

Neural Networks Pt. 4 Spiking Neuron Models

Lecture 9 I400/I590

Artificial Life as an approach to Artificial Intelligence

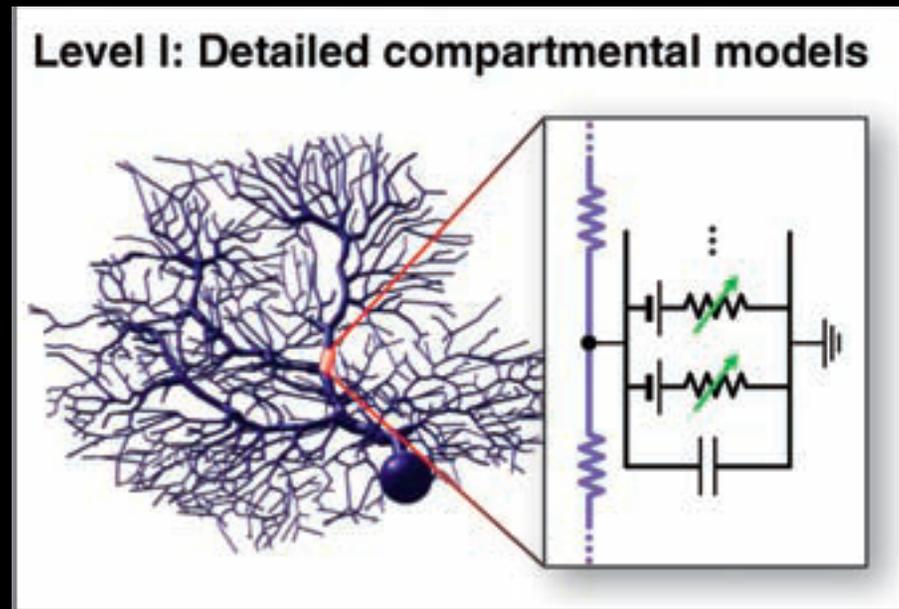
Larry Yaeger

Professor of Informatics, Indiana University

Brain Modeling—Neurons

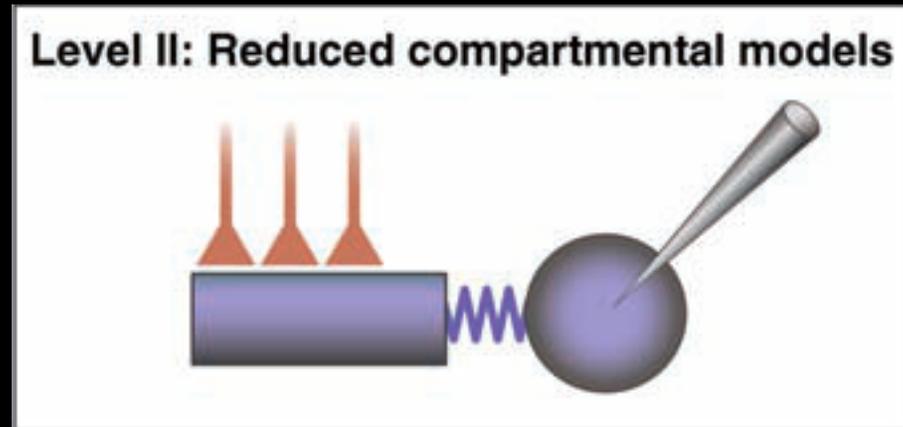
- There is a tradeoff between detail and speed
- Modeling always entails a balance between level of abstraction and computational tractability
- Ultimately we need to look at large networks of neurons, yet both single-neuron and whole-network behaviors may hinge on details of individual components
- One way of partitioning models of individual neurons...

