Integrate and Fire Model

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BENG 207
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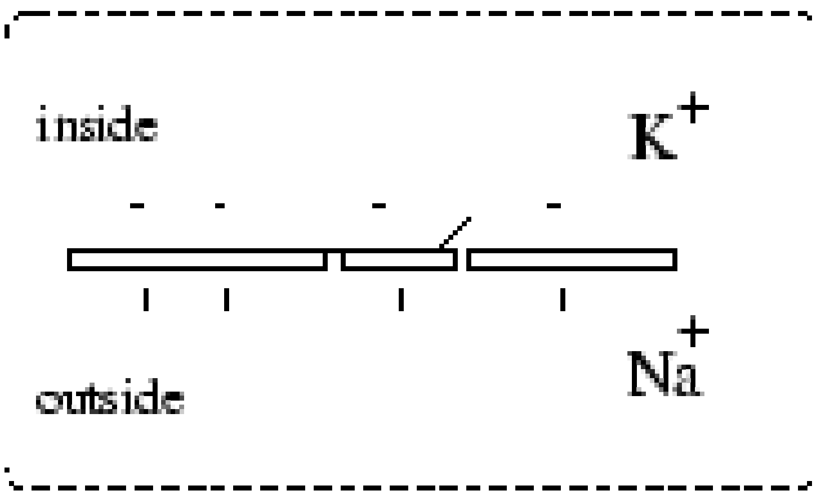
Outline

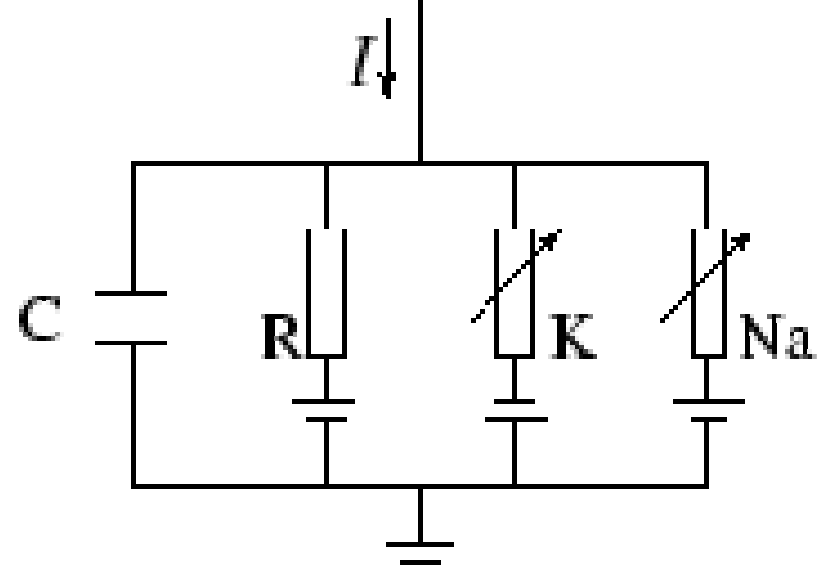
- **Review of Hodgkin-Huxley Model**
- Motivation for Integrate-and-Fire Model
- Linear “Leaky” Integrate-and-Fire Model
- Non-linear Integrate-and-Fire Models
- Current Input Analysis
- Comparison of IF vs HH Models
- Hardware Implementation
- Conclusion

Review of Hodgkin-Huxley

- Input current does one of the following:
  - Charges membrane or
  - Leaks through membrane (through channels R)
- Nerst potentials generated by ion channels
  - Conductance is a function of membrane potential

$$\sum_k I_k = g_L\,(u - E_L) + g_K\, n^4\,(u - E_K) + g_{Na}\, m^3 h\,(u - E_N$$

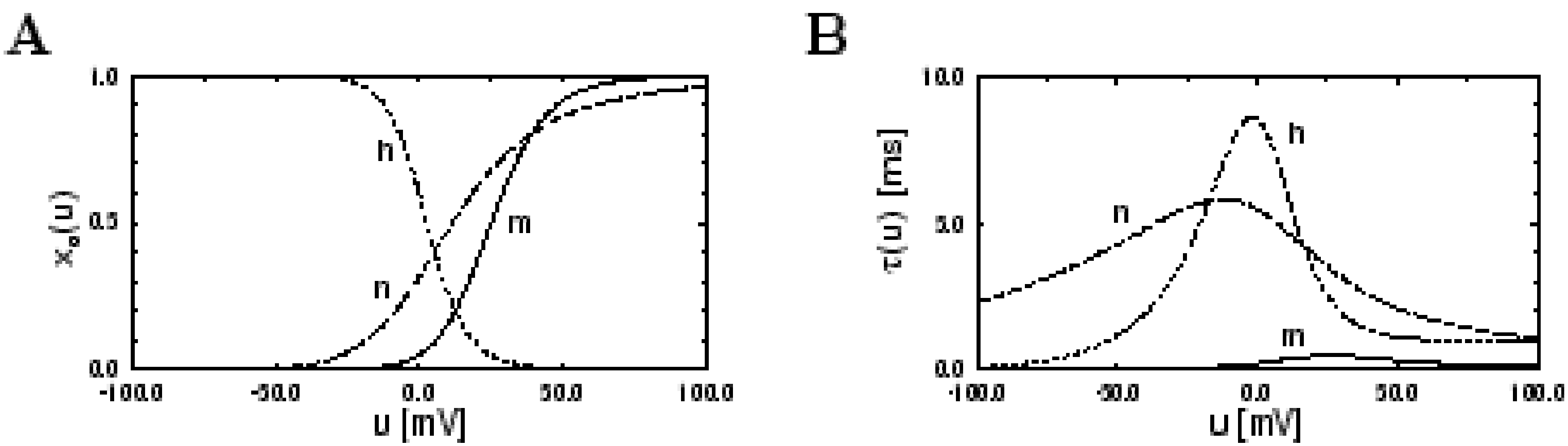




Gerstner and Kistler, Spiking Neuron Models, 2002

Review of Hodgkin-Huxley

- $\sum_k I_k = g_L (u - E_L) + g_K n^4 (u - E_K) + g_{Na} m^3 h (u - E_{Na})$
- Equilibrium Function (A) and Time Constants (B) for h, n, and m
- Leakage current g_L = 1/R (constant)
- *n*,*m* increase with *u* (membrane potential normalized to u_r = 0mV)
- *h* decreases with *u*

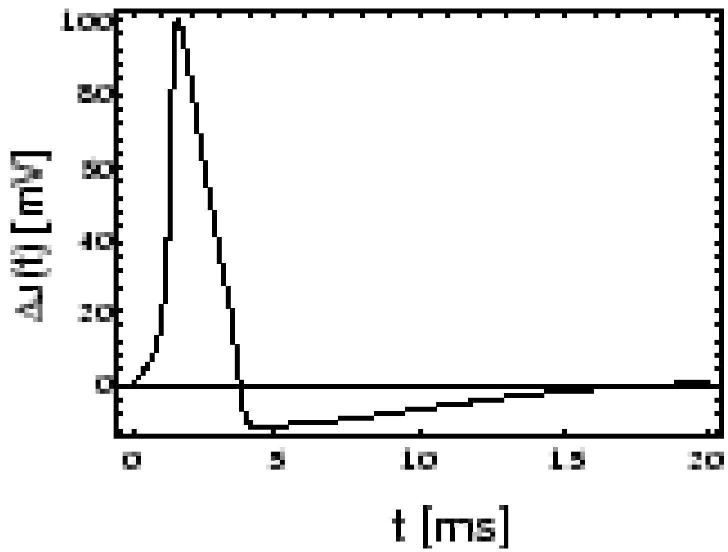


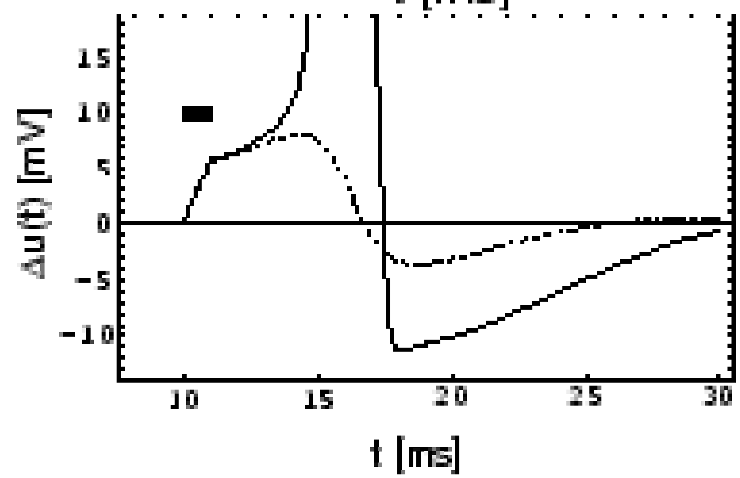
Gerstner and Kistler, Spiking Neuron Models, 2002

Review of Hodgkin-Huxley

- Action potential (top)
  - note refractory period > 10ms

- Threshold effect (bottom)
  - threshold at 10mV
  - initiation of action potential (solid)
    - Na^+ and K^+ channels help
  - insufficient stimulating current pulse (dashed)



