Models of simple spiking neurons

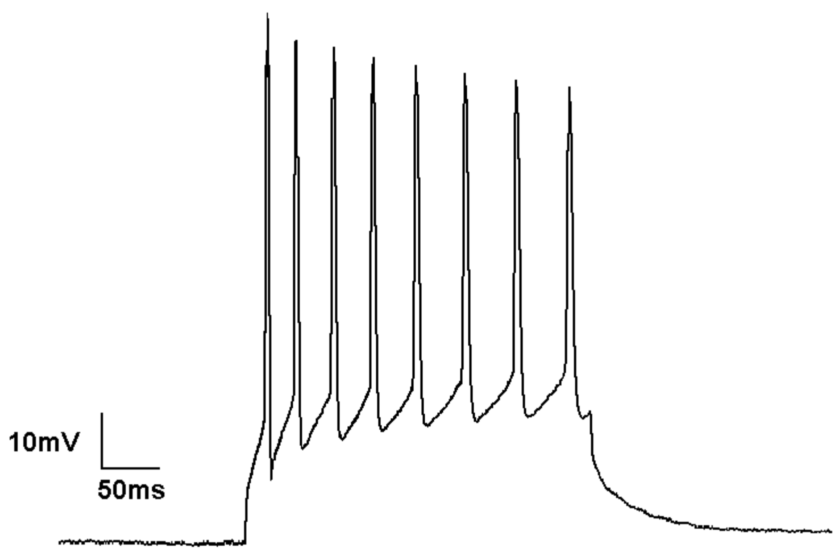
Lecture 3

Why simplified or reduced neuronal models?

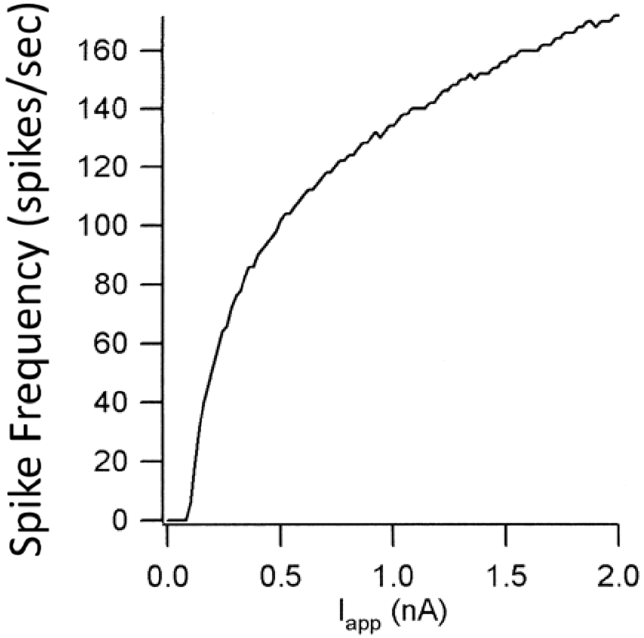
- Depending on the type of questions we are asking!
- Understanding the bare essentials or mechanisms
- Faster to simulate, especially in neuronal network models
- Availability of data
- Conducive for theoretical or mathematical analysis

Temporal and rate coding of neurons

Temporal coding
(Timing of spikes)



Rate coding
(frequency of spikes)



Why spiking neurons?

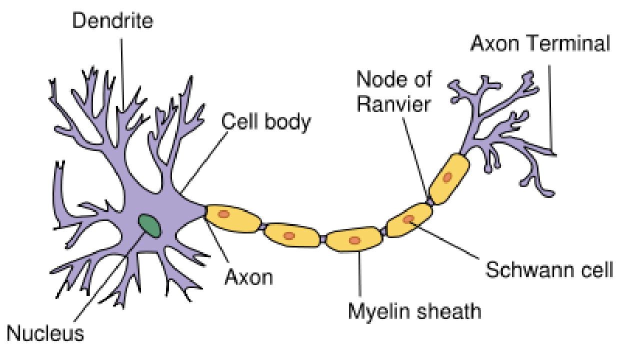
- Model and understand more realistic signal processing in the biological brain

- Can do the same thing as classical (non-spiking) neural network models, but computationally more powerful.

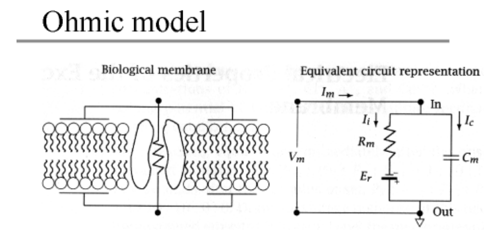
- Help solve engineering problems e.g. signal-processing, auditory systems, event detection, classification, speech recognition, spatial navigation, motor control.

Single-compartmental (point) model

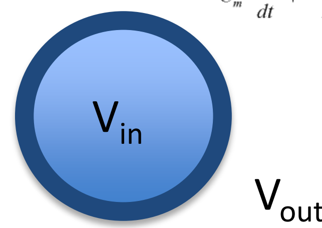
Consider only “single-compartmental” (point) neuronal model and assume iso-potential i.e. membrane potential V is independent of spatial location on the cell membrane.



Simplify



$$C_m \frac{dV_m}{dt} + \frac{V_m - E_r}{R_m} = I_m$$



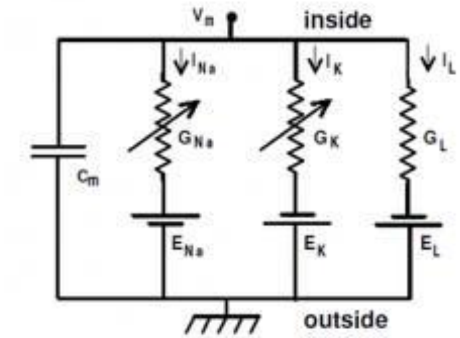
$V = V_{in} – V_{out}$

$C\ dV/dt = dQ/dt$

$= I(V,t)$

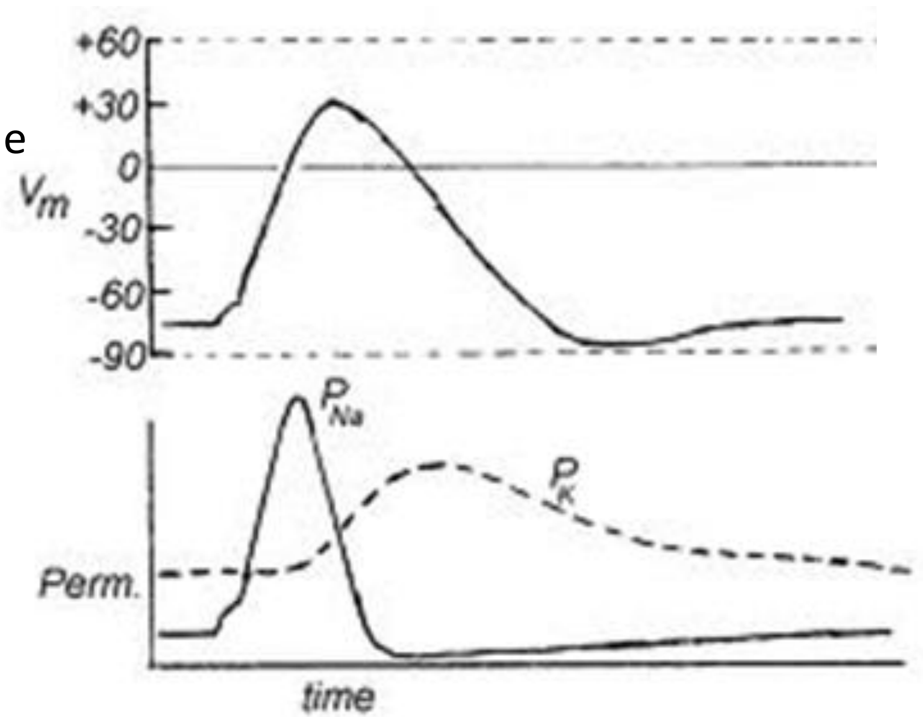
Hodgkin-Huxley Model (1952)

Using motor neuron of a squid giant axon



Membrane potential

“Flow” of Na^+ or K^+



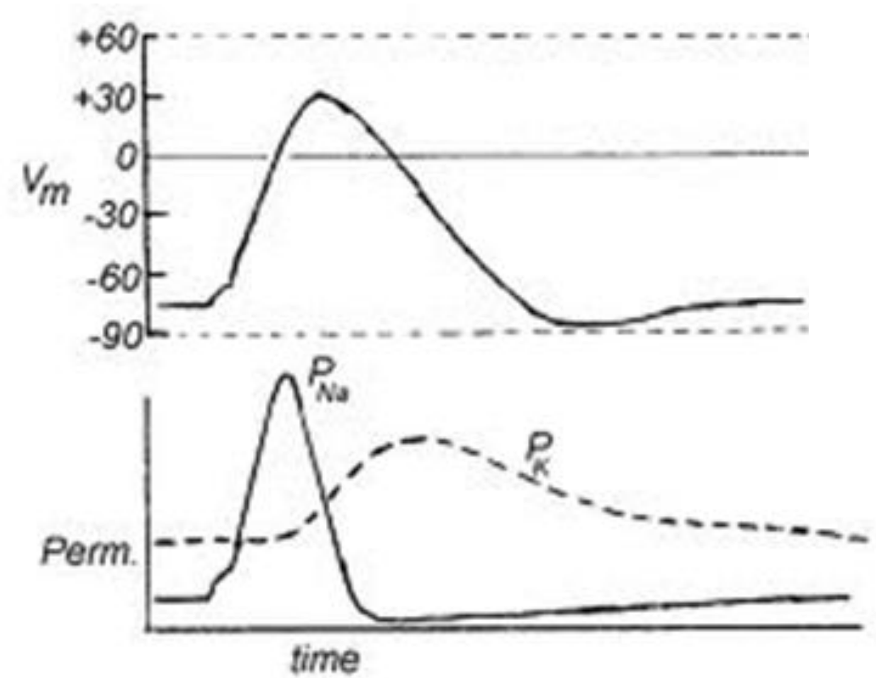
$$C\, dV(t)/dt = I_{Na}(V,t) + I_K(V,t) + I_{Leak}(V,t) + I_{app}$$

Hodgkin, A., and Huxley, A. (1952): A quantitative description of membrane current and its application to conduction and excitation in nerve. *J. Physiol.* **117**:500–544

An all-or-nothing action potential or spike for neuronal information processing

Membrane potential

"Flow" of Na^+ or K^+



- $\tau_m \ll \tau_h \approx \tau_n$ **(can assume *m* has relatively instantaneous dynamics)**
- $h_\infty \approx 1 - n_\infty$ **(replace *h* with *1-n*)**

Morris-Lecar Model (1981)

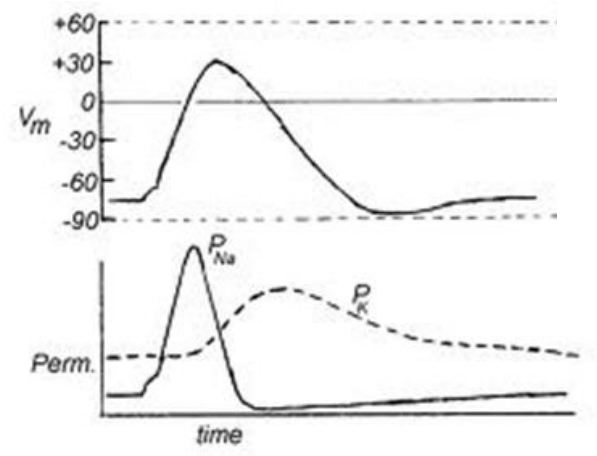
Approximation: Assume Na^+ channel dynamics is very rapid, reducing the HH-model into 2 equations.

$$C\, dV/dt = -\, g_{Na}\, M_{ss}(V)(V-V_{Na}) - g_K W(V-V_K) - g_L(V-V_L) + I_{app}$$

$$dW/dt = (W_{ss}(V) - W)/\tau_W(V)$$

where W is the recovery variable , K^+

(The recovery variable concept is adopted later in simplified spiking neuron models)



Morris, Catherine; Lecar, Harold (July 1981), "Voltage Oscillations in the barnacle giant muscle fiber", *Biophys J.* **35** (1): 193–213

http://www.scholarpedia.org/article/Morris-Lecar_model

Further approximation:

What if we ignore the relatively stereotypical shape action potential (spike) …?

