be approximated as linearly dependent
  - *m* dynamics is almost instantaneous



➢

$C\frac{\mathrm{d}u}{\mathrm{d}t} =$ … $) + I$

$\frac{\mathrm{d}u}{\mathrm{d}t}$ … C



Phase Plot for Spiking Neuron

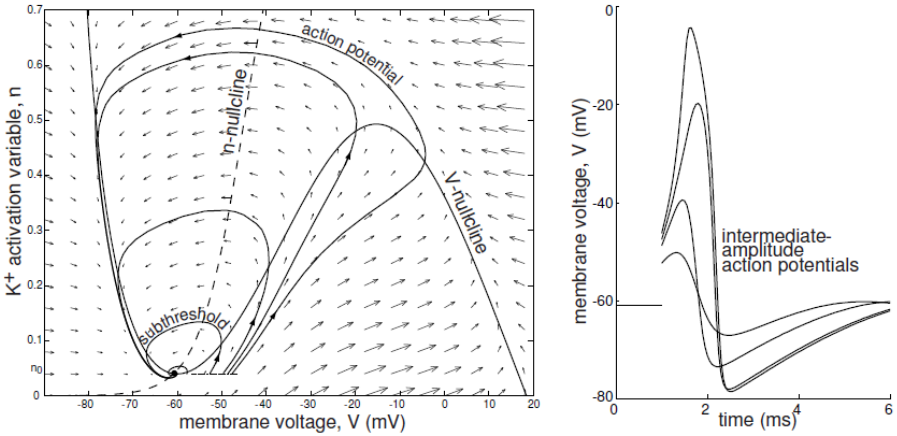


Figure 4.7: Failure to generate all-or-none action potentials in the $I_{Na,p}+I_K$-model.

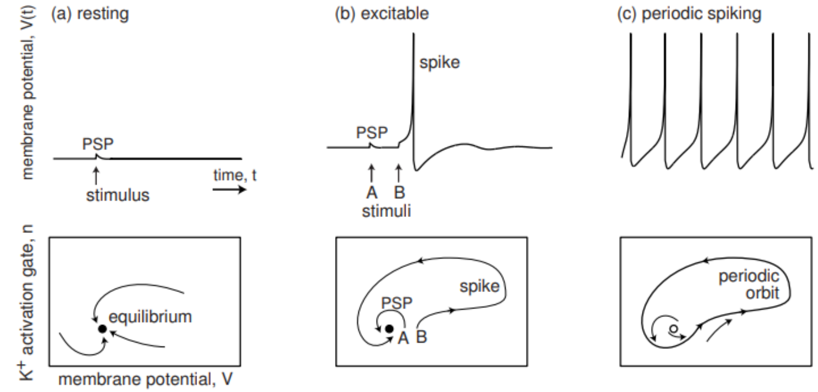
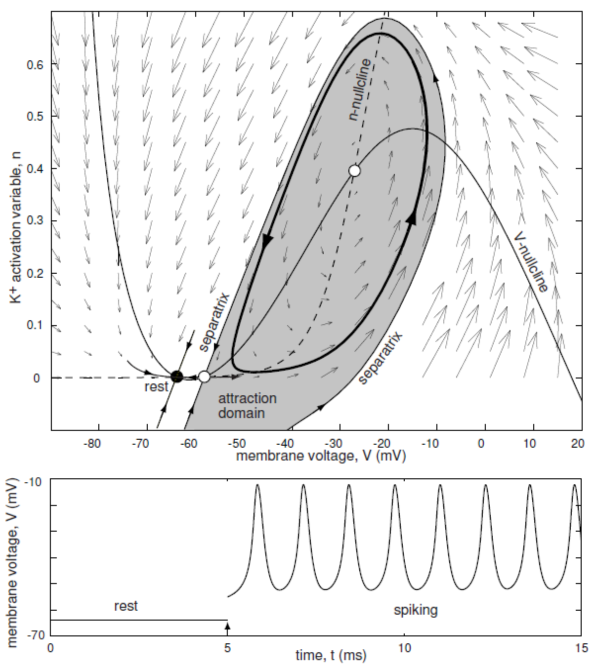
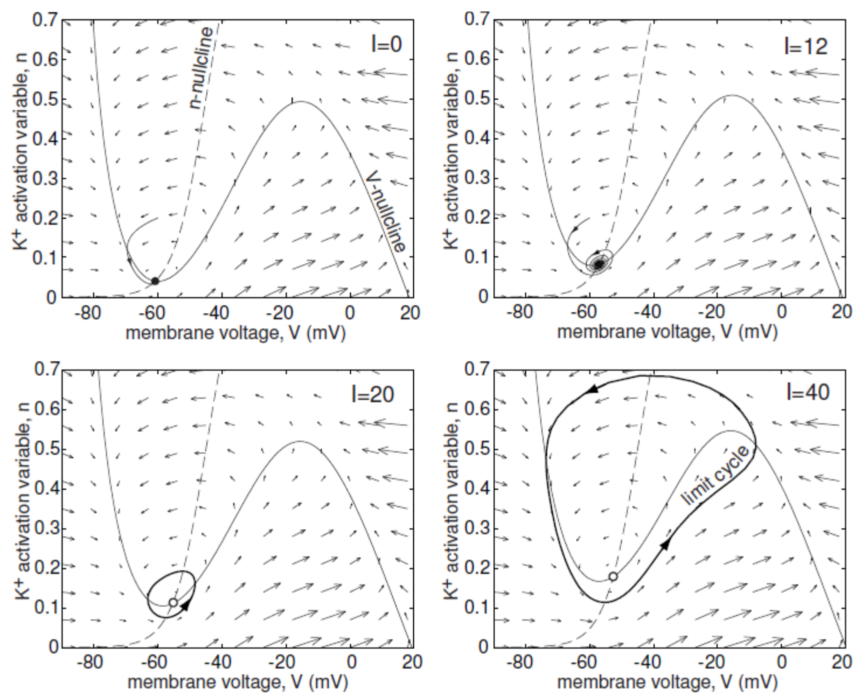