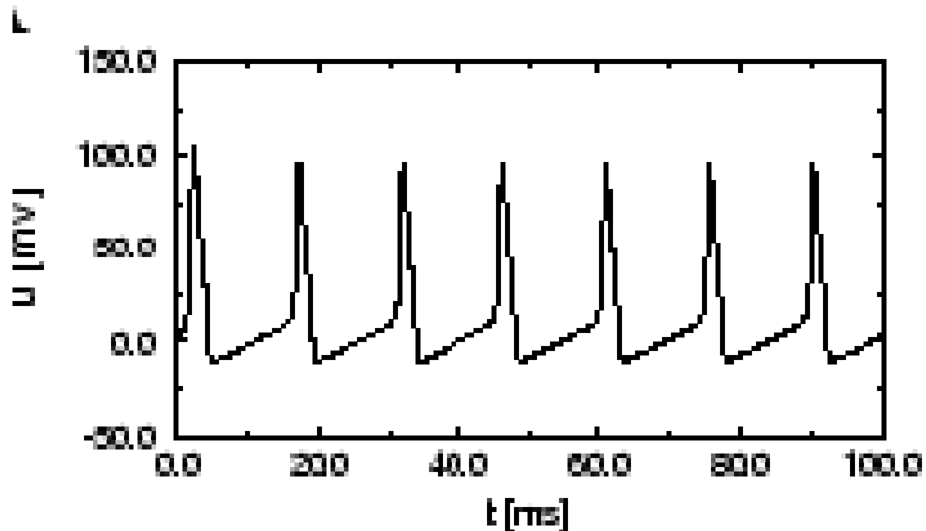


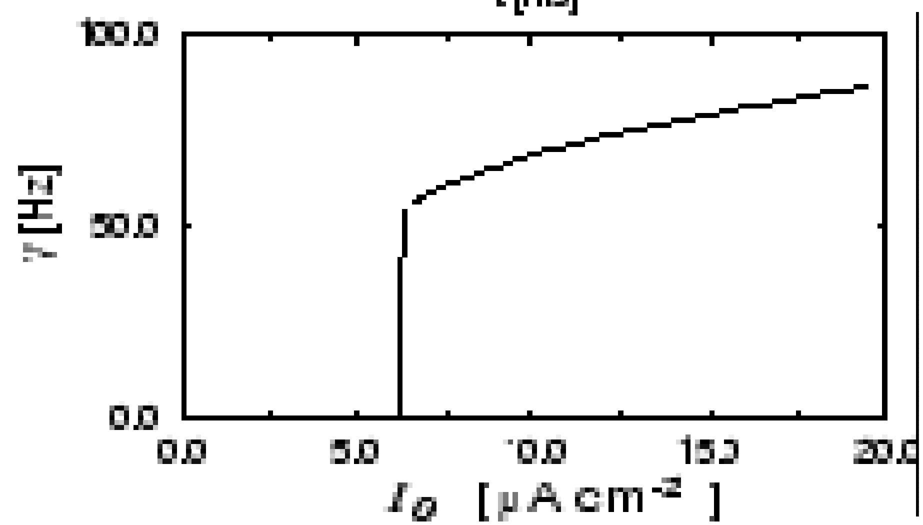
Gerstner and Kistler, Spiking Neuron Models, 2002

Review of Hodgkin-Huxley

- Example of HH output spike train given constant input current (top)
  - Normalized for u_r = 0mV

- Gain function for HH
  - 7uA/cm^2 threshold





Gerstner and Kistler, Spiking Neuron Models, 2002

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Motivation for IF Models

- Practical
  - More accurate models are needed
  - Simpler models are easier to use/troubleshoot
  - Simpler models are easier to implement in hardware
- Theoretical
  - Improve speed/space of modeling
  - Implement timestepping vs. exact solutions

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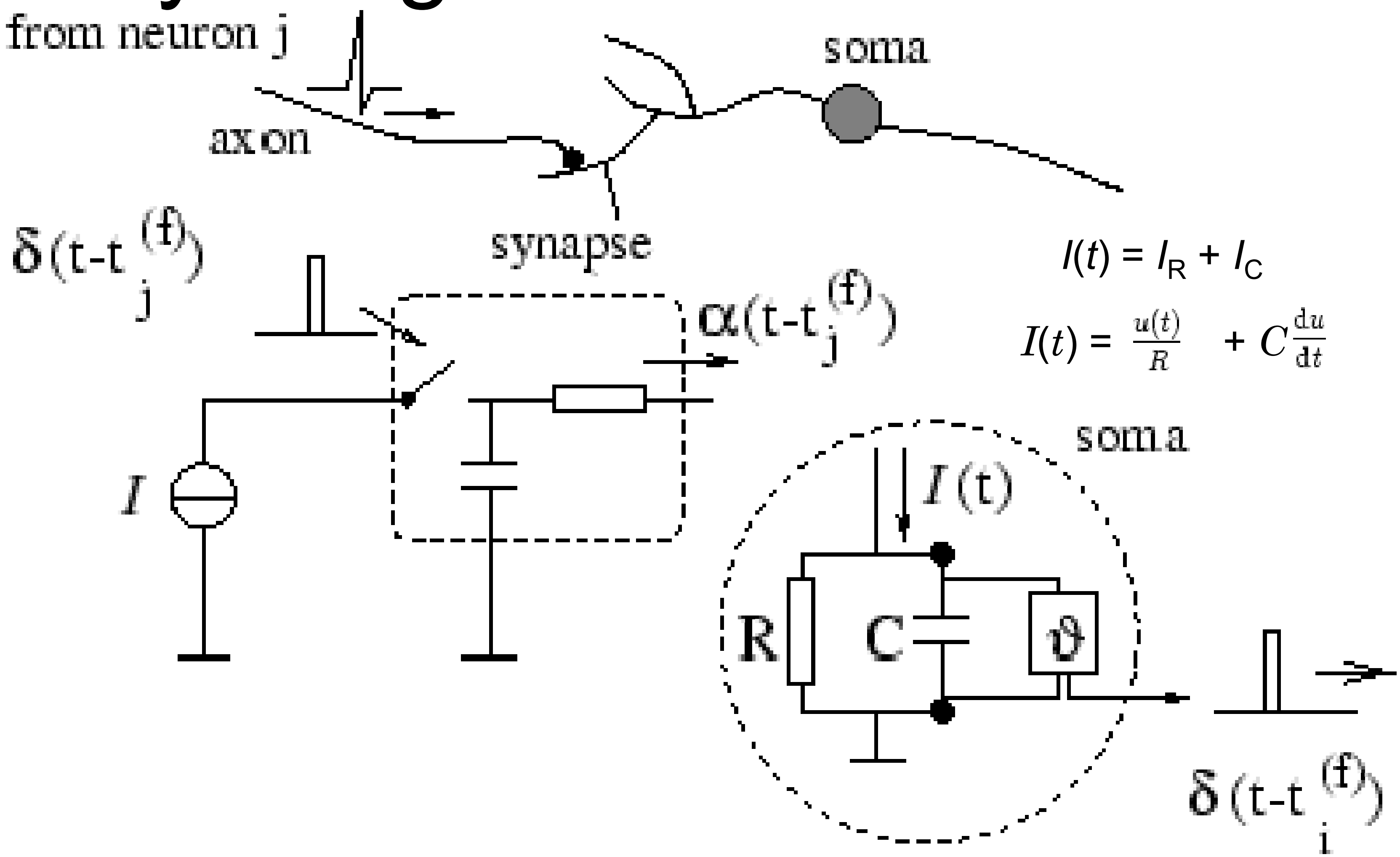
Leaky Integrate-and-Fire Model



$I(t) = I_R + I_C$

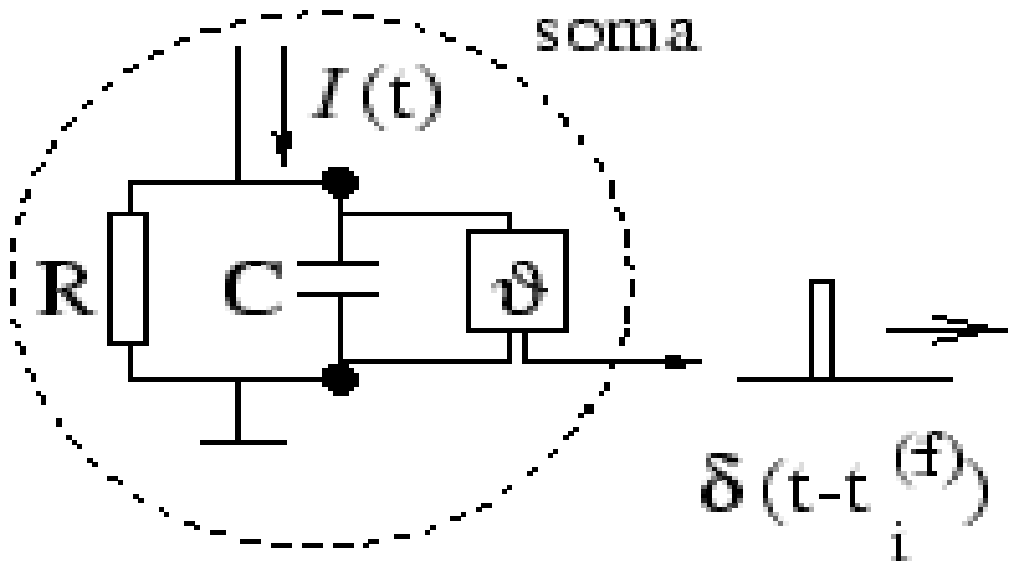
$$I(t) = \frac{u(t)}{R} + C\frac{du}{dt}$$

Gerstner and Kistler, Spiking Neuron Models, 2002

Leaky Integrate-and-Fire Model

- Membrane time constant $\tau_m = R\,C$
- Membrane potential $u(t)$
- $I(t) = \frac{u(t)}{R} + C\,\frac{\mathrm{d}u}{\mathrm{d}t}$
- Multiply by R to get

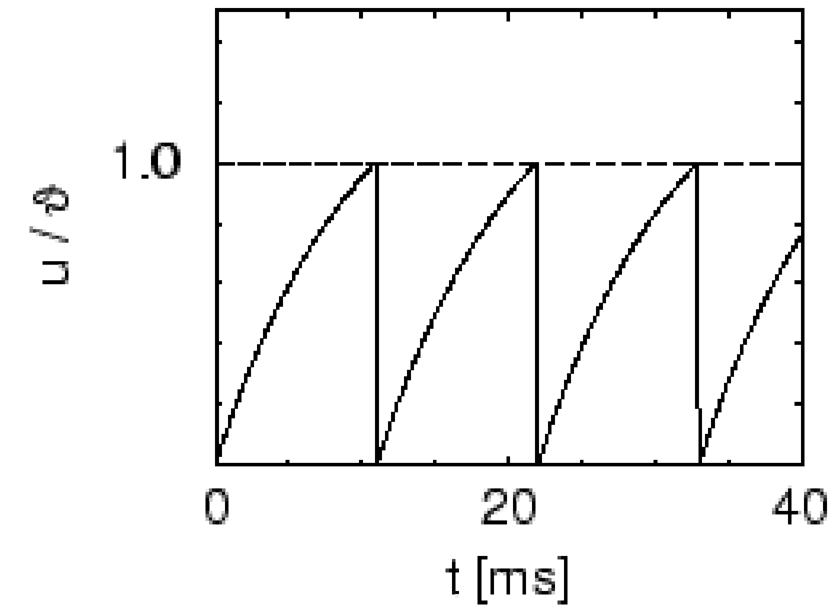
$$\tau_m \frac{\mathrm{d}u}{\mathrm{d}t} = - u(t) + R\,I(t)\ .$$



