Nonlinear Dynamics of Neural Systems

Excitability/Oscillations : fast autocatalysis + slower negative feedback

Value of reduced models

Time scales and dynamics

Phase space geometry

Different dynamic states – “Bifurcations”; concepts and methods are general.

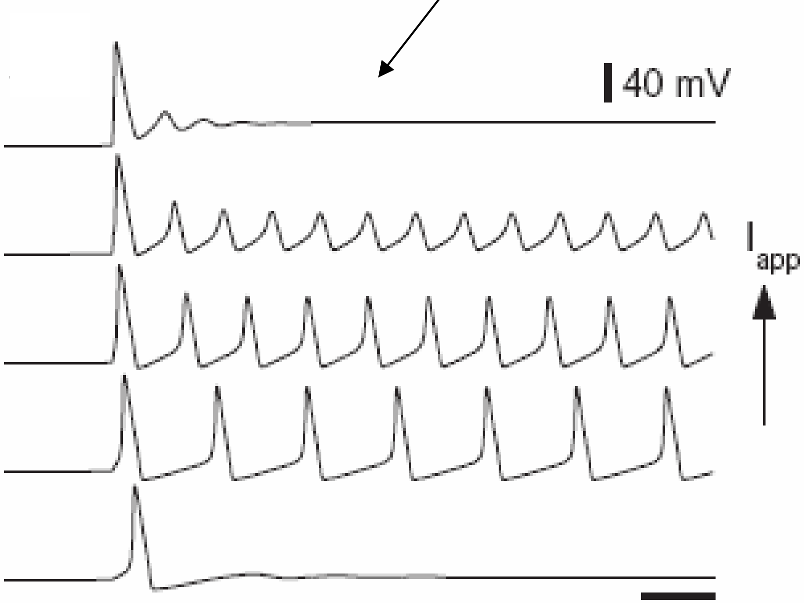
http://www.cns.nyu.edu/doctoral/courses/2005-2006/fall/compNeuro05/

XPP software:http://www.pitt.edu/~phase/ (Bard Ermentrout’s home page)