Level I: Detailed compartmental models



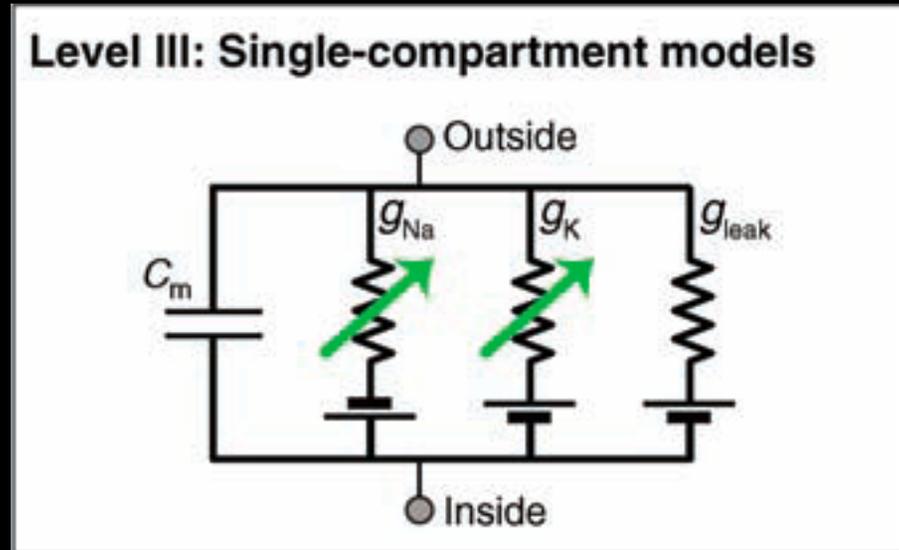
- Morphology, spatial structure are realistic
- Discretized dendrites require numerical integration
- Asymmetric voltage attenuation (Rall "cable theory")
- Supports dendritic computation and axonal signal filtering (coincidence detection, motion detection, gain modulation)
- Mathematical analysis intractable
- Computationally expensive (single cell mostly)

Level II: Reduced compartmental models



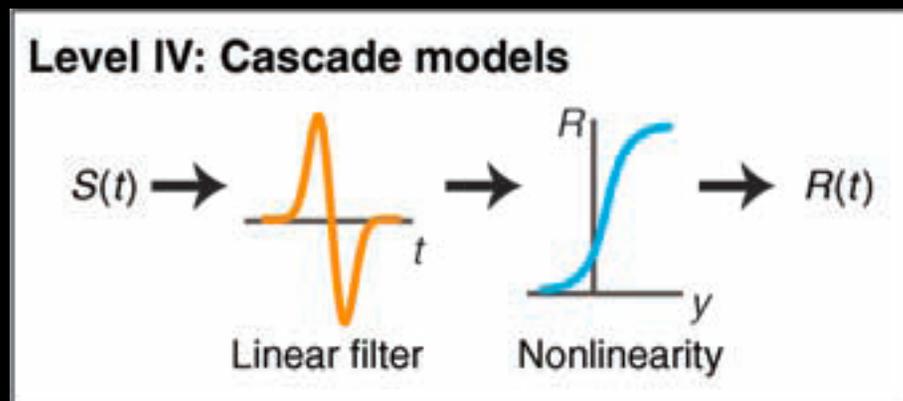
- Sufficient for some somatodendritic interactions
- May retain multiple time scales
- May retain dendritic interactions
- Can model temporal aspects of learning and spiking
- Have been used to model short term memory, cortical gamma oscillations, slow-wave sleep oscillations
- Lose spatial fidelity
- Still computationally expensive (max around 3,000 cells)

Level III: Single-compartment models



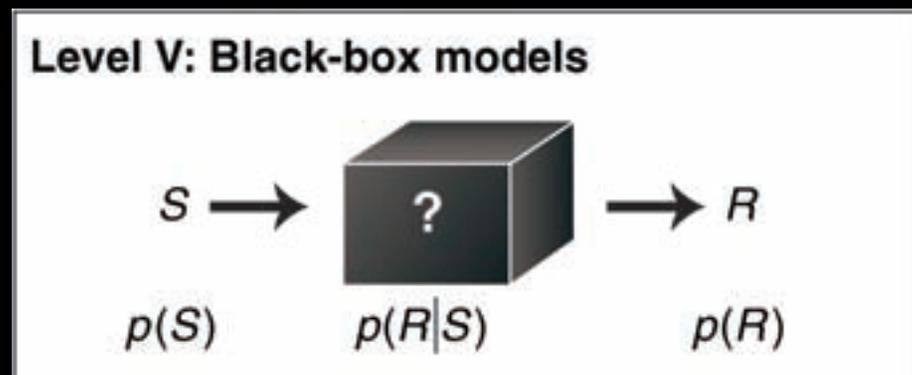
- Focus on ionic currents' production of subthreshold and spiking voltage traces
- Is itself a broad class (Hodgkin-Huxley, Leaky-Integrate-and-Fire, Izhikevich)
- Model phasic, chattering, tonic, and adaptive spiking, relating cell characteristics to observed spike trains
- Capture "synaptic noise" effects on probabilistic spiking, neuron sensitivity, network stability
- Computationally tractable (100,000s to 10^{11} neurons)