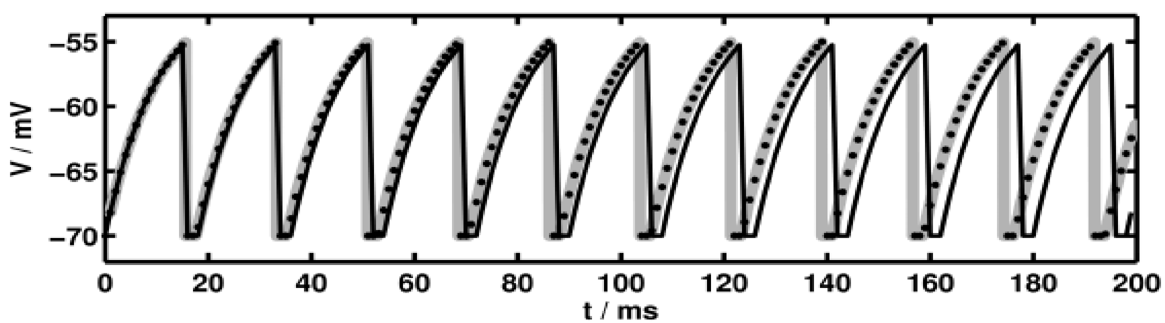
Gerstner and Kistler, Spiking Neuron Models, 2002

Leaky Integrate-and-Fire Model

- Firing Time $t^{(f)}$ when $u(t^{(f)}) = \vartheta$
- RESET: Immediately after $t(f)$,
  $u(t(f) + \Delta_{abs}) = u_r$ (resting potential)
  - Δ_{abs} is the absolute refractory period
- After reset, integration restarts



Gerstner and Kistler, Spiking Neuron Models, 2002



Morrison, 2005

Example: Constant Stimulation

- $I(t) = I_0$, $u_r = 0$, $u(t^{(1)}) = u_r$
- Without reset, max $u(t) = RI_0$:

$$u(t) = R\,I_0 \left[\ 1 - \exp\left(- \frac{t - t^{(1)}}{\tau_m} \right) \right]$$

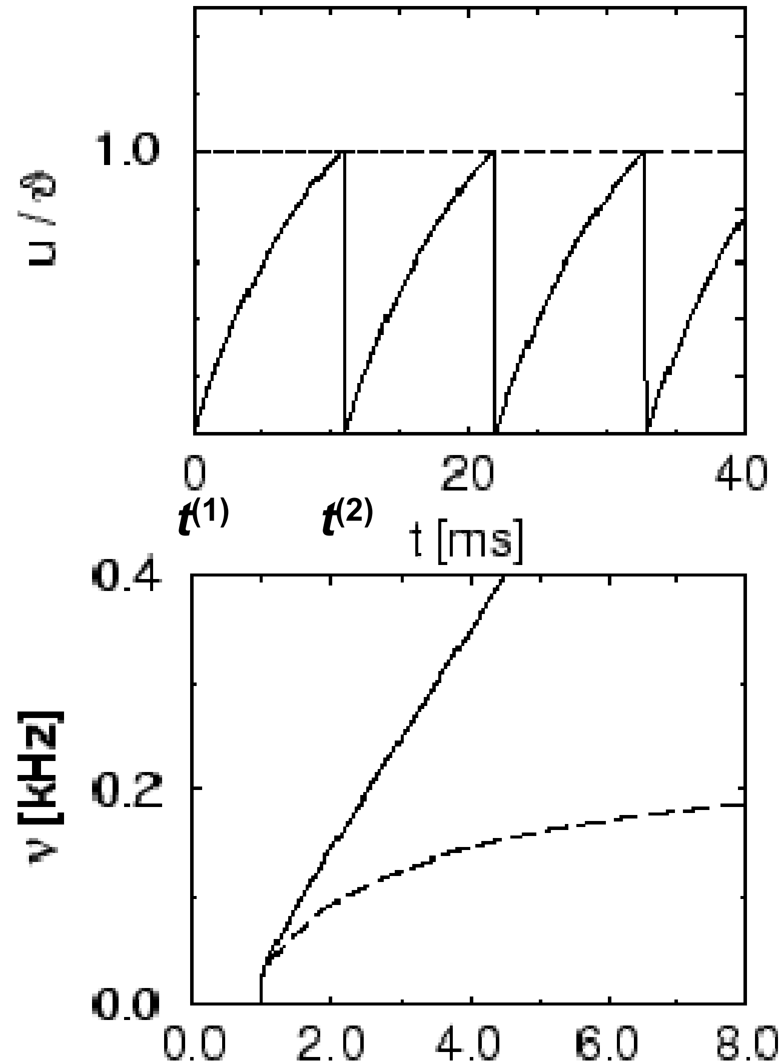
- Next spike at $t^{(2)}$ when $u(t^{(2)}) = \vartheta$

$$\vartheta = R\,I_0 \left[\ 1 - \exp\left(- \frac{t^{(2)} - t^{(1)}}{\tau_m} \right) \right] .$$

- So total period $T = t^{(2)} - t^{(1)}$ is

$$T = \tau_m \ ln \frac{R\,I_0}{R\,I_0 - \vartheta} + \Delta_{abs}$$

- Constant stimulation = regular firing at frequency 1/T

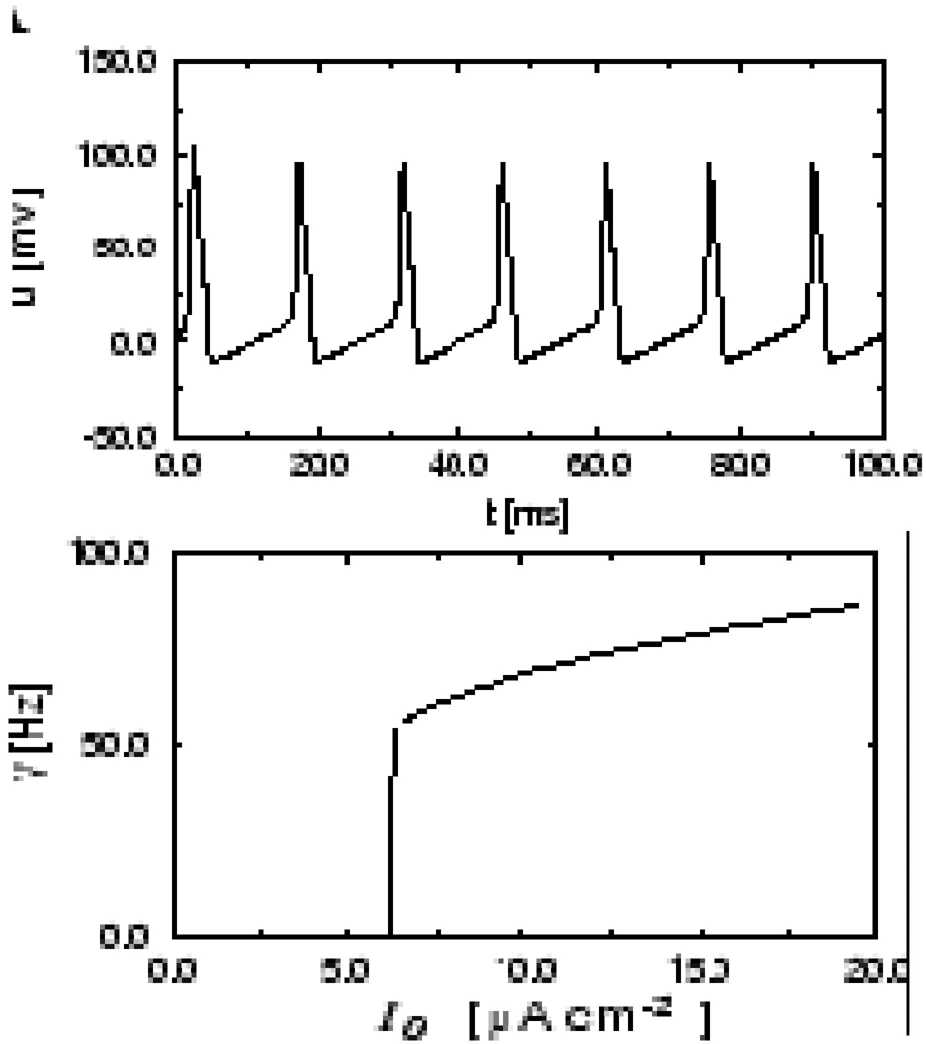


Gerstner and Kistler, Spiking Neuron Models, 2002

I_0

Hodgkin-Huxley Constant Stimulation

- Example of HH output spike train given constant input current (top)
  - Normalized for u_r = 0mV
- Gain function for HH
  - 7uA/cm^2 threshold

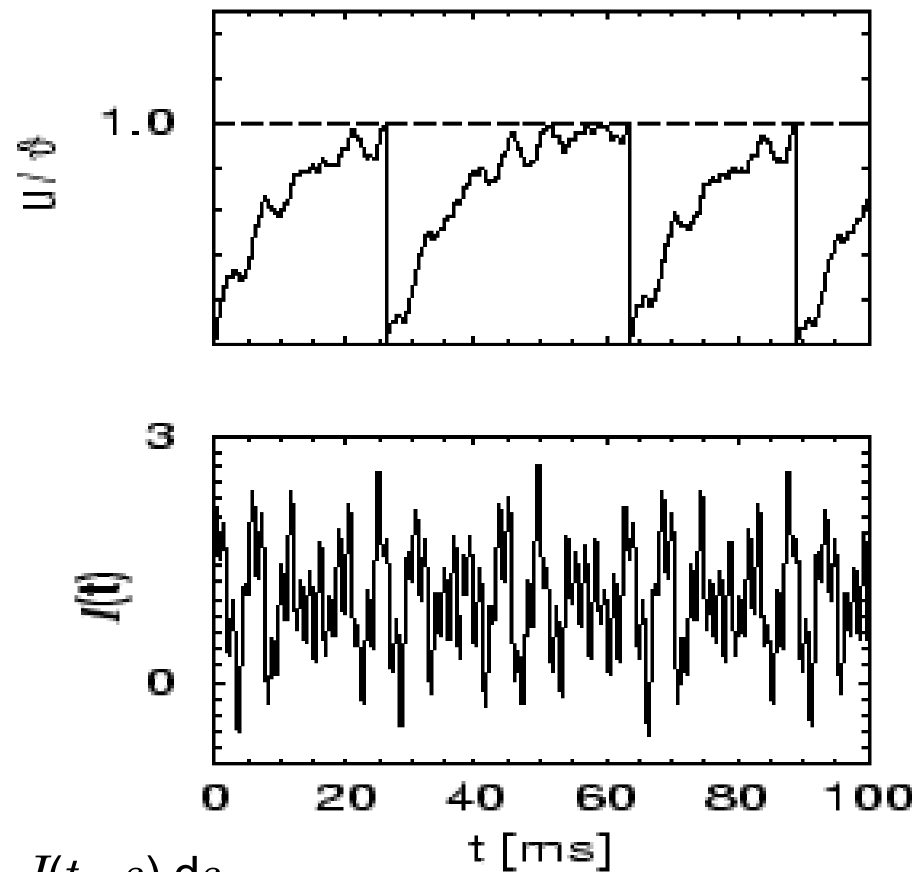


Gerstner and Kistler, Spiking Neuron Models, 2002

Example: Arbitrary Stimulation

- Last spike at $\hat{t}$, $u_r < \vartheta$
- Input $I(t)$ is sum of four sin() waves at random frequencies + $I_0 = 1.2$
- Δ_{abs} is neglected
- Output spike train is more regular (low-pass filter)
- Defining eqn:

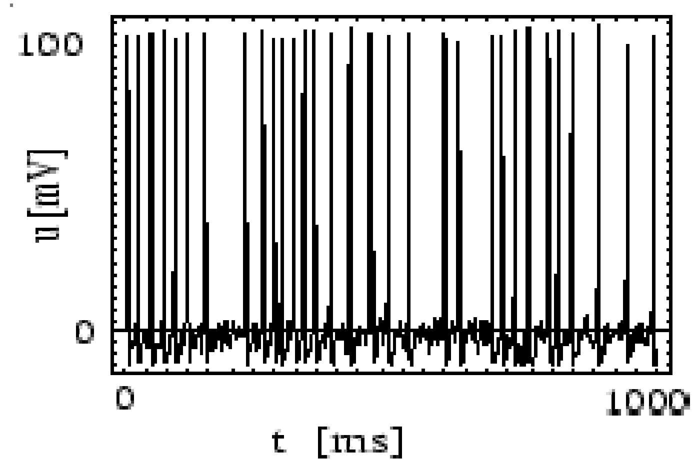
$$u(t) = u_r \exp\left(-\frac{t - \hat{t}}{\tau_m} \right) + \frac{1}{C} \int_0^{t-\hat{t}} \exp\left(-\frac{s}{\tau_m} \right) I(t - s)\, ds$$



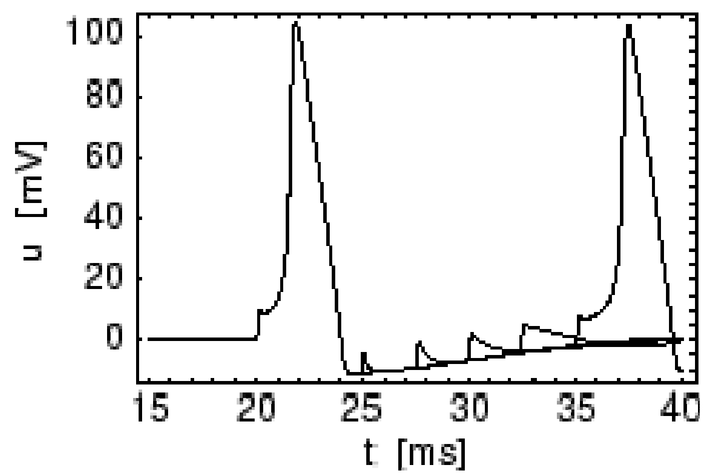
Gerstner and Kistler, Spiking Neuron Models, 2002

Hodgkin-Huxley Arbitrary Stimulation

- Arbitrary stimulation yields irregular spike train



- Emphasis on single, large stimulus over several smaller stimuli



Gerstner and Kistler, Spiking Neuron Models, 2002

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Nonlinear Integrate-and-Fire Models

- Several in use, we'll discuss these:
  - Quadratic
  - Exponential
  - Multicurrent

Nonlinear Integrate-and-Fire Model

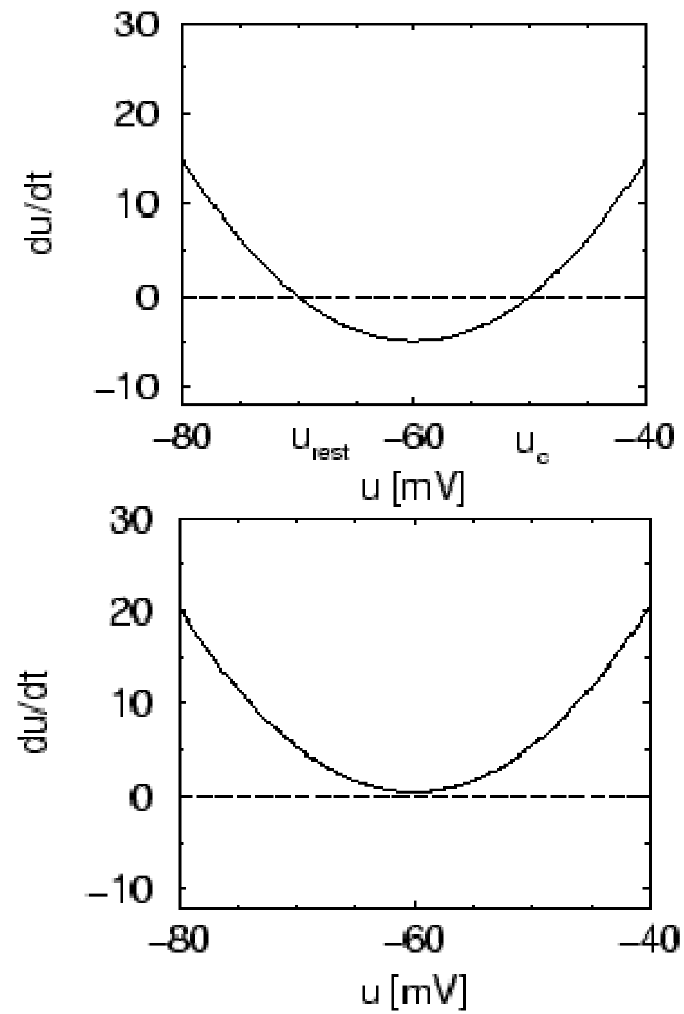
- Replace $\tau_m \frac{du}{dt} = -u(t) + R\,I(t)$

  with $\tau \frac{d}{dt} u = F(u) + G(u)\,I(t)$

- e.g. Quadratic Model

  $$\tau \frac{d}{dt} u = a_0 (u - u_r)(u - u_c) + RI(t)$$

  - $a_o > 0$, $u_c > u_r$ $I(t) = I_0$ (constant)
  - ϑ = -40mV
  - $I_0 = 0$ (top), I_0 = super-threshold (bottom)
  - u_c is critical voltage



Abbott and van Vreeswijk, 1993

Exponential NLIF Model

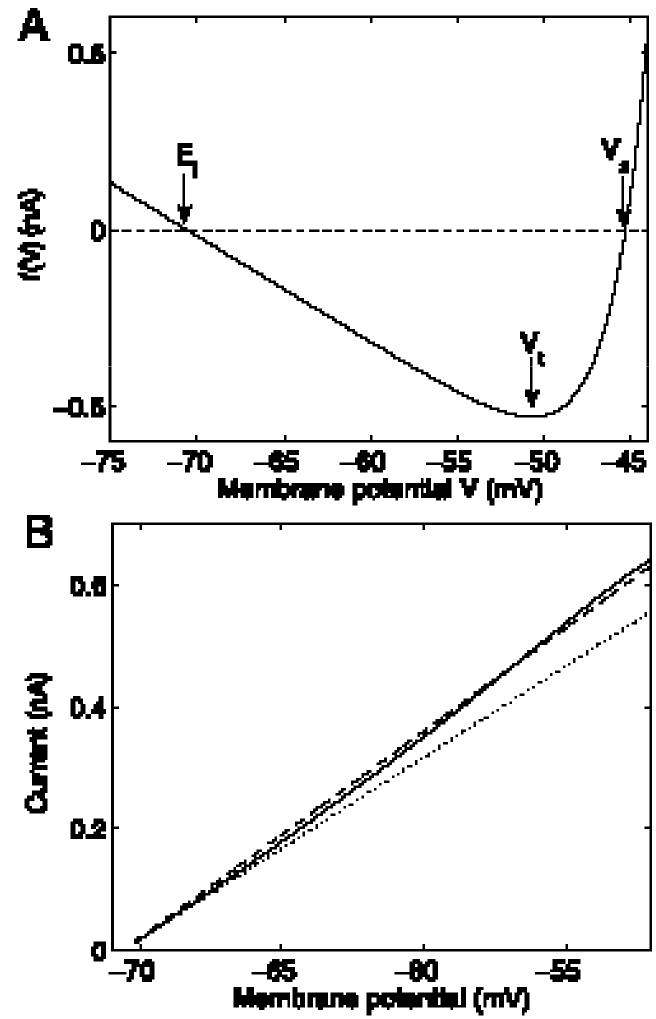
- Replace $\tau \frac{\mathrm{d}}{\mathrm{d}t} u = F(u) + G(u)\, I(t)$

  with $$C\frac{dV}{dt} = f(V) - w + I$$

  - where $f(V) = -g_L(V - E_L) + g_L \Delta_T \exp\left(\frac{V - V_T}{\Delta_T}\right)$
  - and *w* is an spike-triggered adaptive function:

    $$\tau_w \frac{dw}{dt} = a(V - E_L) - w$$

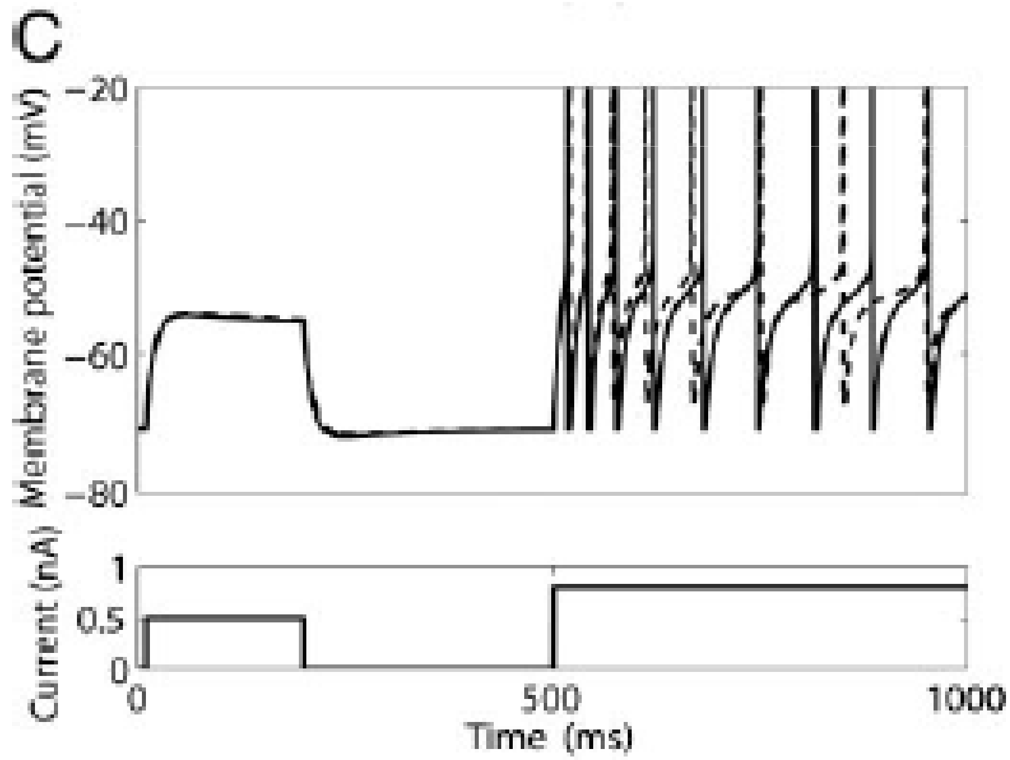
    - a represents sub-threshold adaptation
    - at each firing, w is increased by a set amount



Romain Brette, *J Neurophysiol*, 2005

Exponential NLIF Model

- Exhibits drawbacks of oversimplification
  - Fairly accurate representation without computation intensity
  - Misses spikes (~5%)

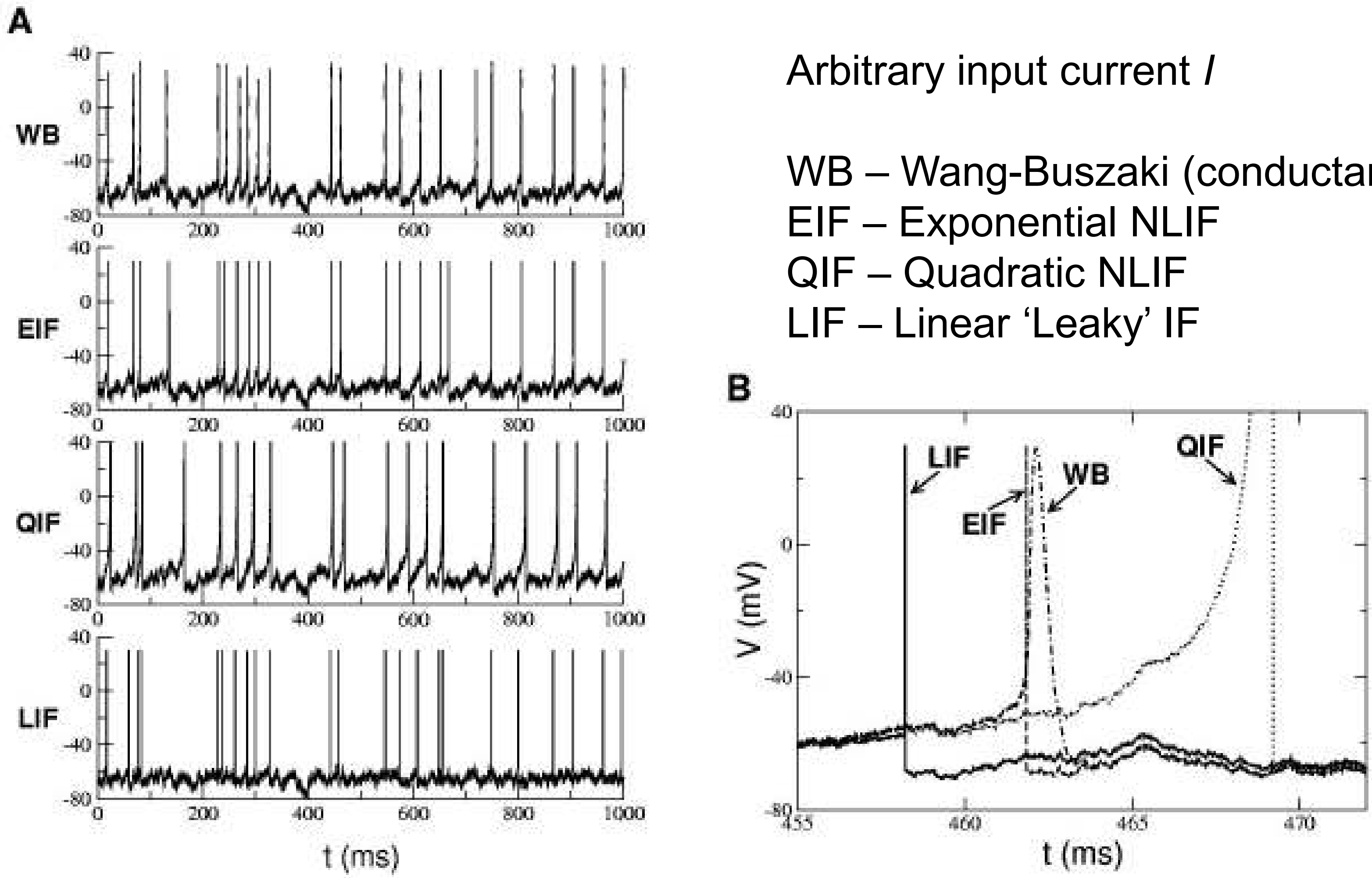


Romain Brette, *J Neurophysiol*, 2005

Multicurrent IF Model

- Compromise between HH and LIF
- Start with HH Model
  - Use firing threshold ϑ and define Δ_{abs}
  - Use standard action potential shape instead of calculating diff eqns
  - Don't integrate during refractory period
  - Reset gating variables m, h, n_1, and n_2 according to input scenario
- Reduce to one-variable dependence ($u(t)$)
  - Sort variables by speed relative to u
    - m is fast ($0.08 < \tau_m < 0.25$ms), replace with equilibrium $m_0[u(t)]$
    - h, n_1, and n_2 are slow ($4.28 < \tau_h < 14.45$ ms; $44.66 < \tau_{n1} < 144.10$ ms; $0.44 < \tau_{n2} < 4.19$ ms), replace with h_{avg}, n_{1avg}, and n_{2eq} (these depend on scenario)

Comparison of IF Membrane Voltage Traces



Arbitrary input current *I*

WB – Wang-Buszaki (conductance)
EIF – Exponential NLIF
QIF – Quadratic NLIF
LIF – Linear 'Leaky' IF

Romain Brette, *J Neurophysiol*, 2005

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Current Input Analysis

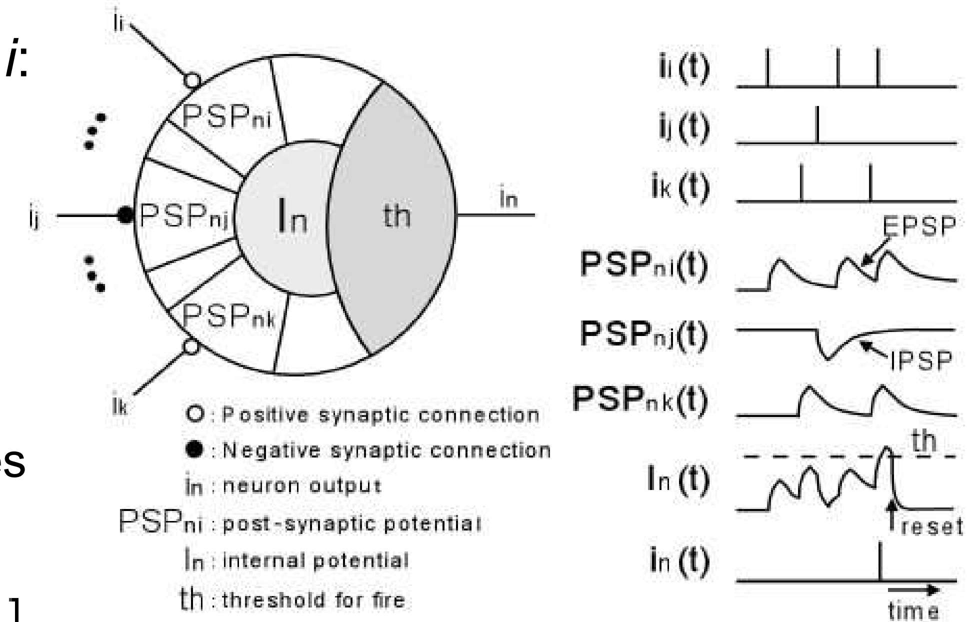
- Input from neuron *j* to neuron *i*:

  $$I_i(t) = \sum_j w_{ij} \sum_f \alpha\,(t - t_j^{(f)})$$

  - neuron j fires at $t_j^{(f)}$ with efficacy w_{ij} and postsynaptic current α
  - Each presynaptic AP changes conductance, so

$$\alpha\,(t - t_j^{(f)}) = -\,g(t - t_j^{(f)})\,[\,u_i(t) - E_{syn}]$$

E_{syn} synapse reversal potential



Takashi Morie, Kyushu Institute of Technology, 2006

Current Input Analysis

$$\alpha\,(t - t_j^{(f)}) = -\,g(t - t_j^{(f)})\,[\,u_i(t) - E_{syn}]$$

Excitatory Synapses

- $E_{syn} >> u_r$, $E_{syn} > \vartheta$
- I_i from presynaptic spike is positive – increases u_i
- Higher u_i, smaller input current
- Saturation when u_i approaches E_{syn}, thus $E_{syn} >> u_r$ usually

Inhibitory Synapses

- E_{syn} u_r, $E_{syn} > \vartheta$
- I_i from presynaptic spike pulls u_i down towards E_{syn}
- Higher u_i, greater inhibitory current
- Saturation when u_i approaches E_{syn}, thus there is little effect when u_i u_r