… Integrate-and-fire neuronal models (Lapicque 1907; Hill 1936; Stein, Knight, etc)

(Perfect) Integrate-and-fire neuronal model

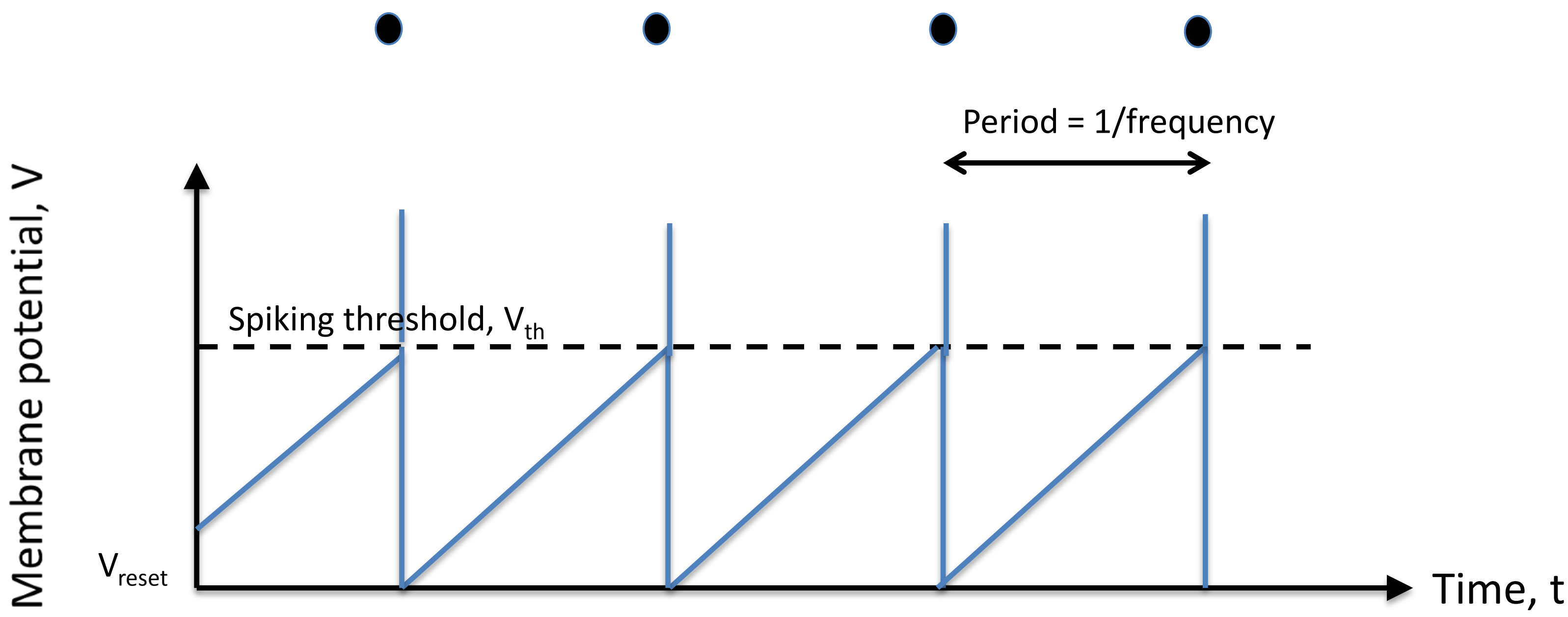
Gerstein and Mandelbrot, "Random walk models for the spike actiity of a single neuron", Biophys. J. (1964)

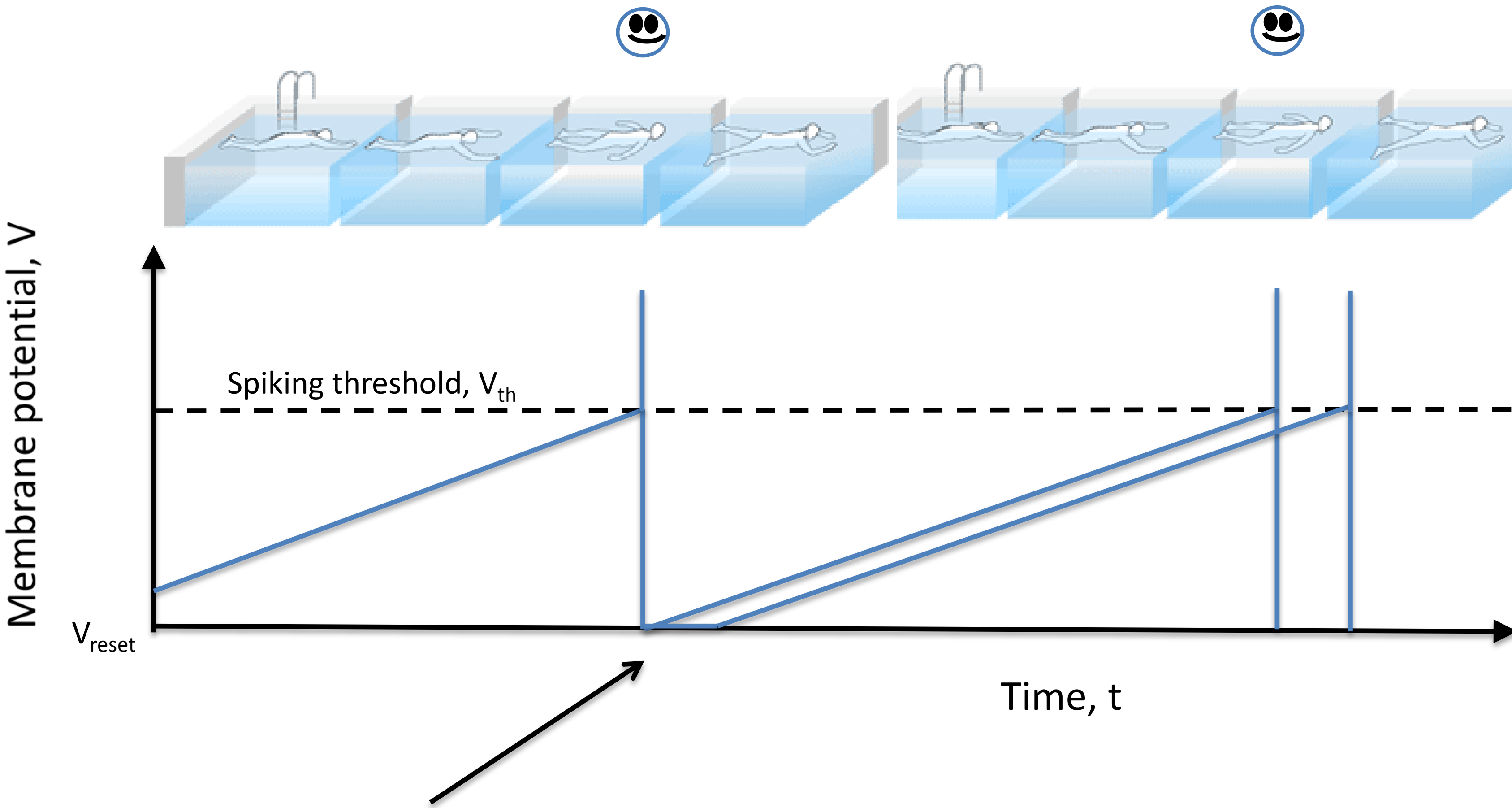
Suppose a current I_{app} is injected to a IF neuron with capacitance C, the sub-threshold membrane potential dynamics V is governed by:

$$C\, dV/dt = dQ/dt = I_{app}$$

i.e. $V \sim (I_{app}/C)t$ and $V \rightarrow V_{reset}$ upon reaching threshold V_{th}.

Note: no leak term





<u>(absolute) refractory period</u>: neuron not responding to any input

Leaky integrate-and-fire (LIF) neuronal model

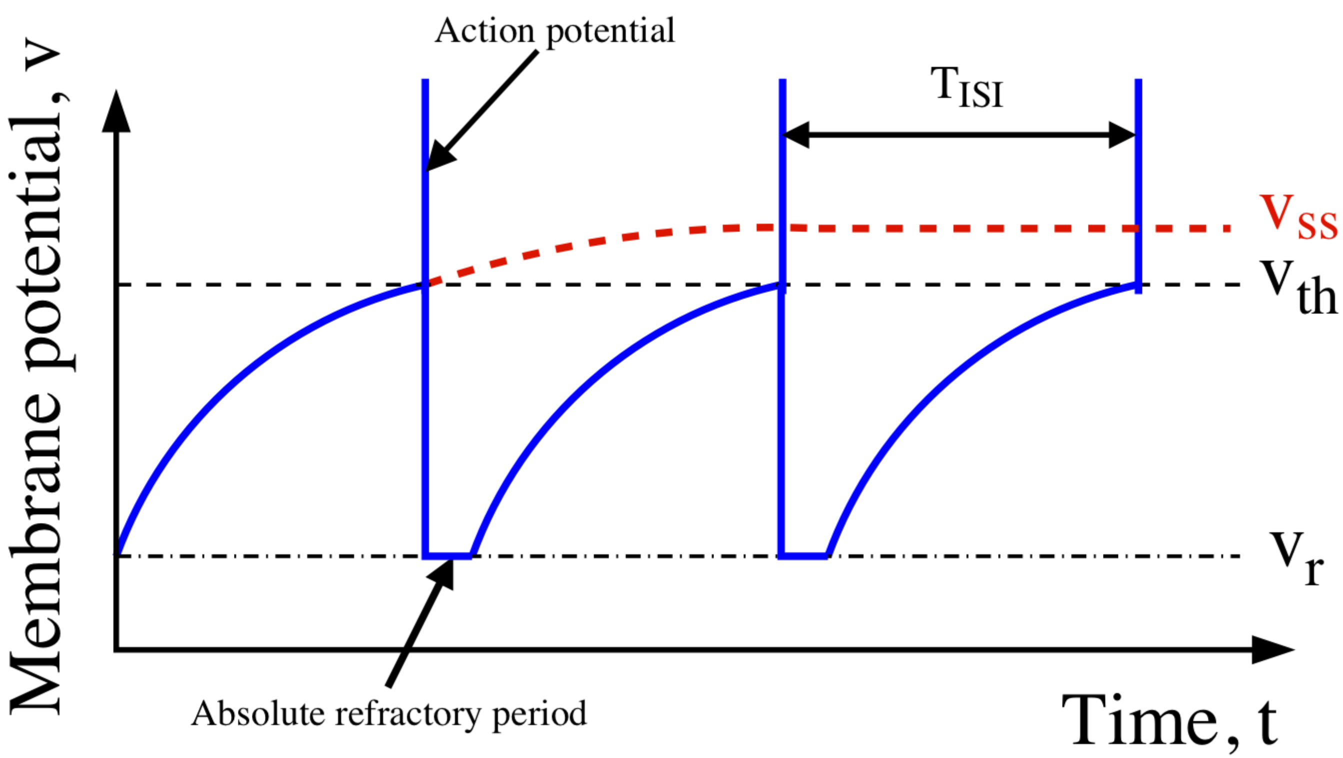
Subthreshold membrane potential dynamics:

Note negative sign

Leak reversal potential ~ -70 mV

$$C\, dV/dt = -g_L(V - E_L) + I_{app}$$

Leak conductance



Demo IF model

http://www.math.pitt.edu/~bard/classes/compneuro/iaf.html

XPPAUT

http://lcn.epfl.ch/tutorial/english/spiking/html/SingleNeuron.html

The applet was written by Florian Seydoux.