Level IV: Cascade models



- Concatenation of linear filters, nonlinear transformations, and random processes
- Includes standard "summing and squashing" models
- Successfully models stimulus-response experimental data
- Used to model visual system, simultaneous adaptation to mean light intensity and light contrast, other features
- Even though rate-based, may incorporate timing information, stochastic firing, and model spike trains
- Ignore dynamics that do affect experimental outcomes
- Yet in specific cases yield accurate information-theoretic description of neuronal responses

Level V: Black-box models

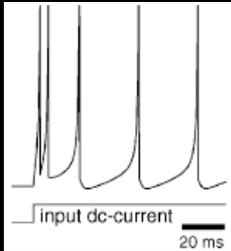


- Model signal-processing characteristics with no consideration of physical machinery
- May reveal general operating points, how inputs modify responses
- Can take $p(R|S)$ directly from experimental data
- Have revealed that sensory neurons operate close to their information-theoretic limit, and how neurons may shift their input-output curves to achieve this
- Good for quantifying some aspects of neuron and network behavior, but difficult to relate to underlying physical mechanisms

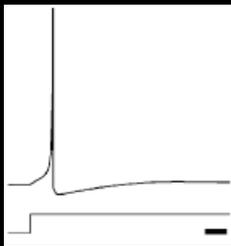
Finding a balance

- "A good theoretical model of a complex system should be like a good caricature: it should emphasize those features which are most important and should downplay the inessential details. Now the only snag with this advice is that one does not really know which are the inessential details until one has understood the phenomena under study."
 - Shriki *et al*, *Neural Comput.* 15, 1809 (2003)
- "Brain function ... relies on the interplay of hundreds to billions of neurons that are arranged in specialized modules on multiple anatomical hierarchies. Even today, it remains unclear which level of single-cell modeling is appropriate to understand the dynamics and computations carried out by such large systems. However, only by understanding how single cells operate as part of a network can we assess their coding and thus the level of detail required for modeling."
 - Herz *et al*, *Science* 314, 80-85 (2006)

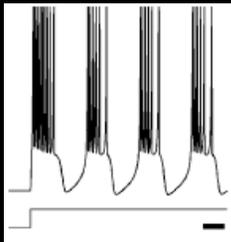
20 Ways to Spike Your Neuron



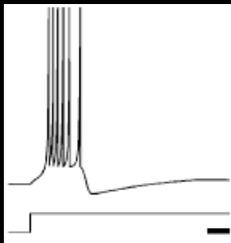
1. Tonic spiking - periodic spikes in response to a step in input current



2. Phasic spiking - single spike in response to a step in input current

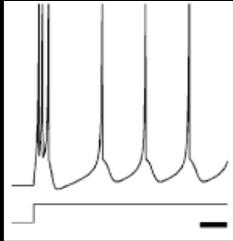


3. Tonic bursting - periodic bursts of spikes in response to a step in input current

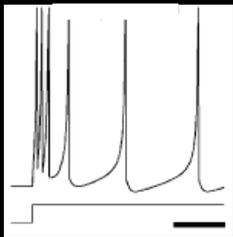


4. Phasic bursting - single burst of spikes in response to a step in input current

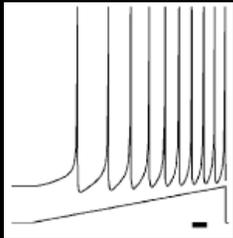
20 Ways to Spike Your Neuron



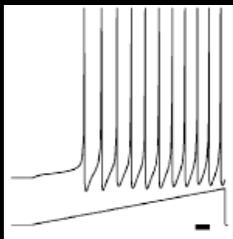
5. Mixed mode - initial burst followed by periodic spiking