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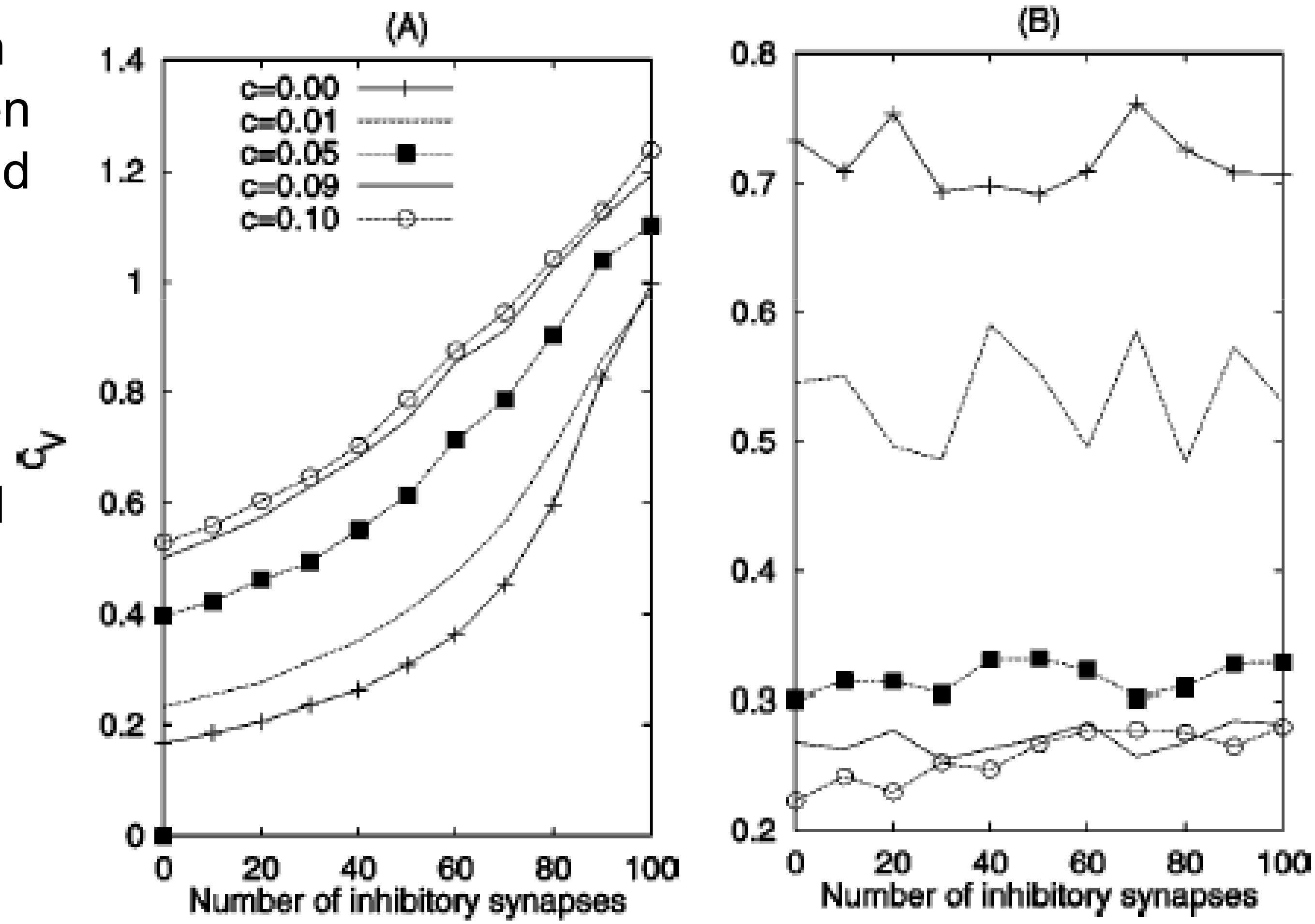
Comparison of IF vs HH

- c, correlation coeff between excitatory and inhibitory synapses
- C_v, coeff of variation (std dev/mean) output



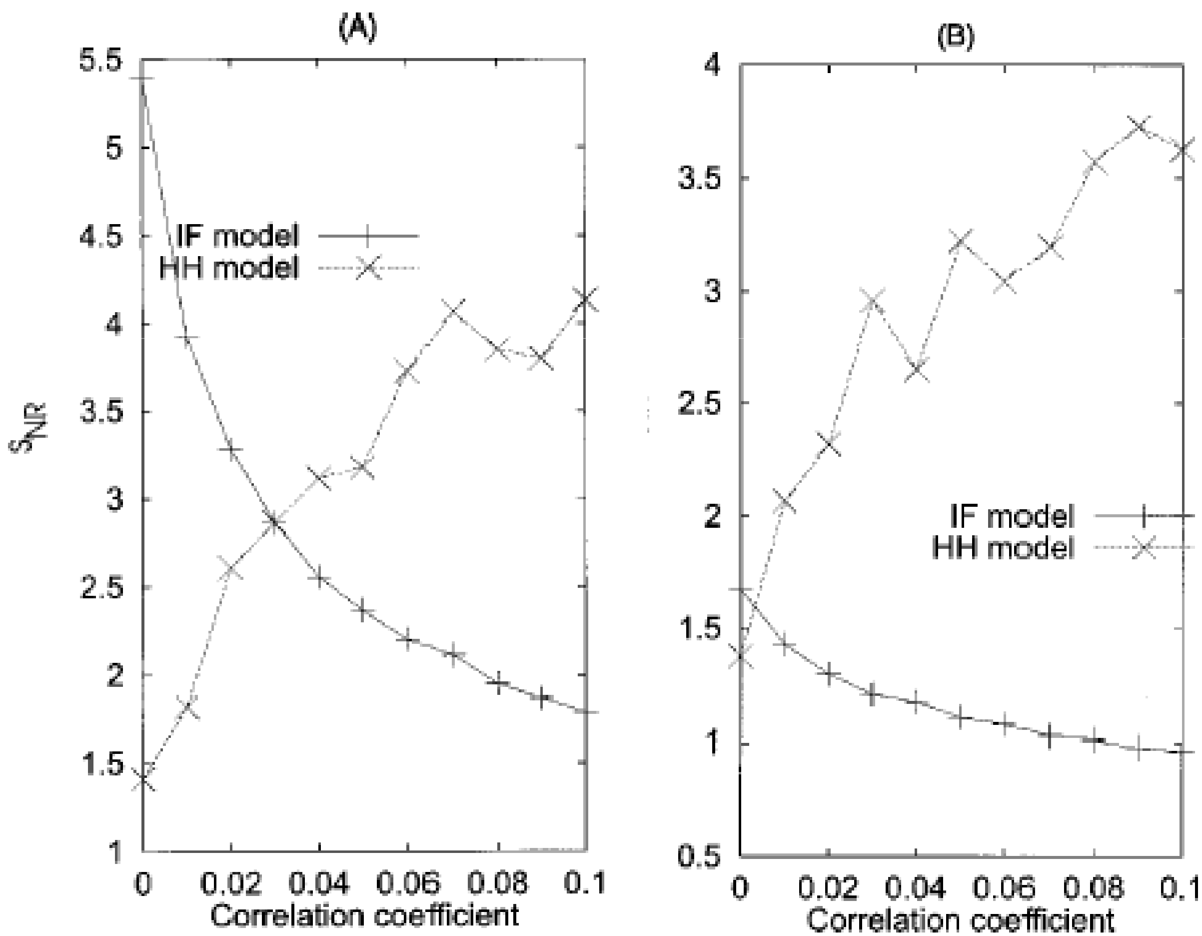
Jianfeng Feng, Sussex Univ, 2001

Comparison of IF vs HH

- 10 synapses (left)
- 80 synapses (right)
- S_{NR} = mean/std deviation

- Linear IF model better for uncorrelated inputs

- HH model better for correlated inputs

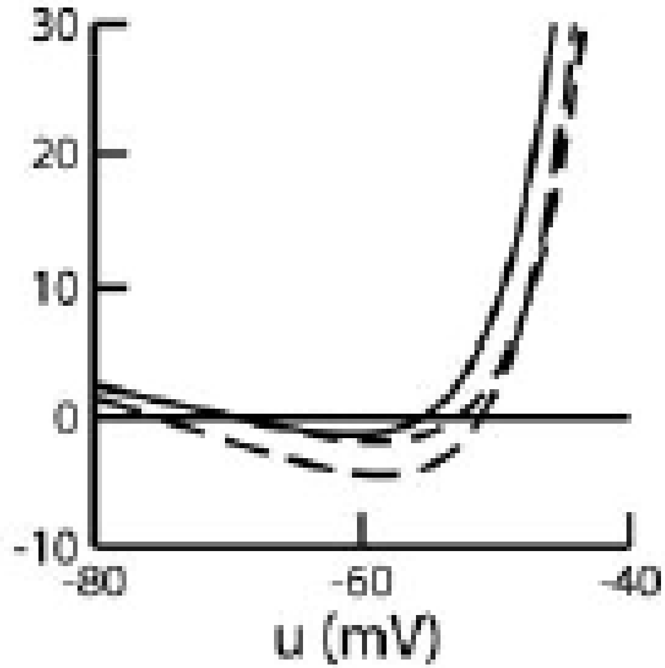


Jianfeng Feng, Sussex Univ, 2001

Comparison of IF vs HH

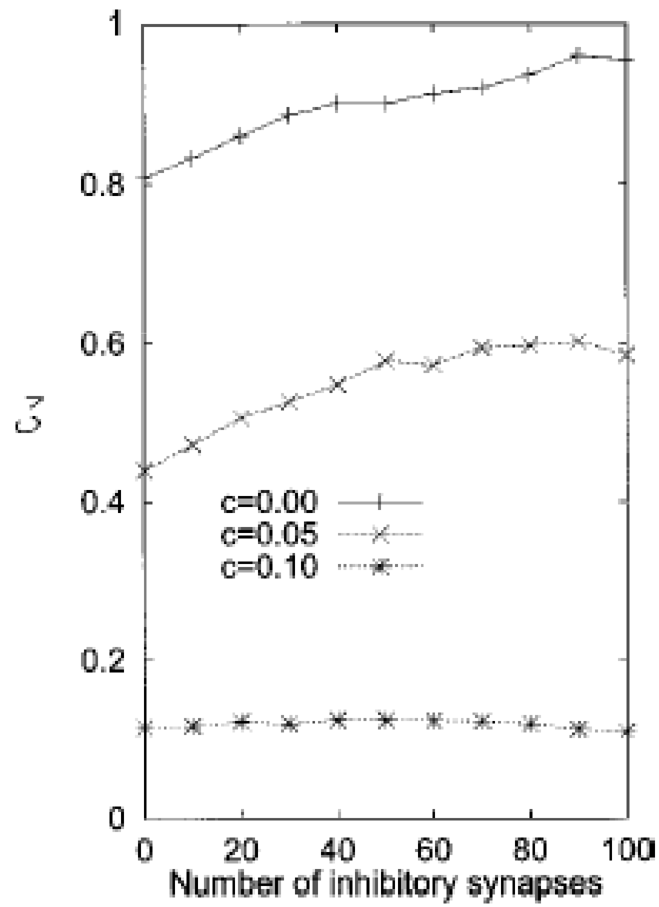
- Non-linear IF model displays beneficial qualities of both HH and linear IF