Figure 1.9: Resting, excitable, and periodic spiking activity correspond to a stable equilibrium (a and b) or limit cycle (c), respectively.

Bistability



Bifurcation



Phase Plot for Spiking Neuron

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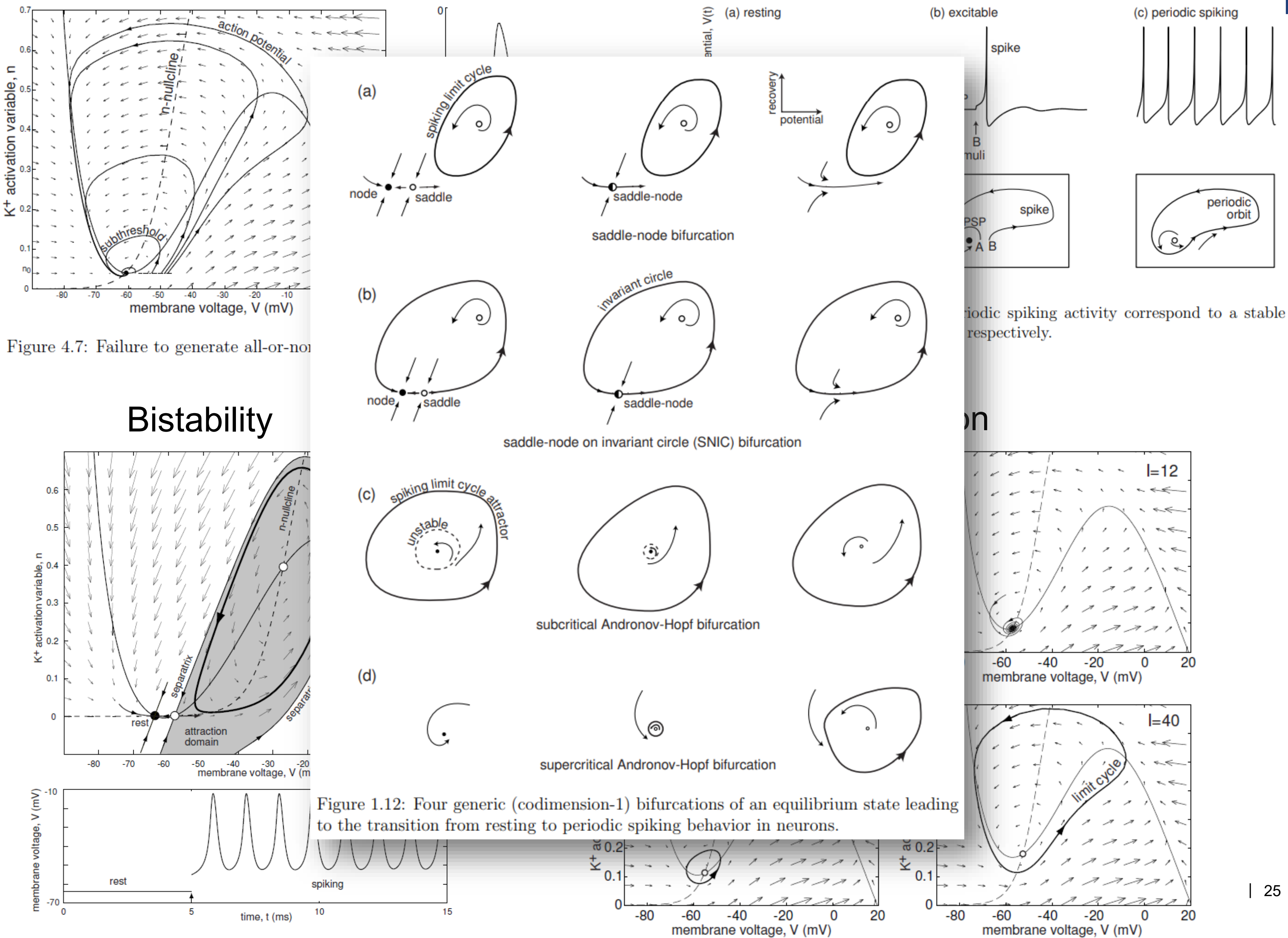