6. Spike frequency adaptation - spike frequency decreases over time

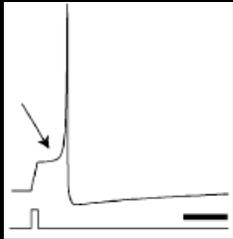


7. Class 1 excitable - fire at low (above threshold) current and spike frequency is proportional to current

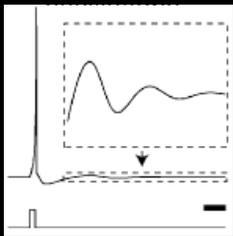


8. Class 2 excitable - requires higher current to fire, then fires at constant, moderate frequency

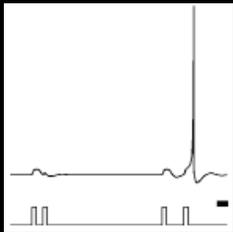
20 Ways to Spike Your Neuron



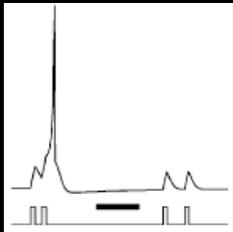
9. Spike latency - spike delay is inversely proportional to current; spike timing encodes strength of input



10. Subthreshold oscillations - membrane potential oscillates after a spike or with subthreshold input

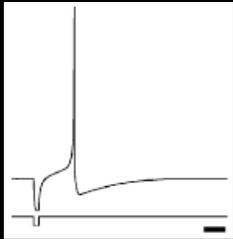


11. Resonator - only spikes when inputs resonate with subthreshold oscillation frequency; can implement frequency modulation & multiplexing

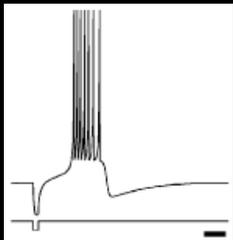


12. Integrator - without subthreshold oscillation, can integrate inputs, prefer high frequency input, perform (near) coincidence detection

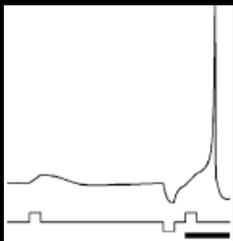
20 Ways to Spike Your Neuron



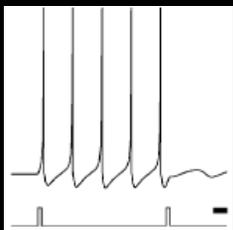
13. Rebound spike - spike upon release from inhibitory inputs



14. Rebound burst - burst of spikes upon release from inhibitory inputs

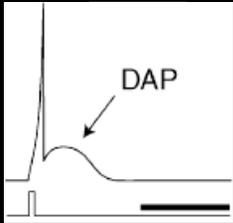


15. Threshold variability - inhibition lowers threshold; excitation raises threshold; same input may be subthreshold or superthreshold



16. Bistable - switch between resting and tonic spiking (or bursting) states; timing of the "off" signal can matter

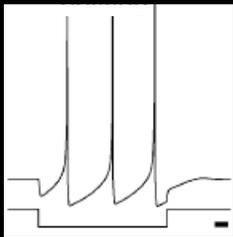
20 Ways to Spike Your Neuron



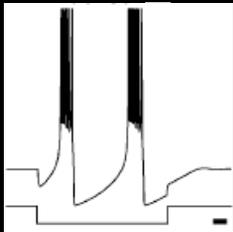
17. Depolarizing after-potential (DAP) - may experience a period of superexcitability after a spike, instead of a refractory period



18. Accommodation - slow increase in current gives neuron time to accommodate; smaller, but sharper current increase may cause spike



19. Inhibition-induced spiking - "bizarre"; current activates the h-current and deinactivates calcium T-current, leading to tonic spiking



20. Inhibition-induced bursting - similar to above; may play role in sleep rhythms

How can we model all of these?