Parameters adapted to:
resting (solid)
constant sub-threshold *I* (short)
periodic 40Hz firing (long)



Abbott and van Vreeswijk, 1993

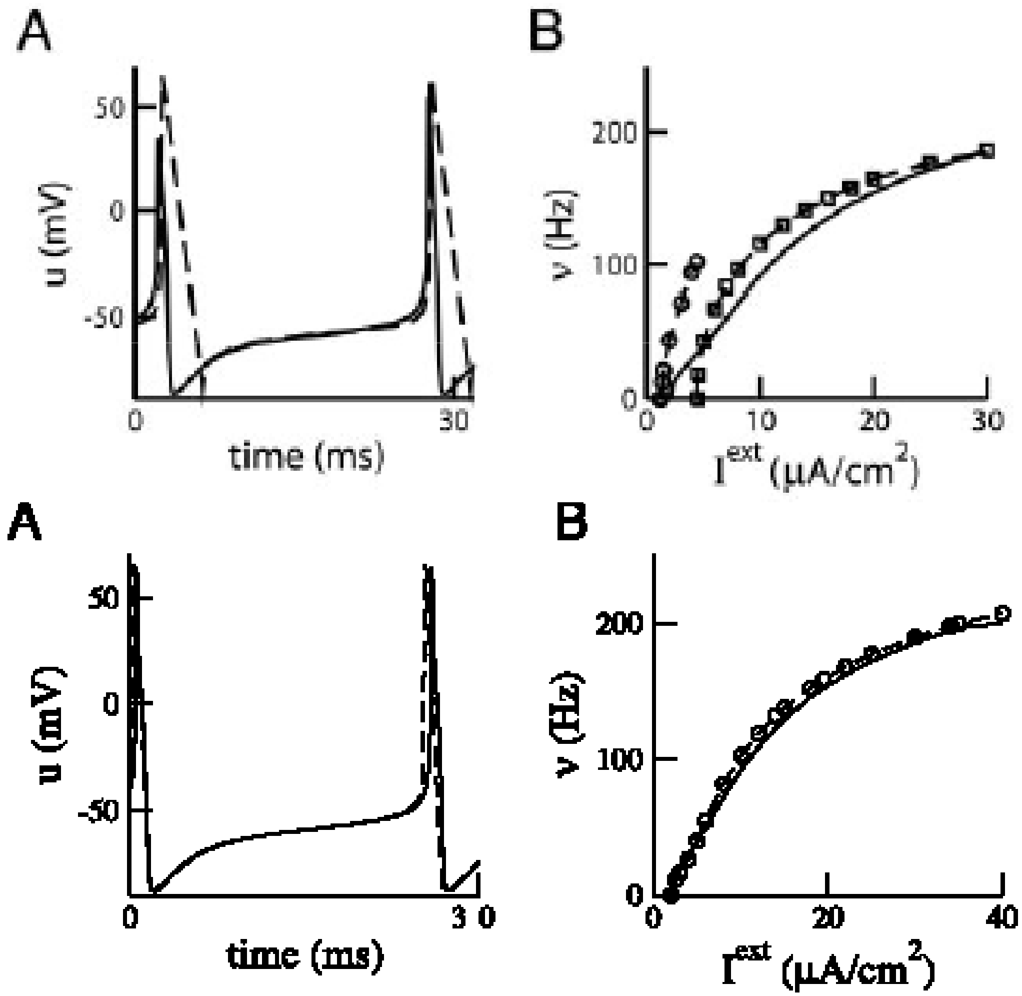
Renaud Jolivet, *J Neurophysiol*, 2004



Jianfeng Feng, Sussex Univ, 2001

Comparison of IF vs HH

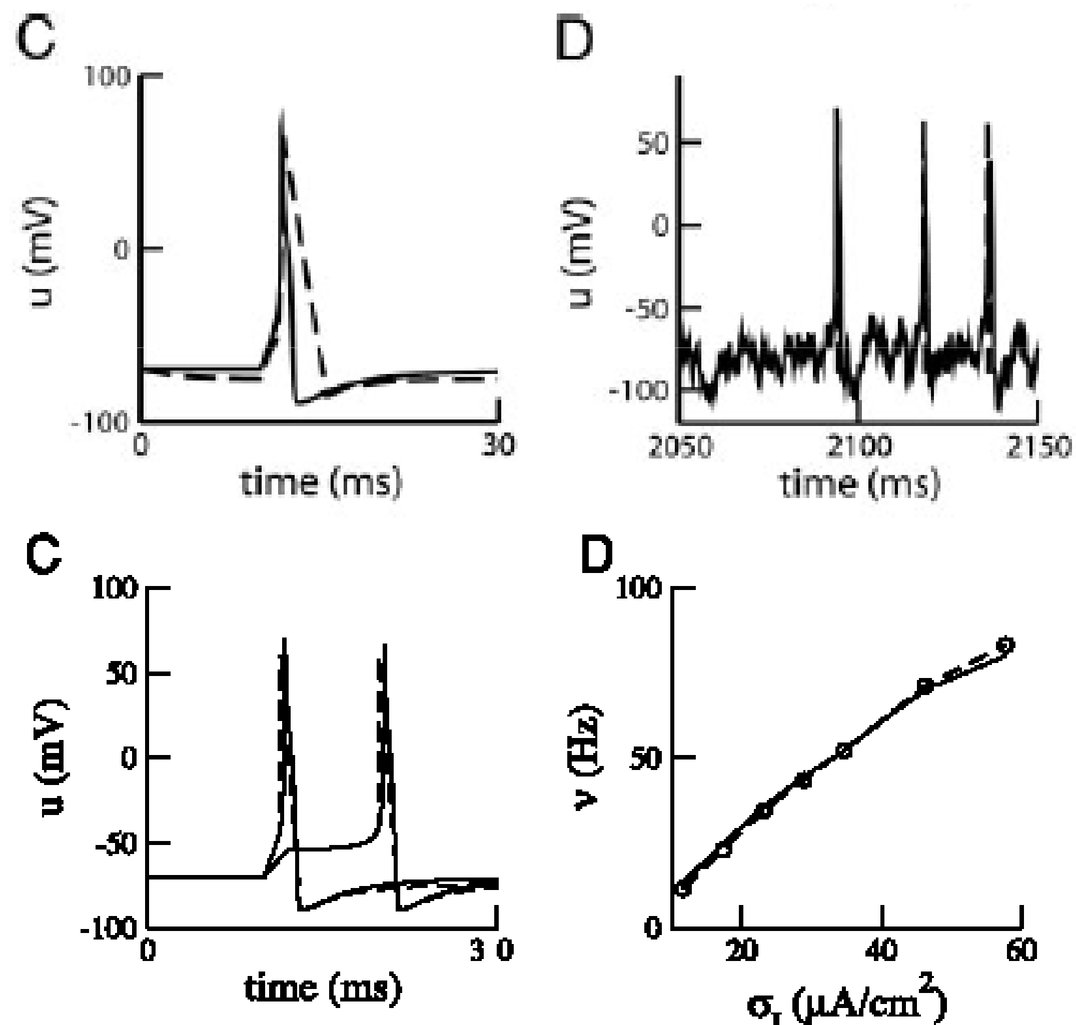
- Constant Input
  - 5uA/cm²
  - 40Hz periodic firing
  - NLIF (top dashed)
  - MCIF (bottom dashed)
  - HH (solid)



Renaud Jolivet, *J Neurophysiol*, 2004

Comparison of IF vs HH

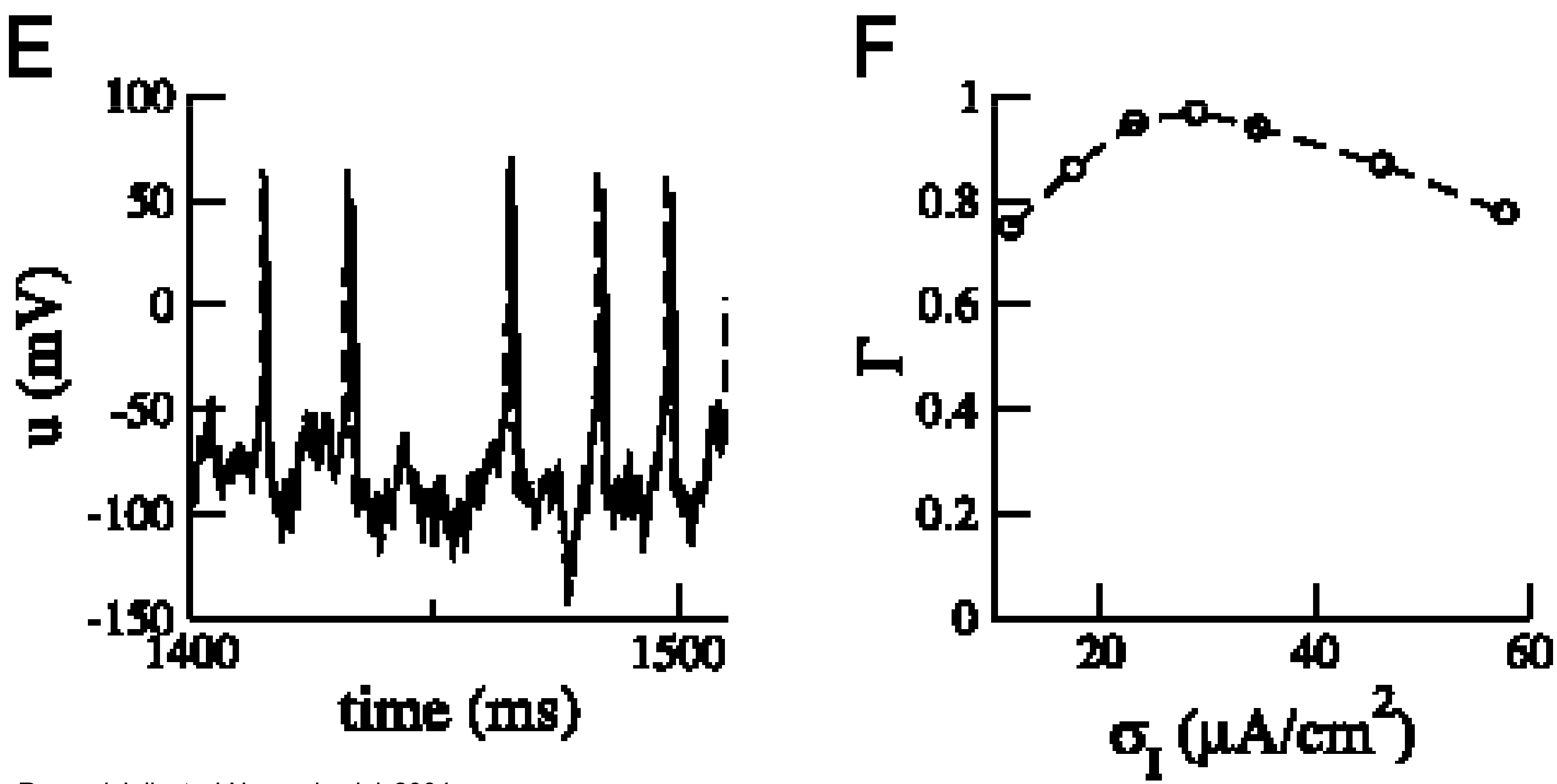
- Pulse input at 10ms $20uA/cm^2$ and $8.8uA/cm^2$
  - NLIF (top dashed)
  - MCIF (bottom dashed)
  - HH (solid)