Analytical form of the input-output (transfer/response) function for a LIF model

Deterministic (i.e. no noise):

$$C\, dV/dt = -g_L\, (V - E_L) + I_{app}$$

The interspike interval or period, T, can found to be

$$T = (C/g_L)\ \ln\left[\{(V_{threshold} - E_L) - I_{app}/g_L\} / \{(V_{reset} - E_L) - I_{app}/g_L\}\right]$$

for $I_{app}/g_L > V_{threshold} - E_L$

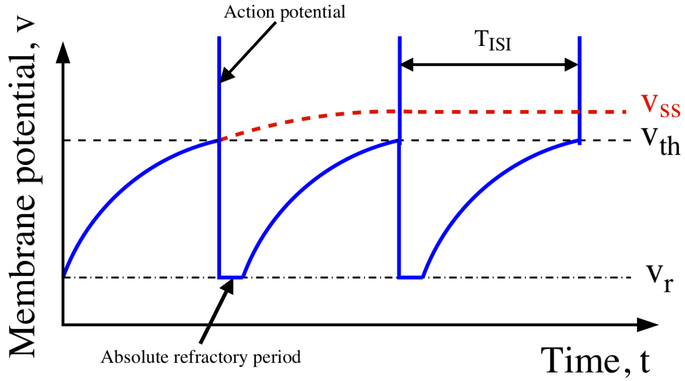
Thus, we can derive the spike frequency or firing rate, $f = 1/T$

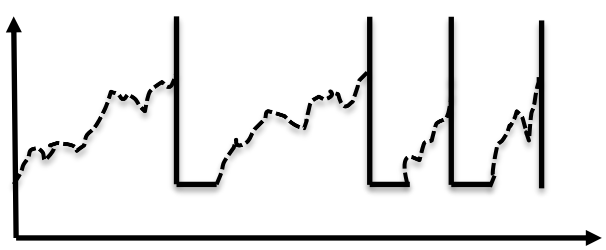
Lab

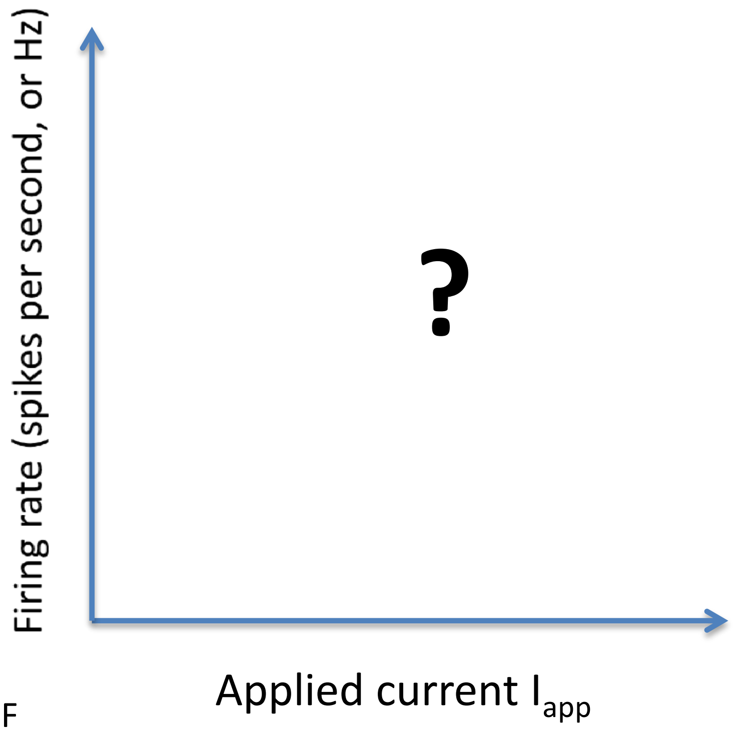
Noise in LIF model

Subthreshold membrane potential dynamics:

$C\ dV/dt = -\ g_L(V - V_L) + I_{app} + I_{noise}$
where e.g. $I_{noise} = \sigma\ \eta$, σ amplitude and η follows a (Gaussian/normal) distribution with zero mean and standard deviation of 1. ("randn" in Matlab)







Good fitting of input-output (response) function of noisy LIF model to experimental data. Rauch et al. (2003)

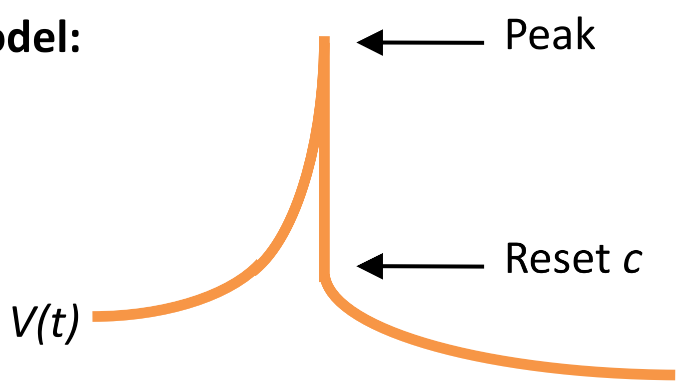
Nonlinear integrate-and-fire neuron

More realistic than the simple integrate-and-fire neuronal models – Accounting for the fast-rising membrane potential right before an action potential, and the finite width of action potentials

- Model behaves closer to that of biophysical (e.g. HH) type model than LIF model
- Powerful and efficient model if an adaptive current is incorporated (next slide)

E.g. The Quadratic Integrate-and-Fire (QIF) model:

$$CdV/dt = dQ/dt$$
$$= V^2 + I$$



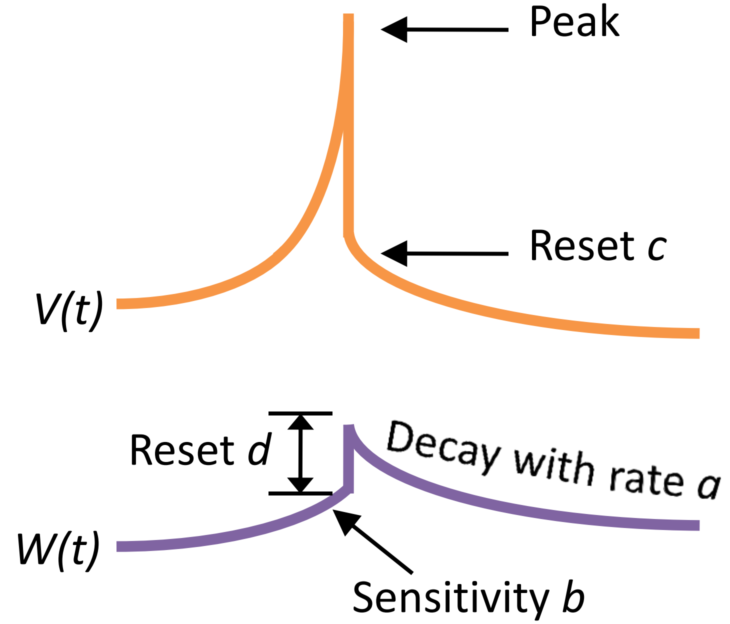
An adaptive quadratic integrate-and-fire neuronal (aQIF) model or Izhikevich model

Membrane potential

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - W + I$$

Additional recovery variable

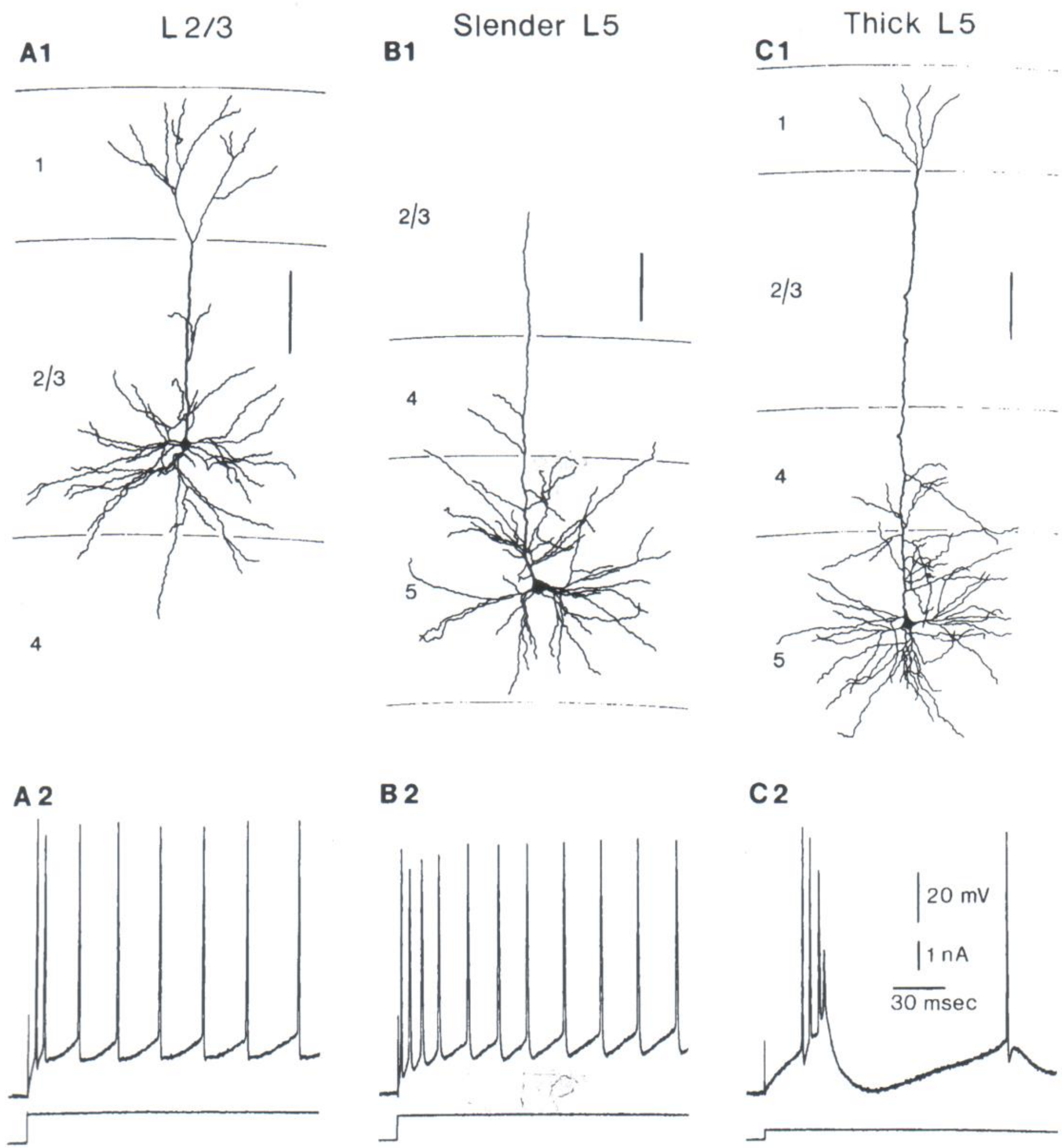
$$\frac{dW}{dt} = a(bV - W)$$



Izhikevich, IEEE Trans. Neural Netw. (2003)