- No model should (or can) exhibit all of these response patterns with a single set of parameters
 - Some of these patterns are mutually exclusive (a neuron cannot be an integrator and a resonator at the same time)
- However, it is possible to achieve all of these behaviors using different parameter settings in a simple neural model involving just four parameters, due to Izhikevich
- Other neuron models can also use adjustment of parameters to achieve some subset of these behaviors
- An optimal model will be able to capture all of these behaviors *and* be computationally efficient

11 Ways to Model Your Neuron

Throughout:

$v \equiv$ membrane potential

$v' \equiv$ derivative of v w.r.t. time

$I \equiv$ input current

All parameters ($a, b, c, \text{etc.}$) are chosen so that
 v is in mV and time is in msec

An integration time step is chosen so as to provide
reasonable numerical accuracy in fixed-step
first order Euler method

11 Ways to Model Your Neuron

1. (Leaky) Integrate & Fire (I&F)

$$v' = I + a - b v$$

if $v \geq v_{\text{thresh}}$ then fire and reset $v = c$

- Class 1 excitable
- Fires tonic spikes at fixed frequency
- Integrator
- Four floating-point operations, plus one compare, per ms
- Fast, but extremely limited repertoire of behaviors
 - No phasic spiking, bursting, rebound responses, threshold variability, bistability, autonomous chaotic dynamics, or latencies
 - Only 3 of the 20 identified behaviors are modeled

11 Ways to Model Your Neuron

2. Integrate & Fire with Adaptation (I&FA)

$$v' = I + a - b v + g (d - v)$$

if $v \geq v_{\text{thresh}}$ then fire and reset $v = c$

$$g' = (e \delta(t) - g) / \tau$$

- Like I & F, but adapts firing rate over time
- 10 floating-point operations, plus compare, per ms
- Reasonably fast, but still a limited repertoire of behaviors (5 of 20)

11 Ways to Model Your Neuron

3. Integrate & Fire or Burst (I&FB)

$$v' = I + a - b v + g H(v - v_h) h (v_T - v)$$

if $v \geq v_{\text{thresh}}$ then fire and reset $v = c$

$$h' = \begin{cases} -h / \tau^- & , \text{ if } v > v_h \\ (1 - h) / \tau^+ & , \text{ if } v < v_h \end{cases}$$

- h describes the inactivation of the calcium T-current
- Remaining parameters describe T-current dynamics
- H is the Heaviside step function
- Between 9 and 13 operations per ms (depending on v)
- Adds bursting, rebound spiking and bursting, bistability, and DAP
- 9 to 11 behaviors still unmodeled

11 Ways to Model Your Neuron

4. Resonate & Fire (R&F)

$$z' = I + (b + i\omega) z$$

if $\text{Im}(z) \geq a_{\text{thresh}}$ then fire and reset $z = z_0(z)$

- $\text{Real}(z)$ is the membrane potential, v
- b , ω , and a_{thresh} are parameters
- $z_0(z)$ is an arbitrary function describing the activity-dependent after-spike reset
- 10 operations, plus compare, per ms
- No bursting, but adds Class 2 excitable, subthreshold oscillations, resonator, rebound spike, bistability, DAP, accommodation, and chaotic
- 9 behaviors unmodeled

11 Ways to Model Your Neuron

5. Quadratic Integrate & Fire (QI&F)

$$v' = I + a(v - v_{rest})(v - v_{thresh})$$

if $v \geq v_{peak}$ then fire and reset $v = v_{reset}$

- Canonical — any Class 1 excitable system described by smooth ODEs can be transformed into this form
- 7 operations, plus compare, per ms
- Adds threshold variability, bistability, and latency to I&F, but lacks bursting and 15 of the 20 behaviors

11 Ways to Model Your Neuron

6. Izhikevich spiking model (ISM)

$$v' = 0.04 v^2 + 5 v + 140 - u + I$$

$$u' = a (bv - u)$$

if $v \geq 30$ mv then has fired, so reset:

$$v = c$$

$$u = u + d$$

- u is a membrane recovery variable
 - Accounts for activation of K^+ ionic currents
 - Accounts for inactivation of Na^+ ionic currents
 - Provides negative feedback to v
- Constants chosen so that v is in mv and t is in ms
- 30 mv is peak, not threshold (threshold varies)
- 13 floating point operations, plus compare, per ms in most regimes
- Time step in chaotic domains may need to be smaller
- Produces all 20 behaviors with different parameters

11 Ways to Model Your Neuron

7. FitzHugh-Nagumo

$$\begin{aligned}v' &= a + b v + c v^2 + d v^3 - u \\u' &= \varepsilon (e v - u)\end{aligned}$$

- 18 floating point operations, per *step*
 - But due to necessity of simulating spike shape, four time steps per ms are required, hence...
- 72 operations per ms
- Can model many resonator neurons, but still misses 9 or 10 of the defined 20