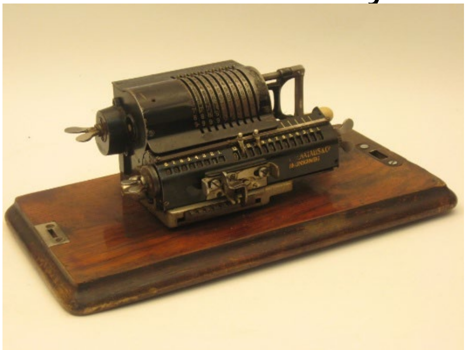
Figure 1.12: Four generic (codimension-1) bifurcations of an equilibrium state leading to the transition from resting to periodic spiking behavior in neurons.

Outline for today

- Lecture Overview
- The Hodgkin- Huxley Equation
- Phase Plane Analysis
- **Temporal Discretization & Numerical Solving**
- NEURON
- Summary of Today's Lecture & Outlook

Numerical Time Integration

- we cannot numerically solve a differential equation with infinitesimally fine temporal resolution (remember the Brunsviga?)
- instead, temporal discretization is combined with numerical time integration



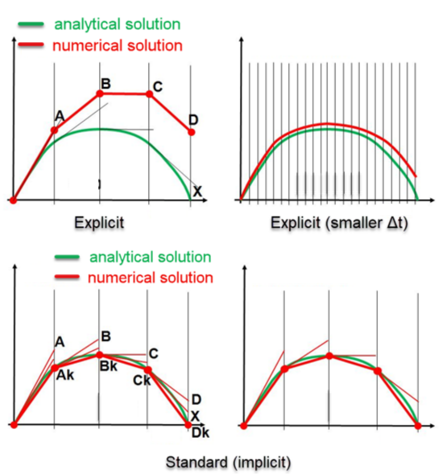
key issues:

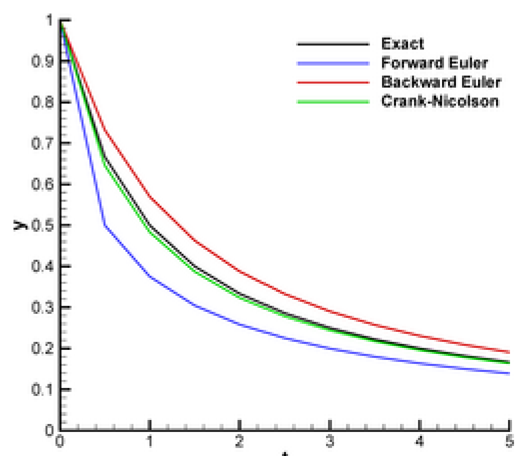
- instability: growth of numerical errors and/or small fluctuations in initial data, which might cause a large deviation of final answer from the exact solution
  - important factor: Eigenvalues (EV) of the time stepping scheme with |EV| >1 (amplification, growing oscillations)
- stiffness: *“If a numerical method with [...] stability, [...] is forced to use [..] a step length which is excessively small in relation to the smoothness of the exact solution”* [J.D. Lambert]
  - important factor: stiffness ratio of largest to smallest |*Re(EV)*| (large time-scale differences, related to condition number)