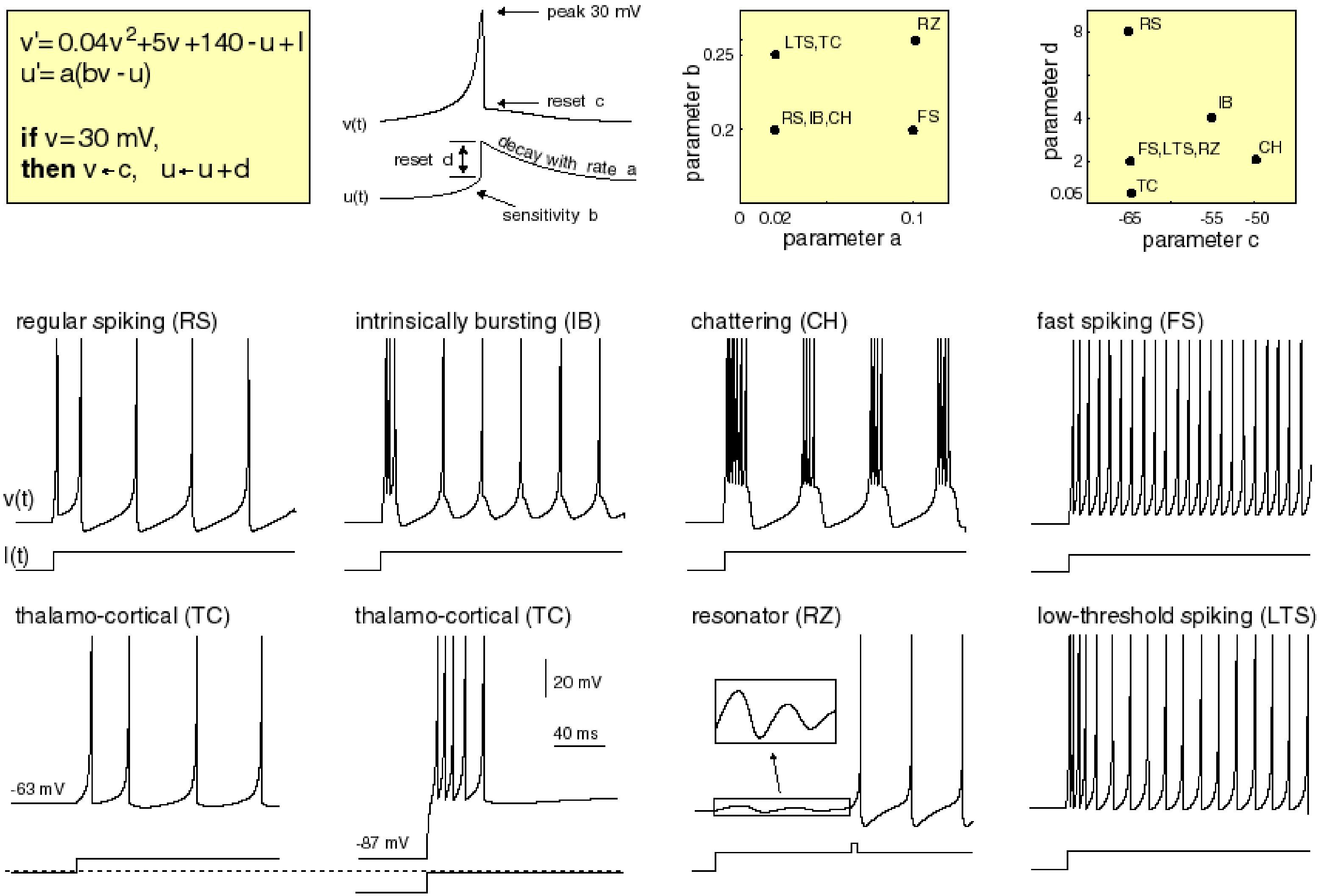
Lab

Excitatory pyramidal neurons at different cortical layers



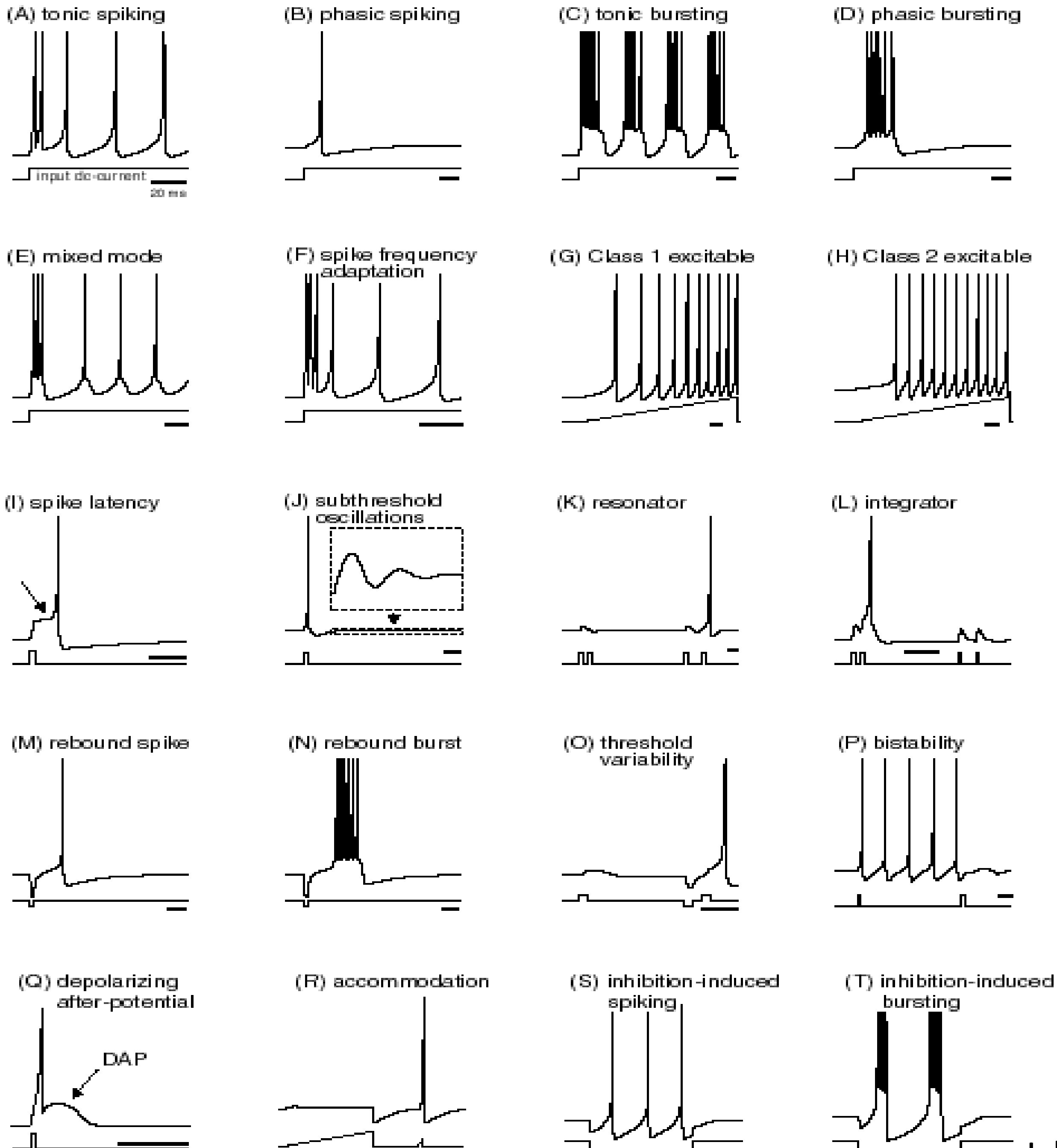
Mason and Larkam (1990)

Adaptive quadratic integrate-and-fire model or Izhikevich model

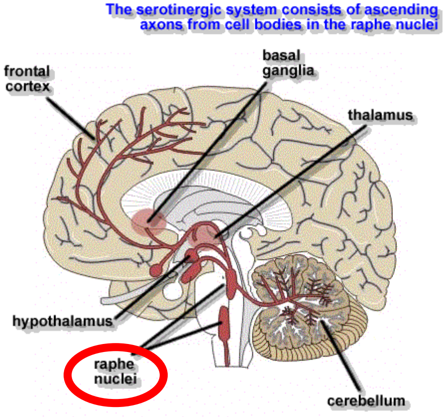


http://www.izhikevich.org/publications/whichmod.htm

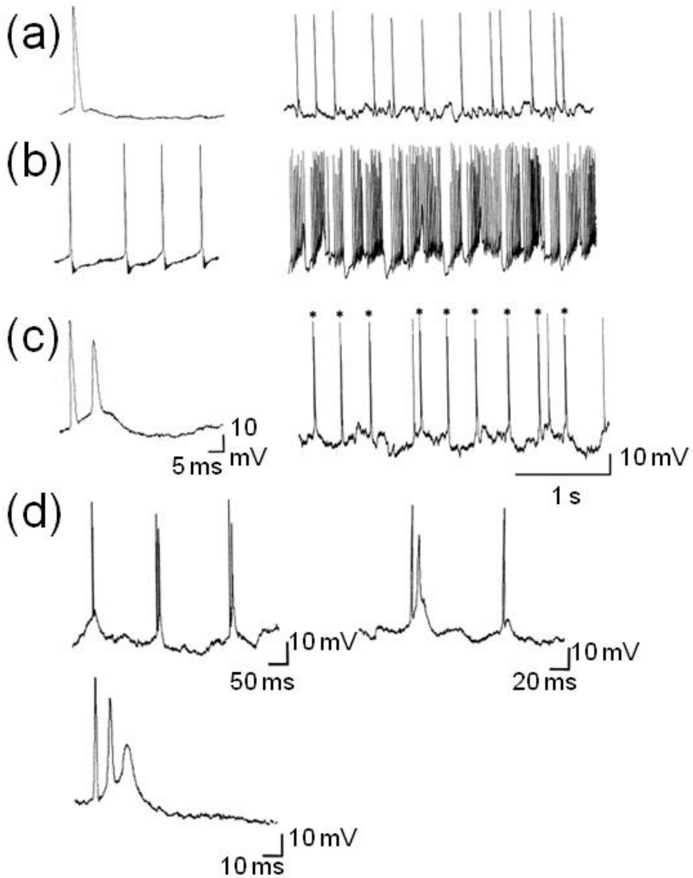
Izhikevich (2003)