11 Ways to Model Your Neuron

8. Hindmarsh-Rose

$$v' = u - F(v) + I - w$$

$$u' = G(v) - u$$

$$w' = (H(v) - w) / \tau$$

- F , G , and H are arbitrary functions
- In principle can model all 20 spiking behaviors, however finding these functions can be difficult
- Assuming the functions can be found and of polynomial degree 3 (best case)...
- 30 floating point operations, per *step*
 - But due to necessity of simulating spike shape, four time steps per ms are required
- 120 operations per ms
- Izhikevich was unable to find suitable functions for 3 of the 20 behaviors

11 Ways to Model Your Neuron

9. Morris-Lecar

$$\begin{aligned}C\dot{V} &= I - g_L(V - V_L) - g_{Ca}m_\infty(V) \\ &\quad \times (V - V_{Ca}) - g_Kn(V - V_K) \\ \dot{n} &= \lambda(V)(n_\infty(V) - n)\end{aligned}$$

$$\begin{aligned}m_\infty(V) &= \frac{1}{2} \left\{ 1 + \tanh \left[\frac{(V - V_1)}{V_2} \right] \right\} \\ n_\infty(V) &= \frac{1}{2} \left\{ 1 + \tanh \left[\frac{(V - V_3)}{V_4} \right] \right\} \\ \lambda(V) &= \bar{\lambda} \cosh \left[\frac{(V - V_3)}{(2V_4)} \right]\end{aligned}$$

- Consists of a membrane potential equation with instantaneous activation of Ca current and an additional equation giving slower K current
- Requires 12 parameters, but they are biophysically meaningful and measurable
- To produce tonic bursting requires additional equation, making it equivalent to Hodgkin-Huxley
- 60 floating-point ops per step, but requires $\tau = 0.1$ ms
- 600 ops per ms
- 6 to 8 behaviors unmodeled

11 Ways to Model Your Neuron

10. Wilson polynomial neurons

(Four differential equations)

- 45 floating-point ops per step, but requires $\tau = 0.25$ ms
- 180 ops per ms
- Can theoretically produce all 20 behaviors, but Izhikevich was unable to find parameters for 6 of them

11 Ways to Model Your Neuron

11. Hodgkin-Huxley

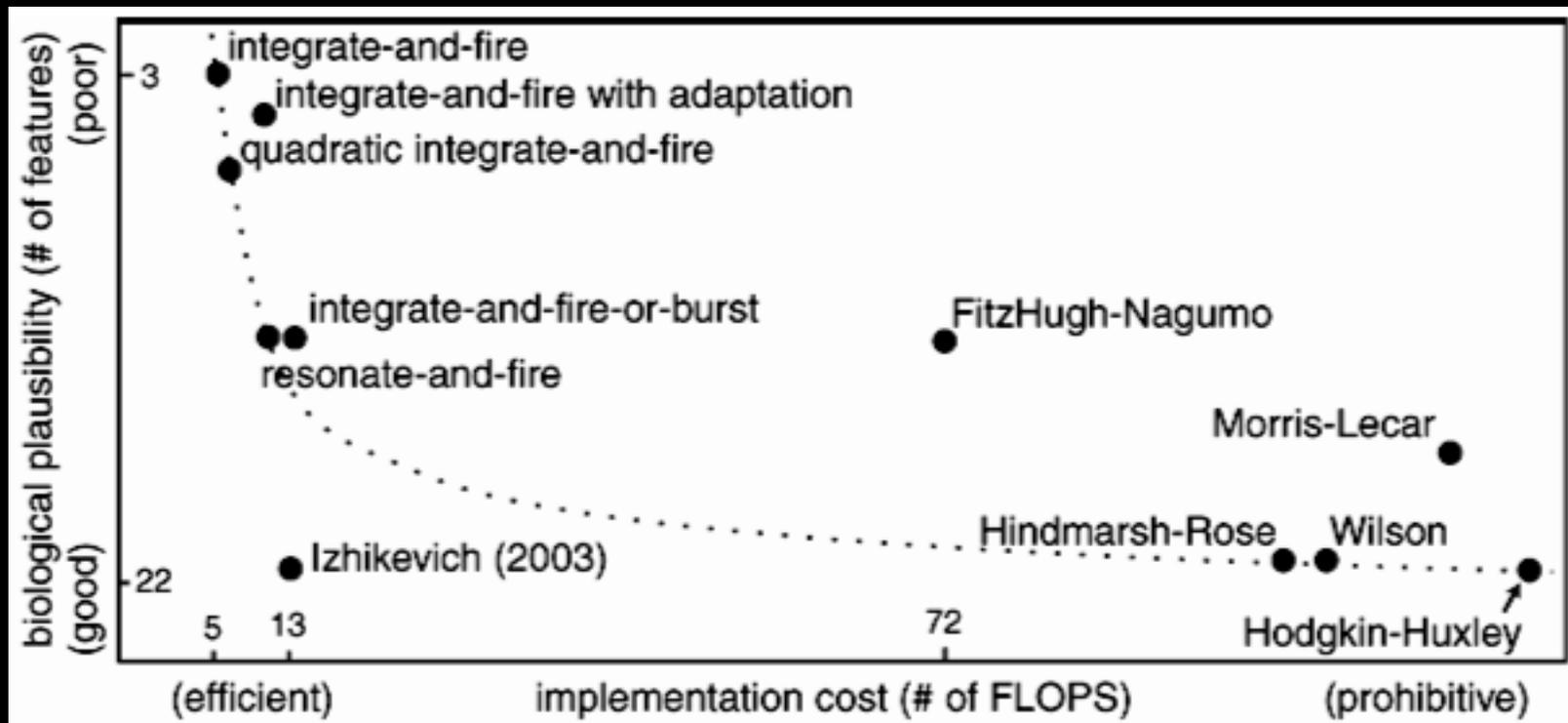
(Four equations)