➢ Hodgkin-Huxley-type models are stiff ODE system with both fast and slow variables

explicit vs. implicit time integration

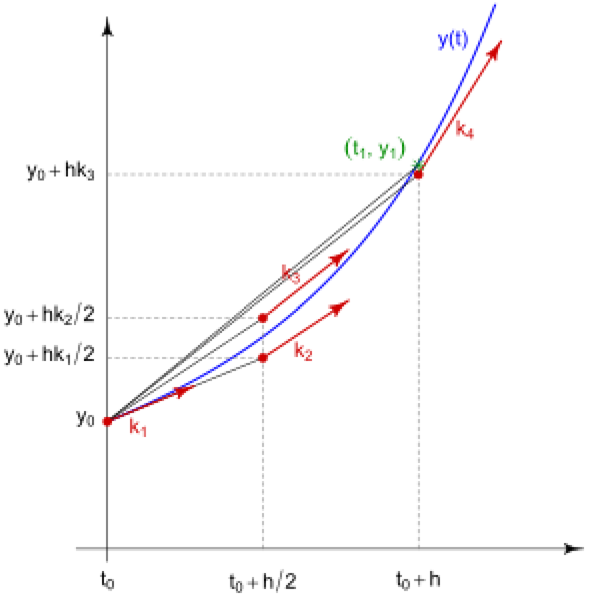
- explicit: project from past; computationally cheap & easy
- implicit: solve self-consistency of past and future; often requires solving of non-linear system, but can be unconditionally stable and support large time steps
- example: $\frac{dy}{dt} = -y^2,\ t \in [0, a]$
  - forward Euler: $\left(\frac{dy}{dt}\right)_k \approx \frac{y_{k+1} - y_k}{\Delta t} = -y_k^2$ ➡ $y_{k+1} = y_k - \Delta t y_k^2$
  - backward Euler: $\frac{y_{k+1} - y_k}{\Delta t} = -y_{k+1}^2$ ➡ $y_{k+1} = \frac{-1 + \sqrt{1 + 4\Delta t y_k}}{2\Delta t}$
  - Crank-Nicholson: $\frac{y_{k+1} - y_k}{\Delta t} = -\frac{1}{2} y_{k+1}^2 - \frac{1}{2} y_k^2$ ➡ $y_{k+1} + \frac{1}{2}\Delta t y_{k+1}^2 = y_k - \frac{1}{2}\Delta t y_k^2$





https://blog.technia.com/en/simulation/implicit-vs-explicit-finite-element-analysis

- multistep methods
  - leverage information from multiple past time-points to also estimate curvature and higher order features
  - more efficient (no new function evaluations), but more memory required (store previous iterations)
  - e.g., Adams-Bashforth
- higher order schemes
  - perform multiple evaluations at intermeditate points of a single time-step
  - less memory, less efficient, more complex
  - e.g., Runge-Kutta (RK4)
- both of these can be explicit or implicit



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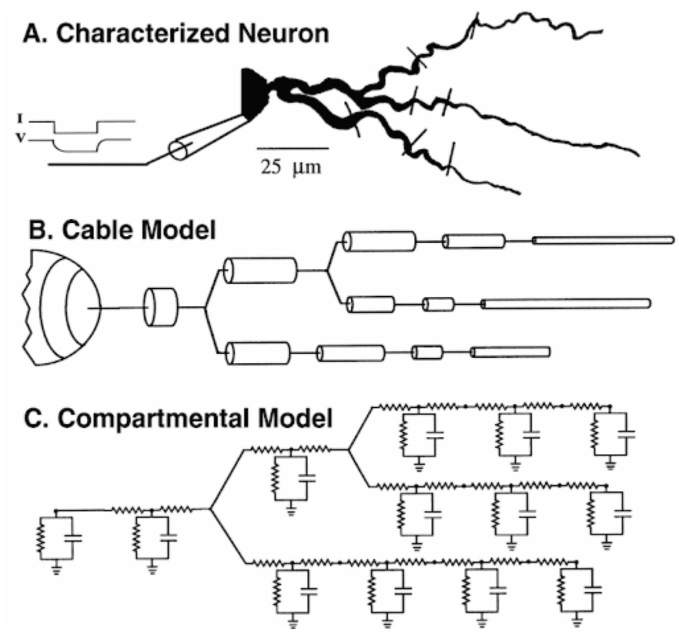
NEURON

- simulation environment for modeling individual and networks of neurons
- primarily developed by Michael Hines, John Moore, and Ted Carnevale at Yale and Duke
- broadly used in computational neurosciences research and education
- compartmental neuron models, with mechanism insertion (NMODL, compilation) for channels, synapses, etc.
- .hoc files, Python API, simple GUIs
- high performance computing support
- large resources available
    - neuron and network models (e.g., ModelDB)
    - computational infrastructure (e.g., eBRAINS)
    - documentation and support
    - wealth of tools
    - integration with open standards