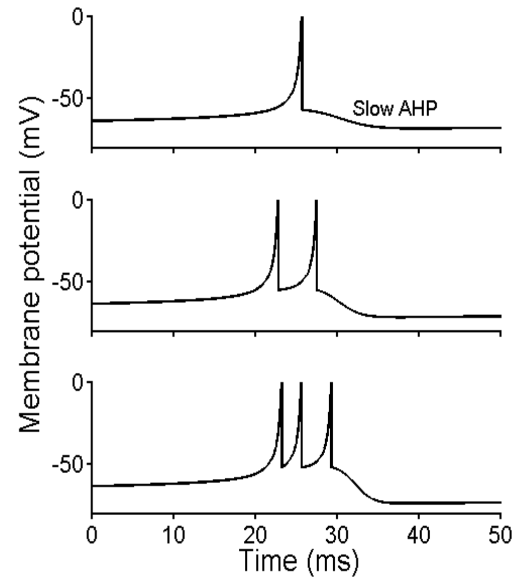


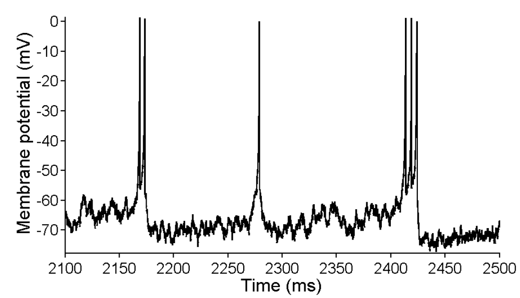
Izhikevich (2004)



Example: Modelling serotonin neurons using aQIF model

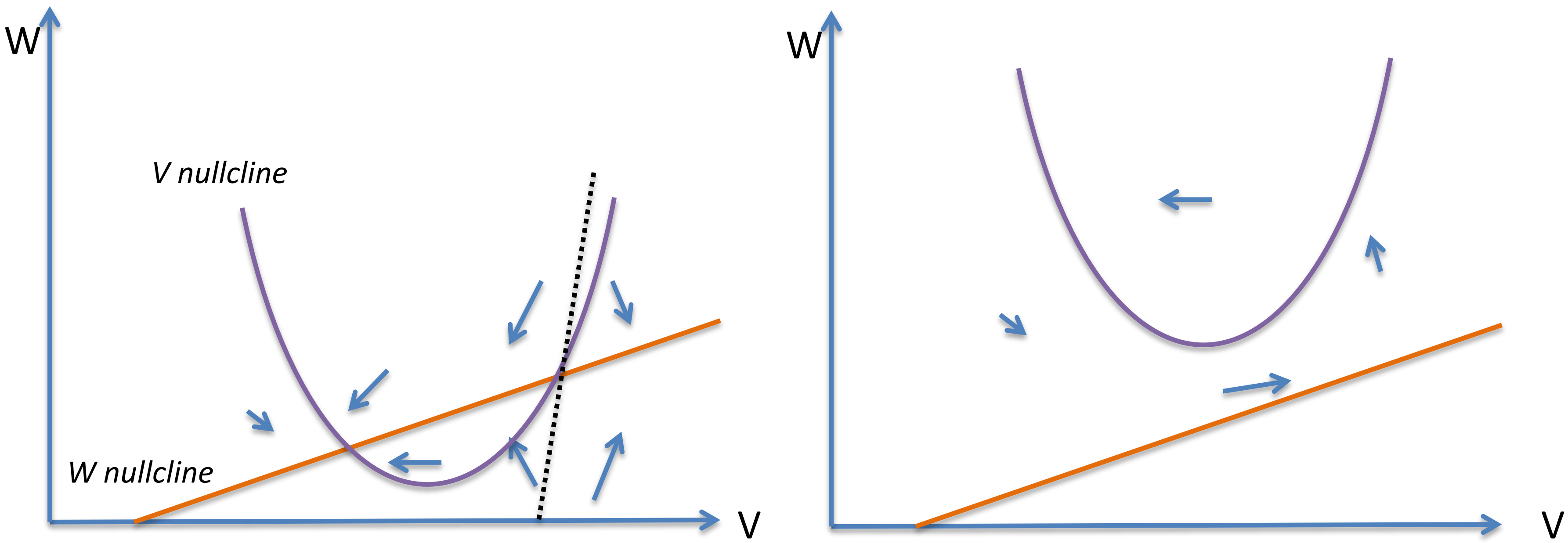


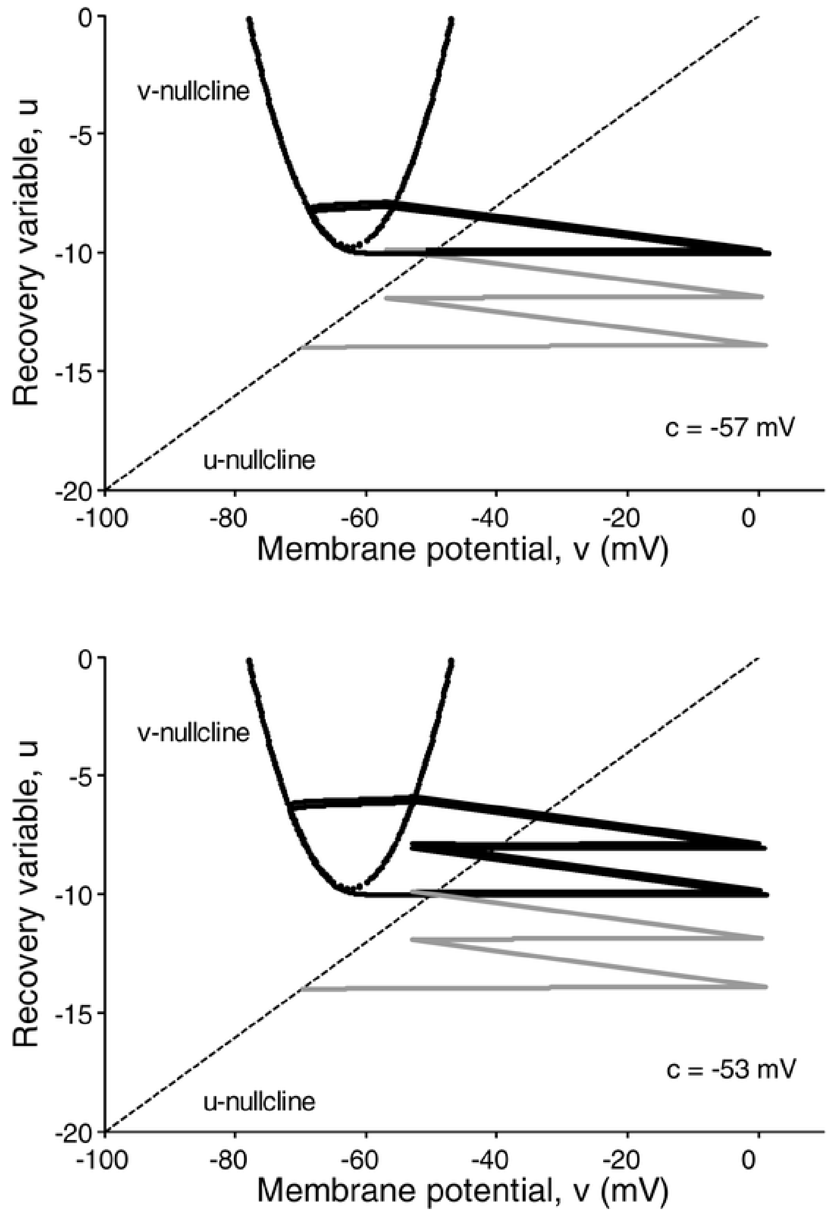




Wong-Lin et al. IJCNN (2011); Wong-Lin et al., Neural Netw. (2012)

Phase planes (portraits)

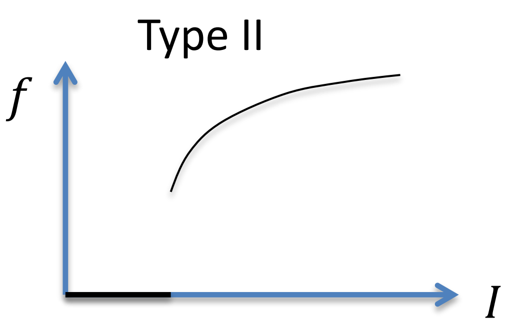


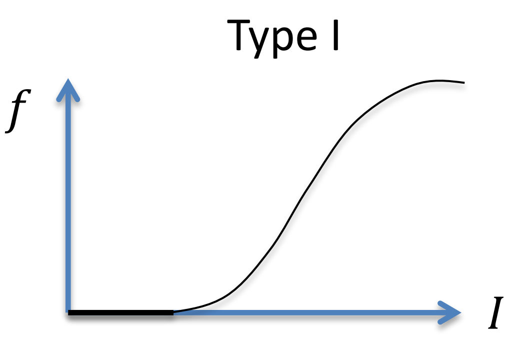


Wong-Lin et al. (2011)
IJCNN Best Paper Award

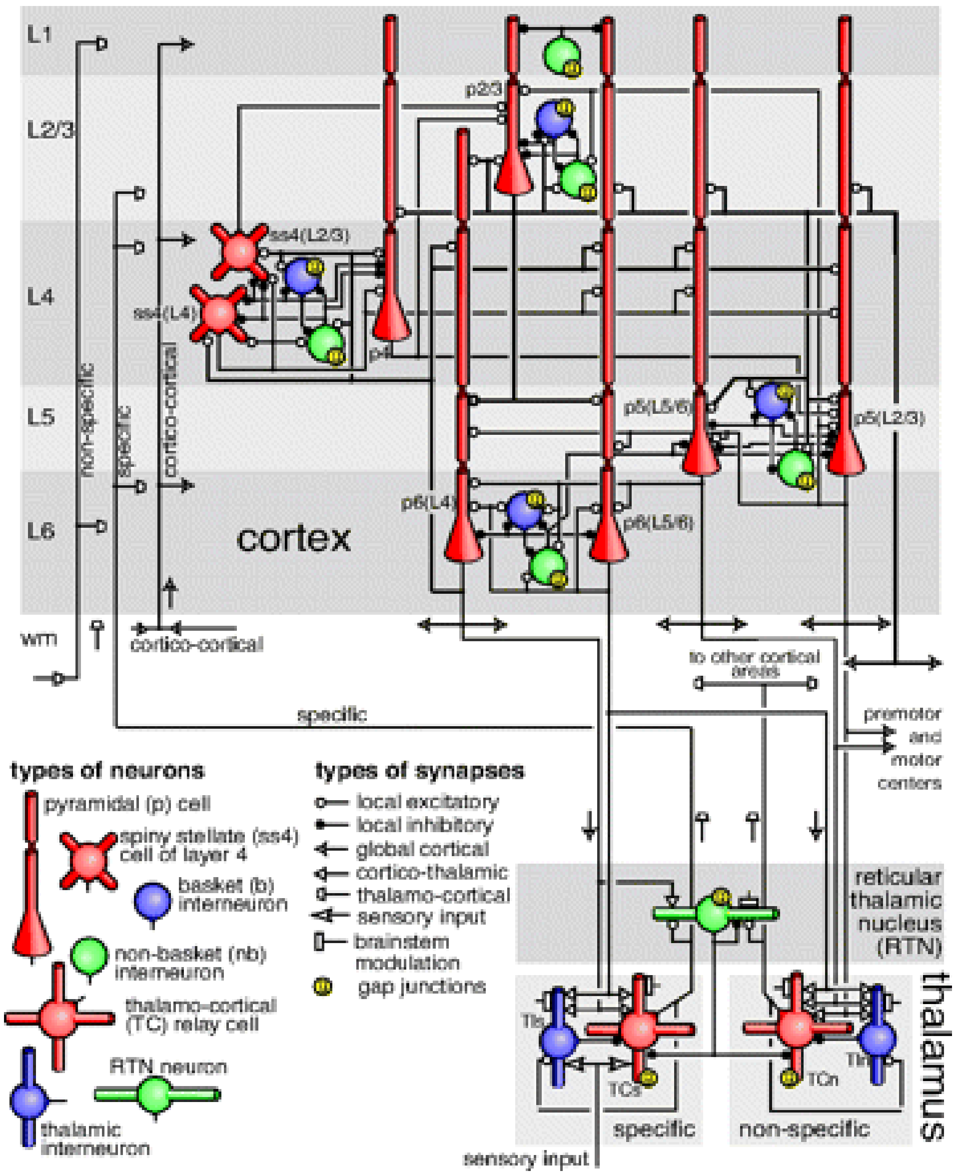
Phase portraits for producing spike singlets and spike doublets at c=-53 and -57 mV. I=6.5. Sharp lines constitute the spikes in the model. Nullclines were plotted by setting each dynamical equations and to be zero and solving algebraically. Bold black (gray) lines: trajectories for tonic (transient) spiking. Initial conditions at (v,u) = (-65, -13).