Renaud Jolivet, *J Neurophysiol*, 2004

Comparison of IF vs HH

- E: Random input (95% of spike times accurate to ✂2ms) NLIF
- F: Coincidence function (for 25 < σ_I < 35, Γ is about 95%)



Renaud Jolivet, *J Neurophysiol*, 2004

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Hardware Implementation Example

- Simple hardware implementation described below
- When V_{thr} is input
  - Spike voltage is quickly output
  - The reset request line is pulled down
  - a delayed reset response is enacted through the pull-down transistor

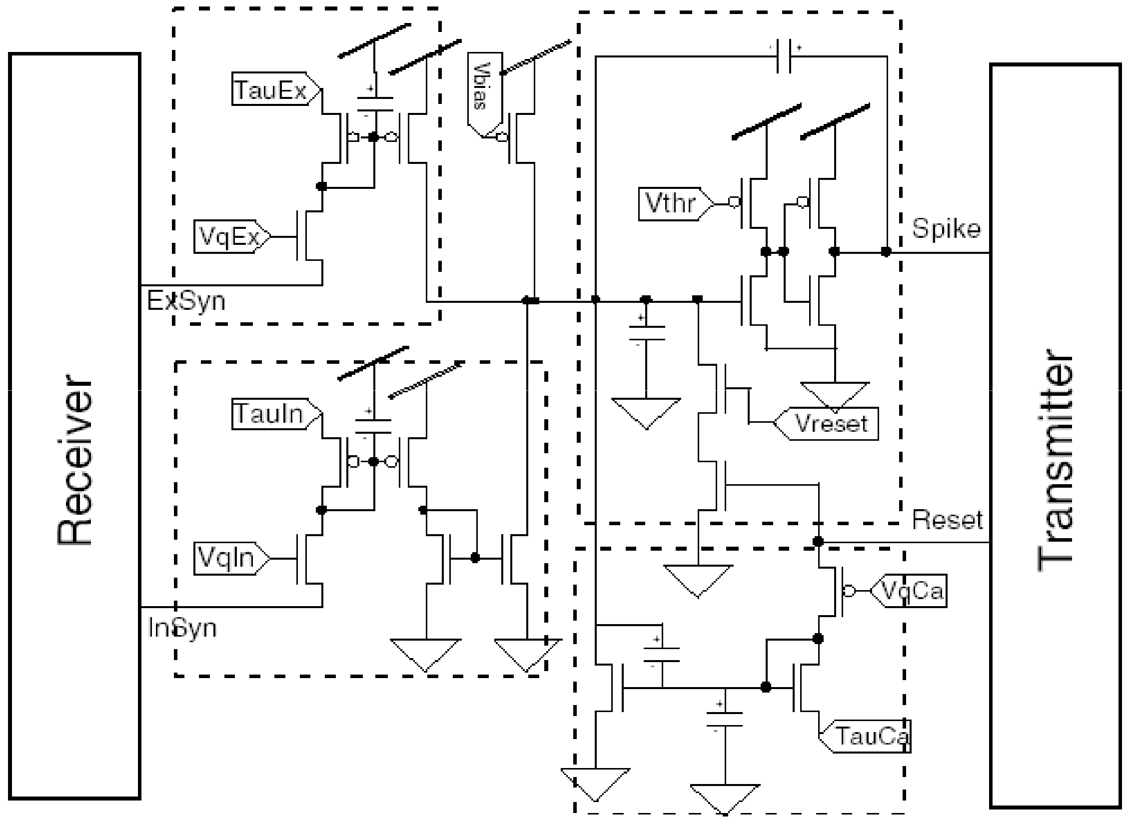

Figure 8.1: Silicon-Neuron Model

Schematic of the silicon neuron with synapses. The Transmitter and Receiver circuitry communicate address events to and from the transceiver chip. The dashed boxes indicate various subcircuits within the neuron. Clockwise from top-right: 1) Integrate & Fire Neuron; 2) Ca^{++} and Voltage dependent K^{+} channels; 3) Inhibitory Synapse; 4) Excitatory Synapse.

McLaughlin, *Proc. Natl. Acad. Sci*

Hardware Applications

- Model of the Lateral Geniculate Nucleus and Primary Visual Cortex
  - Replace random connections with known anatomical data
- Simulate and predict behavior of a cricket (Cornell)
- Implementation of motoneuronal behavior using analog circuits (Georgia Institute of Technology)
- Cortical visual neuro-prosthesis for the blind: Retina-like hardware preprocessor (University of Grenada, Spain)
- Brain-implantable biomimetic electronic prosthesis (DARPA, USC)
- Neuromorphic approaches to rehab for paralysis (Arizona State)
- Vastly parallel computing
- Robotics signal processing

Conclusion

Benefits of IF Models

- Simple
  - Only 3 internal parameters
    - u_r, τ_m, and ϑ
  - Reset is undefined
- Linear model is accurate far from threshold
  - good for quick sub-threshold membrane potentials
- Quadratic model is accurate close to threshold
  - good approximation of current-frequency curve

Drawbacks of IF Models

- Not conductance-based
- Linear model inaccurate near threshold
- MCIF model depends on input scenario
- LIF and NLIF models do not display observed firing correlation tendency

Discussion Questions

- What is the relative importance of membrane threshold voltage accuracy? precision?
- What is lost when unique action potential amplitudes/depolarizations are not modeled?
- What is lost when input correlation is not reflected in output correlation?
- What is the effect of sub-threshold resonance properties on the firing rate?
- What other non-linear models are relevant?

References

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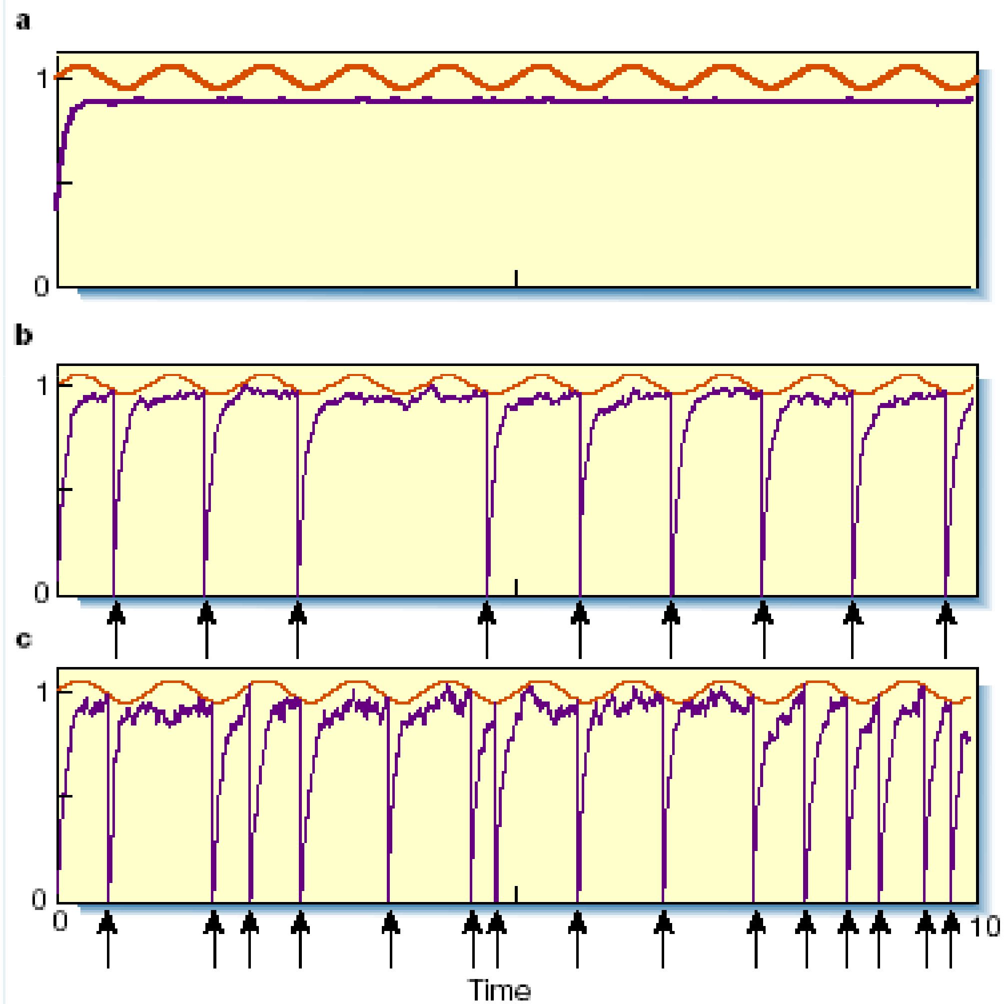
Varying threshold as modulator

- Intermediate level of noise is desirable



Renaud Jolivet, *J Neurophysiol*, 2004

Examples

- IF
- HH