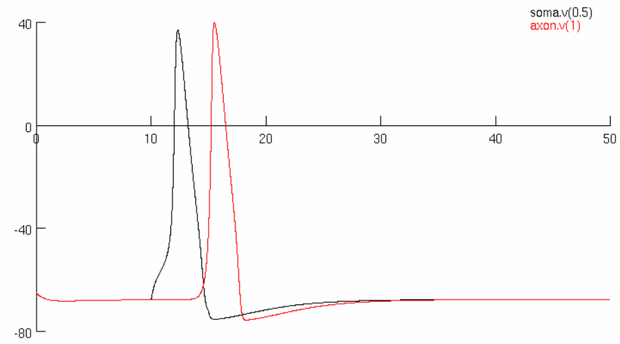


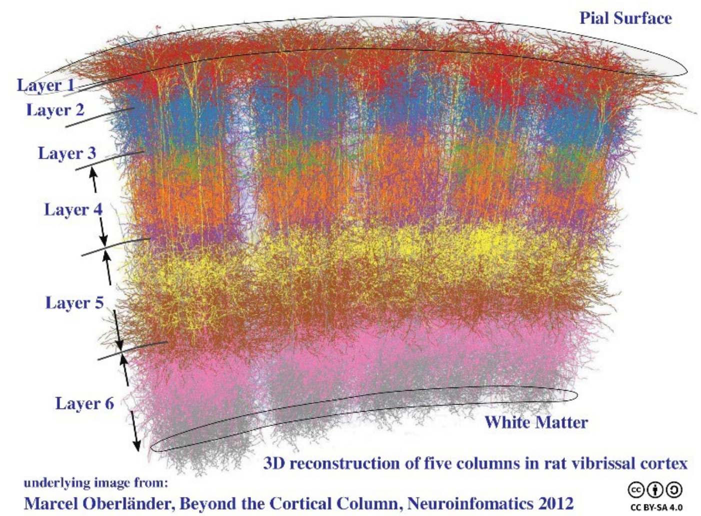
http://www.genesis-sim.org/GENESIS/cnslecs/cns2a.html

NEURON

- simple Hodgkin-Huxley Model with two compartments (soma, axon)
- for more, see exercises

```
//create two sections, the body of the neuron and a very long axon
create soma, axon

soma {
    //length is set to 100 micrometers
    L = 100
    //diameter is set to 100 micrometers
    diam = 100
    //insert a mechanism simulating the standard squid Hodgkin-Huxley channels
    insert hh
    //insert a mechanism simulating the passive membrane properties
    insert pas
}
axon {
    L = 5000
    diam = 10
    insert hh
    insert pas
    //the axon shall be simulated using 10 compartments. By default a single compartment is used
    nseg = 10
}

//connect the proximal end of the axon to the distal end of the soma
connect axon(0), soma(1)

//declare and insert a current clamp into the middle of the soma
objref stim
soma stim = new IClamp(0.5)

//define some parameters of the stimulus: delay, duration (both in ms) and amplitude (in nA)
stim.del = 10
stim.dur = 5
stim.amp = 10

//load a default NEURON library file that defines the run routine
load_file("stdrun.hoc")
//set the simulation to run for 50 ms
tstop = 50

//run the simulation
run()
```





https://en.wikipedia.org/wiki/Neuron_(software)

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Course objectives

At the end of this lecture, you will have

- refreshed your knowledge about how Hodgkin-Huxley modelled neuron dynamics
- an intuitive understanding for non-linear neural dynamics and transitions between behavioural regimes
- started on your road to understand the numerics of neural dynamics simulations and associated challenges
- met the widely applied NEURON software from Yale

Next week: Axon models, activating functions, and electrical stimulation

- The exercise project will revolve around implementing a simplified Hodgkin-Huxley simulator, studying time integration schemes, and performing a phase-plane analysis
- Plus, you get a free rapid intro to NEURON

Exercise Outline

DATE	EXERCISE THEME
19.02	"Hello Neuron": integrate-and-fire in Python/NEURON
26.02	Point neuron phase portrait; basic time integration numerics
05.03	Recruitment prediction for myelinated axon using AF/GAF
12.03	EM (FEM) modeling of transcranial brain stimulation
19.03	Stimulation selectivity and signal content modeling for nerve interfaces
26.03	Guest (SCS – NeuroRestore)
02.04	Mini project work
09.04	No class: Easter break
16.04	Guest (Neuromodulation Spin-Off – Z43)
23.04	Mini project work
30.04	Guest (NIBS – Kinderspital)
07.05	Mini project work
14.05	No class: Ascension Day
21.05	Mini project work
28.05	Project presentations

Room: ETZ E7

13:15-14:00 Lecture

14:00-14:15 Break

14:15-15:00 Lecture

14:00-14:15 Break

15:15-16:00 Exercise