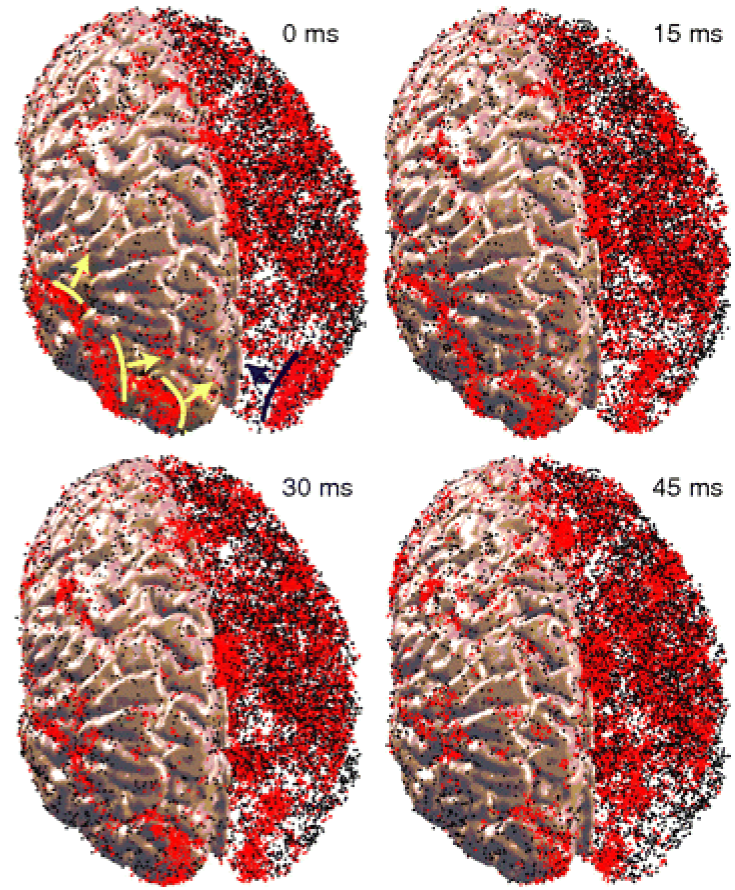
Captures both Type I and II behaviours depending on model parameters





Large-scale model of the thalamocortical network model





Izhikevich and Edelman (2008)

http://www.youtube.com/watch?v=843G1WDnmAU

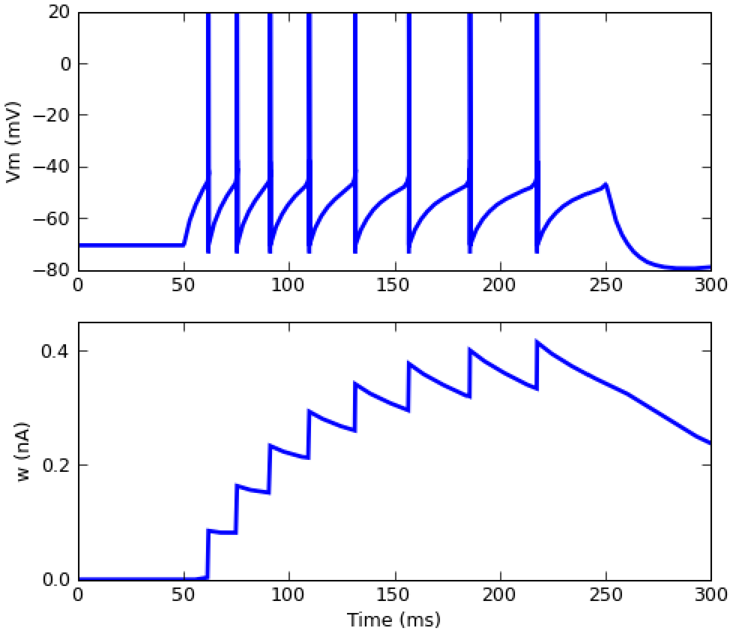
Abuhassan et al. (2013)

Adaptive exponential integrate-and-fire (AdEx) neuronal model

Similar model but more realistic spike form than adaptive QIF (Izhikevich model):

$$C\, dV/dt = -g_L(V-E_L) + g_L \Delta_T \exp((V-V_T)/\Delta T) - W + I$$

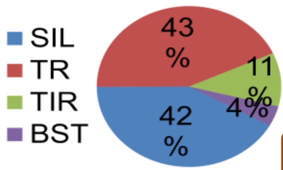
$$\tau_w\, dW/dt = a(V-E_L) - W$$

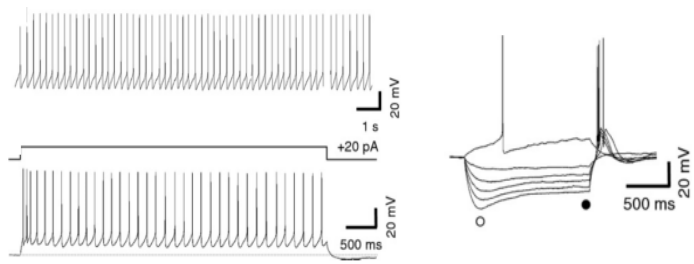
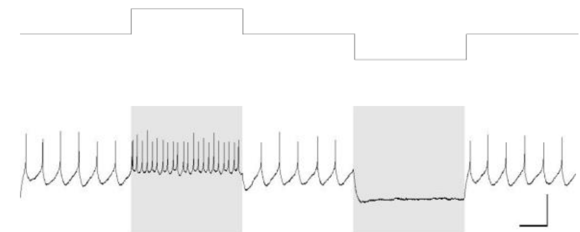
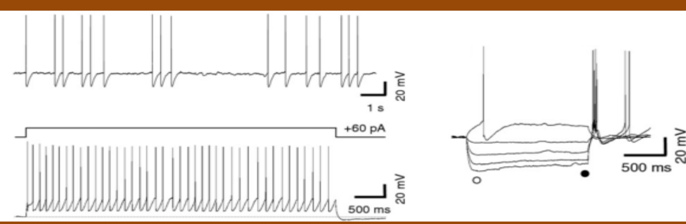
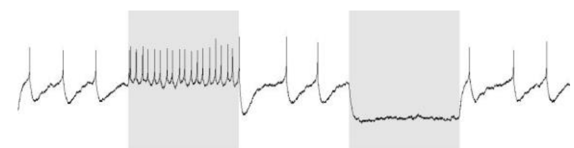
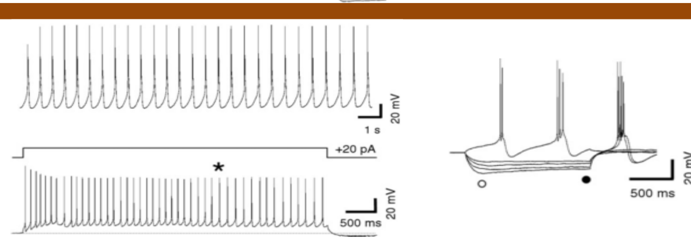
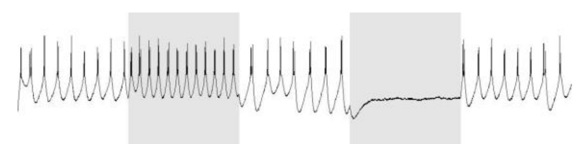
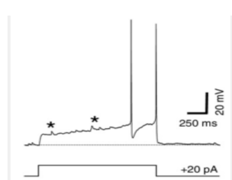
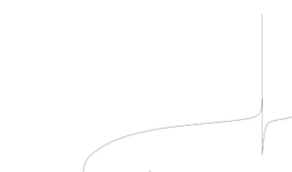


Overall, very similar behaviour as aQIF, but the spikes look more realistic (~exponential)

http://www.scholarpedia.org/article/Adaptive_exponential_integrate-and-fire_model

Spiking neuronal models in the limbic system - lateral habenula. *Laviale et al. (2012; 2013)*



	Electrophysiology	Simulation
Tonic Regular (TR)		
Tonic Irregular (TIR)		
Bursting (BST)		
Neuro-glialform Cells		

Integrate-and-fire neuronal models

$$\begin{aligned} C\,dV/dt &= dQ/dt \\ &= I(t,V) \\ &= F(V) + G(V)I(t) \end{aligned}$$

Generalized integrate-and-fire neuronal model

E.g. for the QIF model

$$\begin{aligned} C\,dV/dt &= F(V) + G(V)I(t) \\ &= F(V) + I, \text{ where } F(V) = V^2 \end{aligned}$$

Lapicque (1907); Review by Brunel and van Rossum (2007)

Conductance-based models: Additional currents

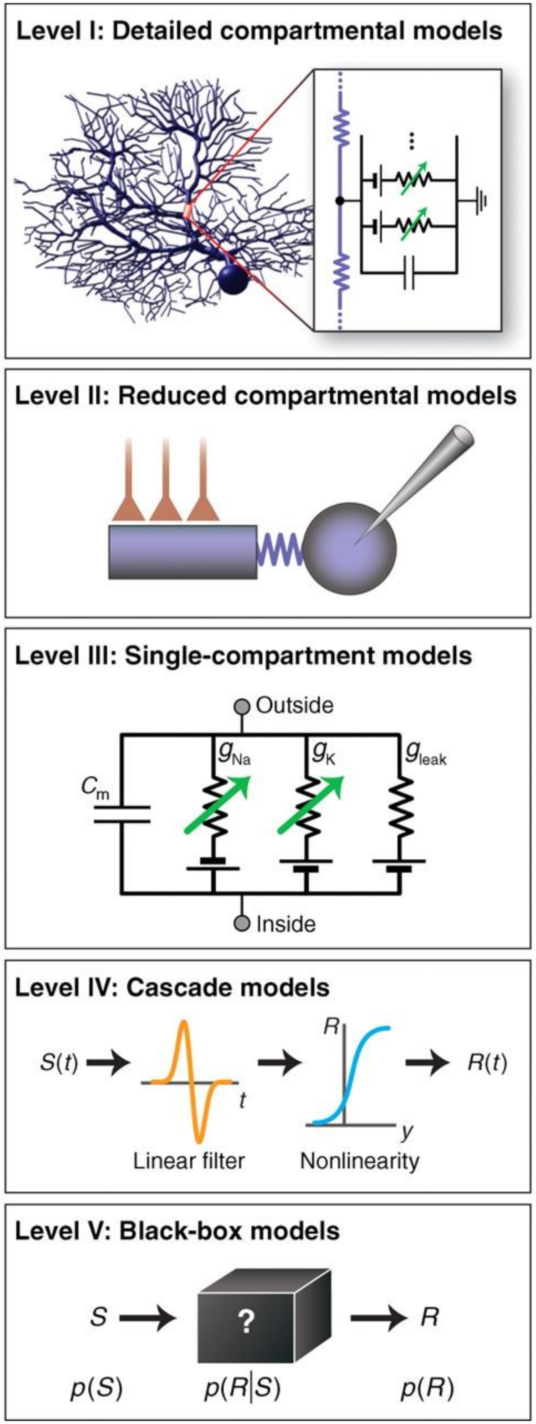
The Hodgkin-Huxley type model belongs to the wider class of conductance-based neuronal models where the conductances are explicitly modelled.