- 10s of parameters, but all biophysically meaningful and measurable
- Describes membrane potential, activation of Na and K currents, and inactivation of Na current
- Original formulation produces limited set of behaviors, but tweaking parameters allows considerable flexibility
- 120 floating-point ops per step, but requires $\tau = 0.1$
- 1200 ops per ms
- Adjusting parameters can theoretically produce all 20 behaviors, but Izhikevich was unable to find parameters for 3 of them

Which model should we choose?

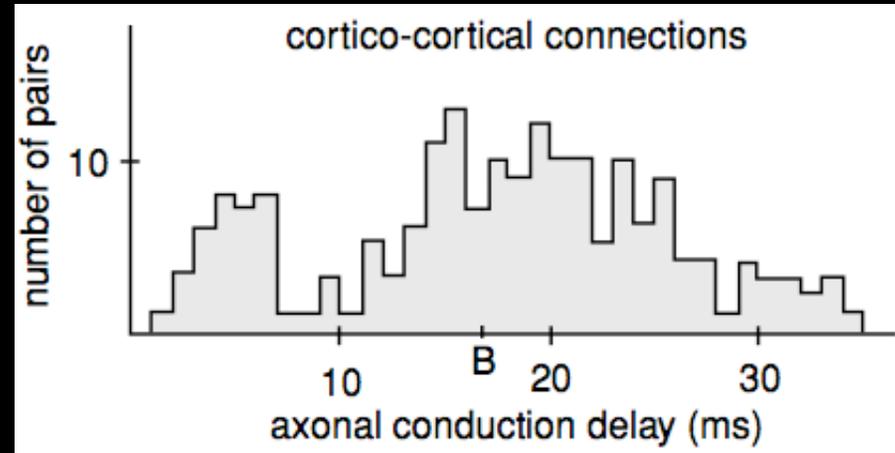
Models	biophysically meaningful	tonic spiking	phasic spiking	tonic bursting	phasic bursting	mixed mode	spike frequency adaptation	class 1 excitable	class 2 excitable	spike latency	subthreshold oscillations	resonator	integrator	rebound spike	rebound burst	threshold variability	bistability	DAP	accommodation	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

Which model should we choose?