There are many other different types of conductances and its associated currents found in experiments (e.g. calcium-related), which can modulate the way a neuron spikes, particularly making the model more “active” due to the “active” channels.

Can also incorporate these various currents into integrate-and-fire neuron models to produce richer and biologically accountable neuronal behaviours.

Which model?

Depends on the question you want to address and availability of data.

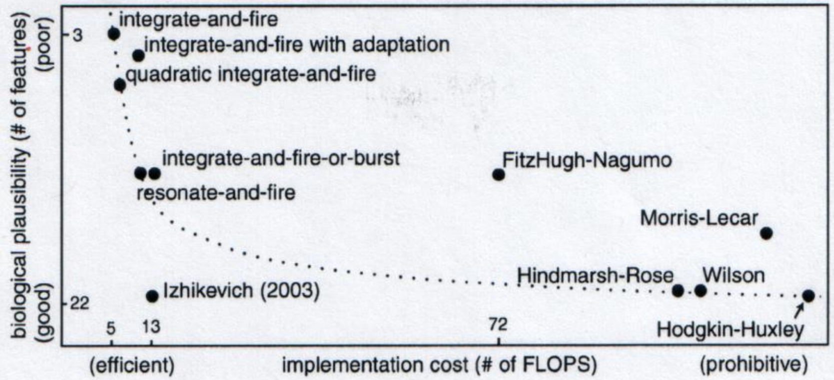


Herz et al., Science (2006)

Which model?

Depends on computational efficiency or accuracy, or both.

Izhikevich (2004)



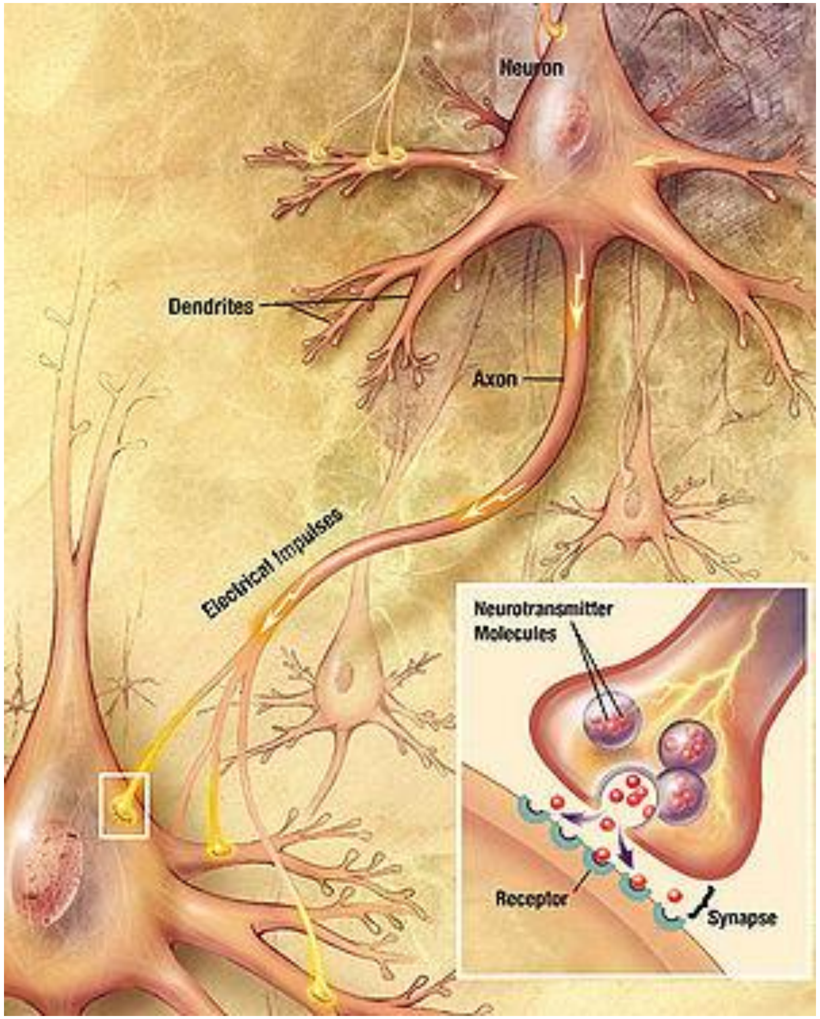
Models	biophysically meaningful	tonic spiking	phasic spiking	tonic bursting	phasic bursting	mixed mode	spike frequency adaptation	class 1 excitable	class 2 excitable	spike latency	subthreshold oscillations	resonator	integrator	rebound spike	rebound burst	threshold variability	bistability	DAP	accommodation	inhibition-induced spiking	inhibition-induced bursting	chaos	# of FLOPS
integrate-and-fire	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	5
integrate-and-fire with adapt.	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-	10
integrate-and-fire-or-burst	-	+	+		+	-	+	+	-	-	-	-	+	+	+	-	+	+	-	-	-		13
resonate-and-fire	-	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+	+	-	-	+	10
quadratic integrate-and-fire	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	+	-	-	-	-	-	7
Izhikevich (2003)	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	13
FitzHugh-Nagumo	-	+	+	-		-	-	+	-	+	+	+	-	+	-	+	+	-	+	+	-	-	72
Hindmarsh-Rose	-	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	120
Morris-Lecar	+	+	+	-		-	-	+	+	+	+	+	+	+		+	+	-	+	+	-	-	600
Wilson	-	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+				180
Hodgkin-Huxley	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	1200

Fig. 2. Comparison of the neuro-computational properties of spiking and bursting models; see Fig. 1. "# of FLOPS" is an approximate number of floating point operations (addition, multiplication, etc.) needed to simulate the model during a 1 ms time span. Each empty square indicates the property that the model should exhibit in principle (in theory) if the parameters are chosen appropriately, but the author failed to find the parameters within a reasonable period of time.

Hooking up spiking neurons with synapses

– to form a network of spiking neurons

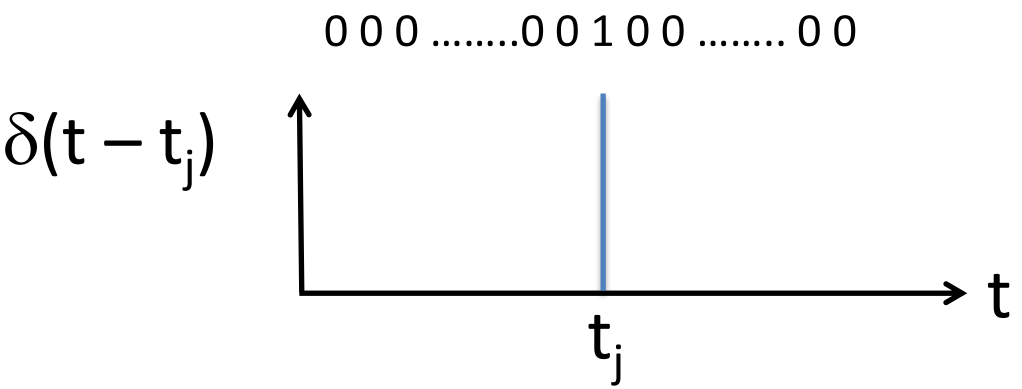
Chemical synapse

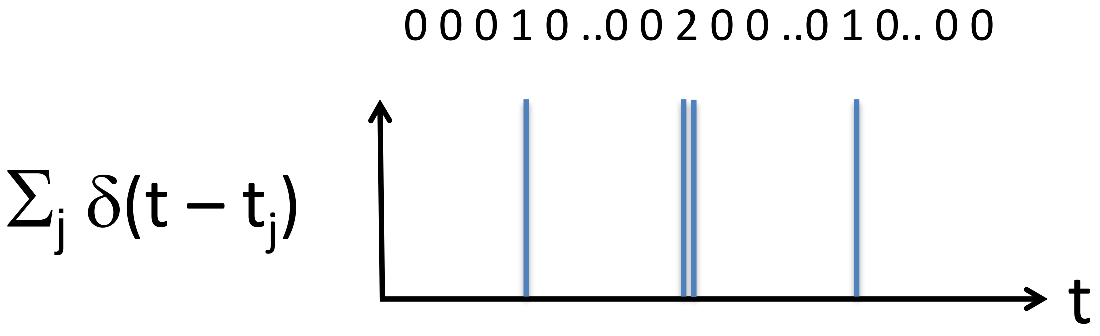


http://www.youtube.com/watch?v=LT3VKAr4roo&feature=related

Using (Dirac) delta function to represent an abstract spike

$\delta(t - t_j) = 1$ when $t = t_j$, otherwise 0





http://en.wikipedia.org/wiki/File:Dirac_function_approximation.gif

Instantaneous synapses – the simplest synapse

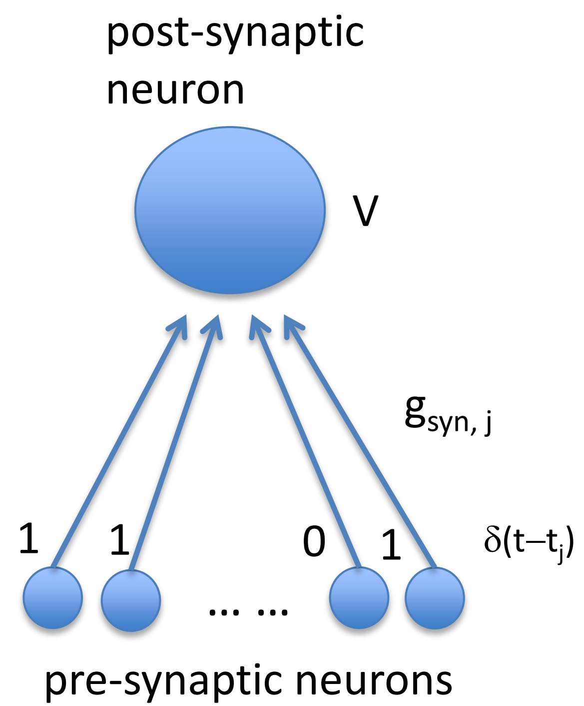
For a single (post-synaptic) neuron, just sum up the (pre-synaptic) spikes

$$CdV/dt = -\, g_L(V - V_L) + I_{app} + I_{syn}$$

where the synaptic current

$$I_{syn} = \Sigma_j\, g_{syn,\, j}\, \delta(t - t_j)$$

is the sum weighted sum of incoming spikes. Treat *synaptic conductance g_{syn}* like the typical synaptic/connection weight/strength. $g_{syn} > 0$ if synapse is excitatory, and < 0 if inhibitory.

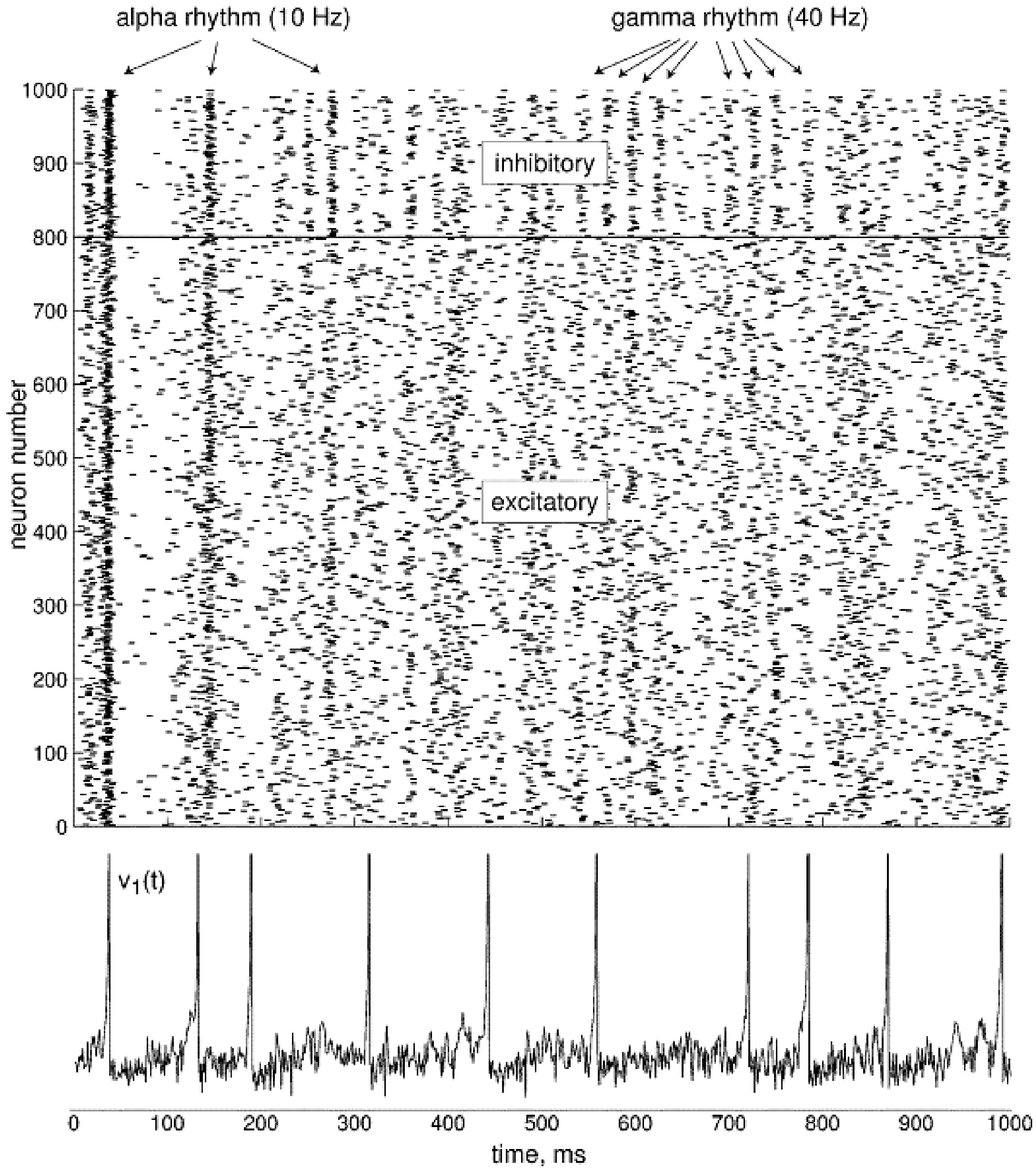


An approximation for fast (chemical) synapses

Spiking neuronal networks with instantaneous synapses

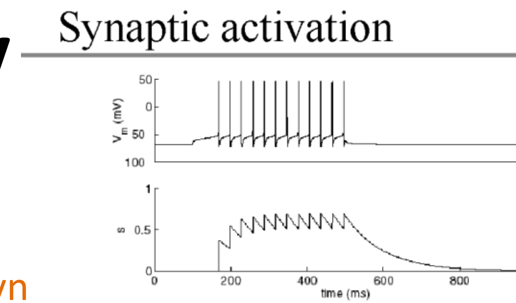
Raster spike diagram

Activity time course of one neuron (neuron 1) selected from network



Lab

Chemical synapse with decay



$$C dV/dt = -\, g_L(V - V_L) + I_{app} - I_{syn}$$

where the synaptic current

Reversible potential, can range from ~ 0 to -90 mV

$$I_{syn} = \Sigma_j\, g_{syn,\,j}\, s_j(t)\, \underbrace{(V - E_{rev})}_{\text{“driving force”}}$$

And s is the *synaptic gating variable* (of the channel), which follows an instantaneous “kick” (opening) after a pre-synaptic spike, followed by a decay (closing):

$$ds_j/dt = -\, \underbrace{s_j/\tau_s}_{\text{decay}} + \underbrace{\alpha}_{\text{“kick size”}}\, \Sigma_j\, \delta(t - t_j)$$

Thus the synapse acts as temporal filters

Chemical synapses with rise and decay

- more realistic and good model for slow synapses

$$C dV/dt = -g_L(V - V_L) + I_{app} - I_{syn}$$

where the synaptic current

$$I_{syn} = \Sigma_j \, g_{syn,j} \, s_j(t) \, (V - E_{rev})$$

And the *synaptic gating variable* (of the channel), which follows a finite rise time (opening) after a pre-synaptic spike, followed by a decay (closing):

$$dx_j/dt = -x_j/\tau_{rise} + \Sigma_j \, \delta(t - t_j)$$
$$ds_j/dt = -s_j/\tau_{decay} + \alpha \, x_j \, (1 - s_j)$$

or

$$\Delta V \sim \alpha \, [\exp(-\frac{t-t_j}{\tau_{rise}}) - \exp(-\frac{t-t_j}{\tau_{decay}})]$$

Synaptic delay

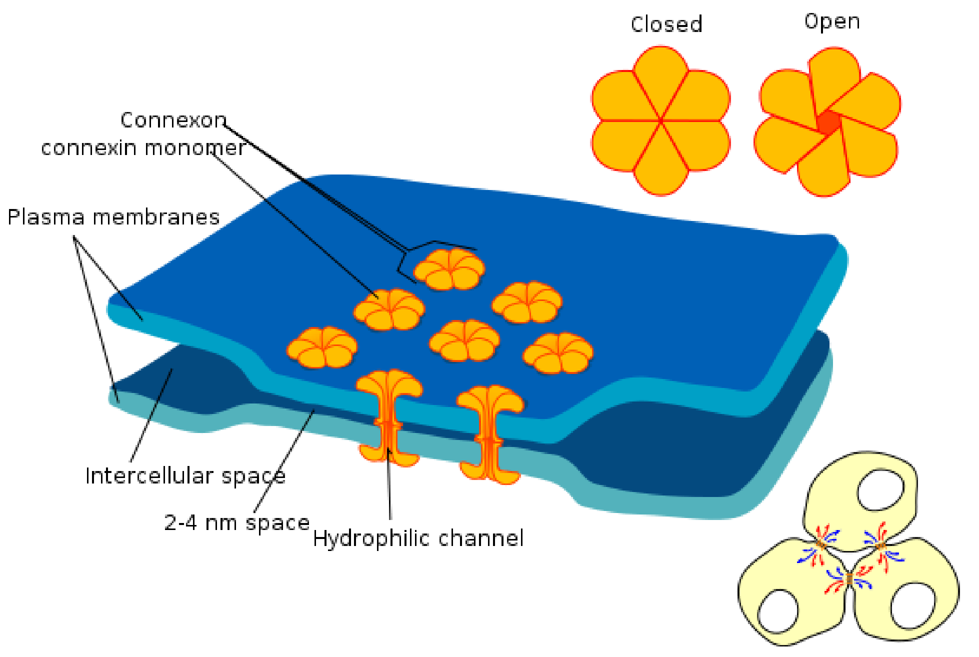
Realistically, it takes time for a spike to travel through an axon and affect another neuron

$$I_{syn} = \sum_j g_{syn,\,j}\, \delta(t - t_j - \Delta_j)$$

where Δ is the delay (~ 0.1 – 50 ms) e.g. depending on the connection distance

Note: Connection delays can easily lead to oscillatory behaviour

Electrical synapses (gap junctions) - instantaneous



$$CdV/dt = -g_L(V - V_L) + I_{app} + I_{gap}$$

where $I_{gap} = g_{gap}(V - V_j)$ for a single synapse

Based on classical NN, NN are the most useful when there is learning.

How can we model synaptic changes (i.e. plasticity) in SNN to allow learning?

– Tune in next week …

Key points and summary

- Appreciate the implication of encoding information in spike times rather than firing rates. But can convert from spiking to firing rates (transfer/response function)
- How a single integrate-and-fire (esp. IF, LIF, QIF) neuronal model can be implemented, and how this class of neurons are approximation of more realistic models or mechanisms.
- Relations among the various IF models. What are their similarities and differences?
- Differences between IF models and classical neural models?
- Understand how to explicitly model various synapses – instantaneous (as an approximation), chemical and electrical.
- Applications? – More next week. Require a network of neurons. Tune in next week.

Readings, practising and revising

- Nicholas Brunel, “Modeling Point Neurons: From Hodgkin-Huxley to Integrate-and-Fire”, Chapter 7, In: Computational Modeling Methods for Neuroscientists, MIT 2009.
- Dayan and Abbott book, chapter 5.1 – 5.4. (Available on Blackboard)
- Izhikevich “Dynamical Systems in Neuroscience” book. Especially Chapter 8.
- Sterratt et al. “Principles of Computational Modelling in Neuroscience” book. Chapter 8.

- Izhikevich, Simple Model of Spiking Neurons, IEEE Trans. Neural Netw. (2003)
- Izhikevich, Which Model to Use for Cortical Spiking Neurons? IEEE Trans. Neural Netw. (2004)
- Herz et al., Science (2006)
- Brunel and van Rossum (2007)

- Keep searching, thinking, and discussing with me regarding topics that interest you!
- Today’s lab (on 10th Feb) will be assessed (10% of overall module marks) through individual reports submitted by the end of the lab.