Incorporating temporal delays

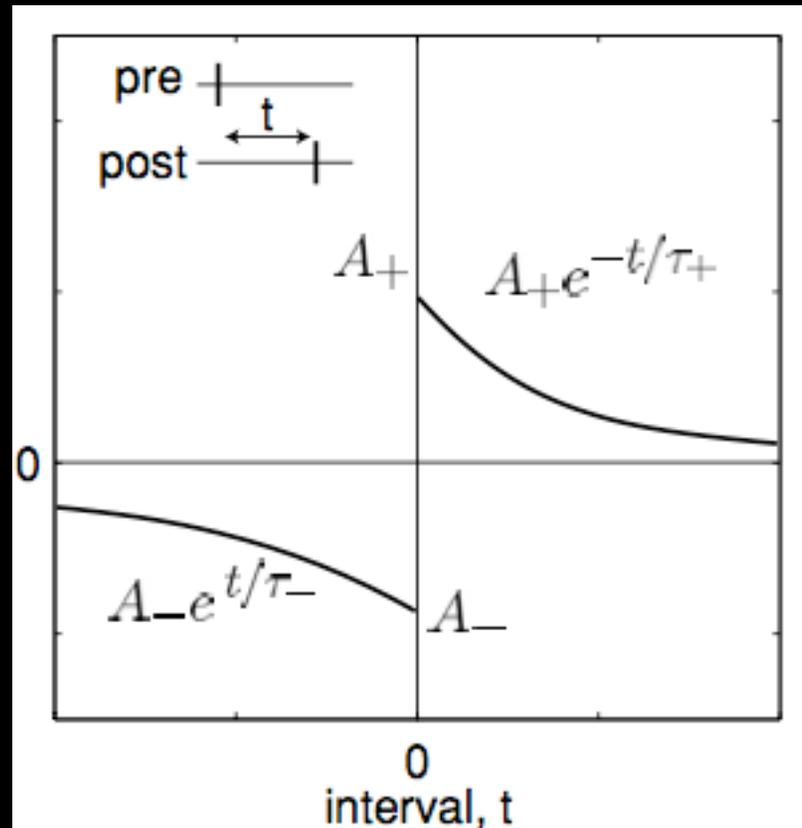
- Axonal conduction delays in mammalian neocortex range from 0.1 ms to 44 ms, depending on neuron type and location



- Yet the propagation delay between two specific neurons is reproducible with submillisecond precision
- Though often ignored, axonal delays confer a substantial advantage on brain networks
 - Results in otherwise impossible stable firing patterns
 - Neurons can participate in multiple, distinct groups
 - The number of such groups exceeds the number of neurons in the network, and possibly the number of synapses

Incorporating learning

- STDP rule – Spike-timing-dependent plasticity, or Hebbian temporally asymmetric synaptic plasticity



$$\tau_+ = \tau_- = 20\text{ms}, A_+ = 0.1, \text{ and } A_- = 0.12$$

How far can we push this model?

- 1,000 cortical spiking neurons in real time in MATLAB on a 1 GHz desktop PC
- 20,000 neurons in real time in C on a 1 GHz desktop PC
- Izhikevich has modeled 100,000 neurons with axonal delays and STDP learning
 - Exhibited delta oscillations early, and as learning progressed generated chaotic, Poisson firing patterns, subsequently settling into gamma rhythms
- "In September 2005, [Izhikevich] simulated a detailed thalamo-cortical system with 10^{11} spiking neurons (size of the human brain), 6-layer cortical micro-circuitry, specific, non-specific, and reticular thalamic nuclei."
 - One second of simulation took over a month on a cluster of 27 3 GHz processors.

References

- Extensive use was made of the three reading assignments:
 - Izhikevich, Eugene M., Simple Model of Spiking Neurons, IEEE Transactions on Neural Networks (2003) 14:1569-1572
<http://www.nsi.edu/users/izhikevich/publications/spikes.htm>
 - Izhikevich, Eugene M., Which Model to Use for Cortical Spiking Neurons? IEEE Transactions on Neural Networks (2004) 15:1063-1070
<http://www.nsi.edu/users/izhikevich/publications/whichmod.htm>
 - Izhikevich, Eugene M., Polychronization: Computation With Spikes, Neural Computation (2006) 18:245-28
<http://www.nsi.edu/users/izhikevich/publications/spnet.htm>
- Some context derived from the review article (in the reading extras area):
 - Herz, Andreas V.M. et al., Modeling Single-Neuron Dynamics and Computations: A Balance of Detail and Abstraction, Science (2006) 314:80