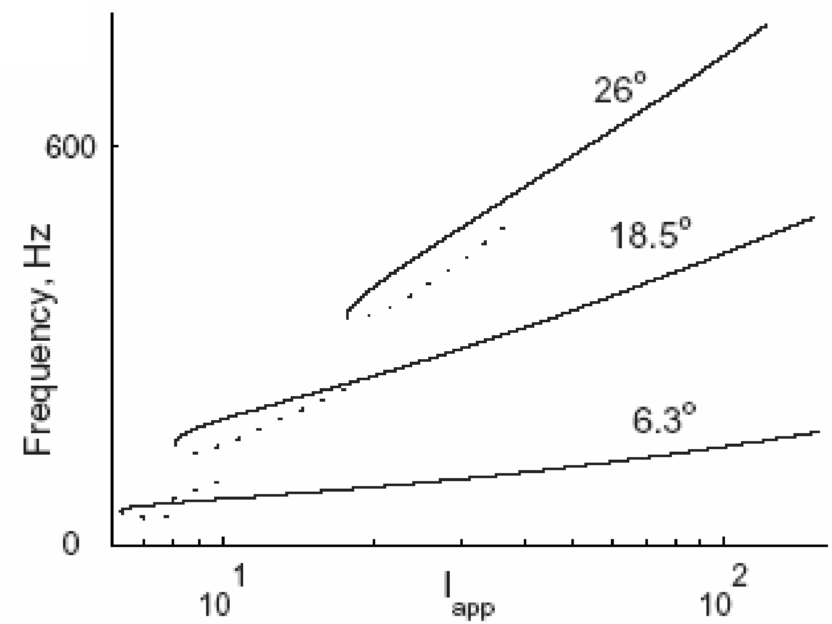
Repetitive Firing, HH model and others

Response to current step

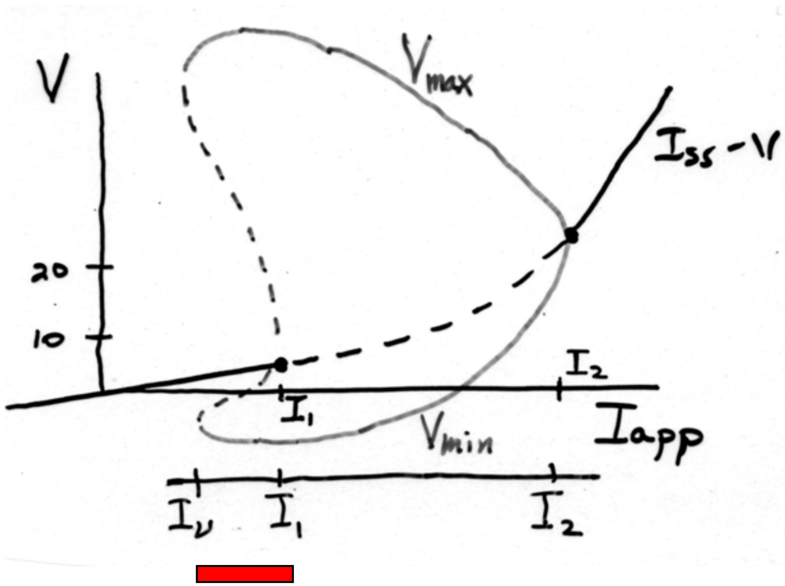
nerve block



Subthreshold



Repetitive firing in HH and squid axon -- bistability near onset

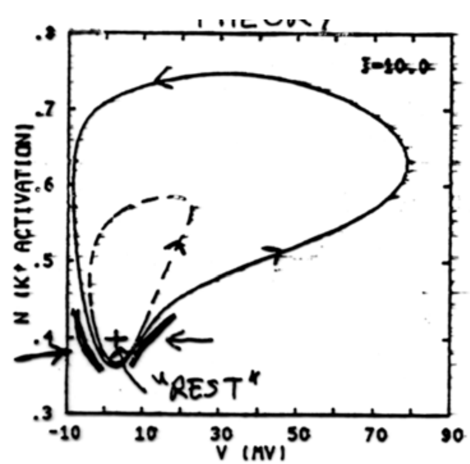


Interval of bistability

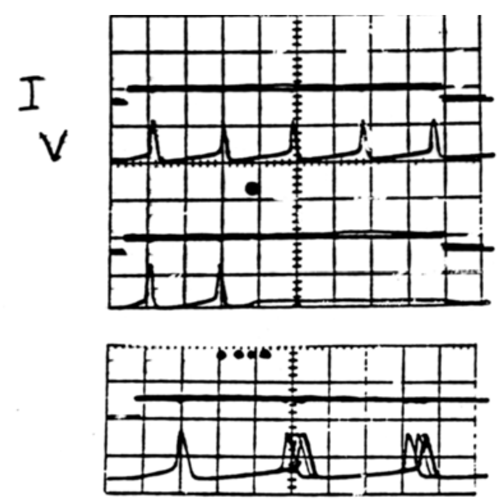
Rinzel & Miller, '80

Linear stability: eigenvalues of 4x4 matrix. For reduced model w/ $m=m_\infty(V)$: stability if $\partial I_{inst}/\partial V + C_m/\tau_n > 0$.

HH eqns

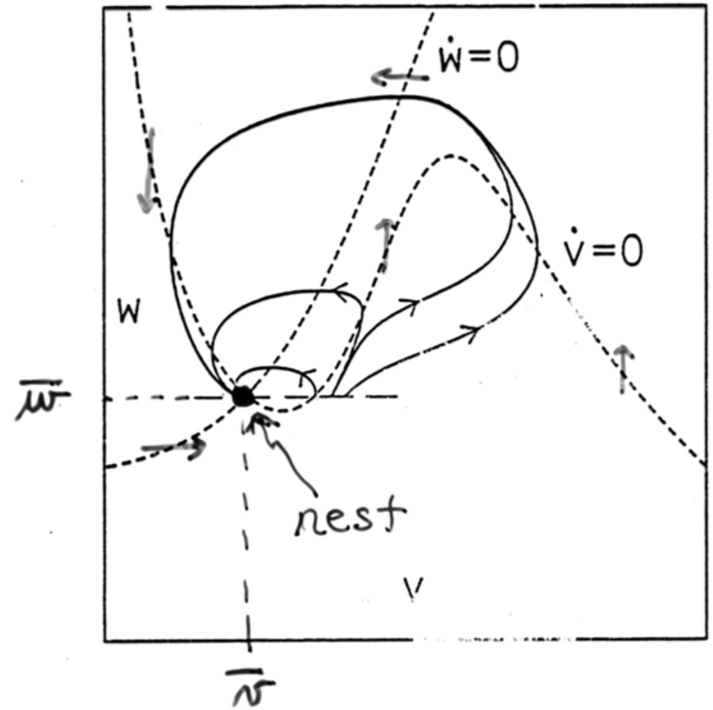


Squid axon



Guttman, Lewis & Rinzel, '80

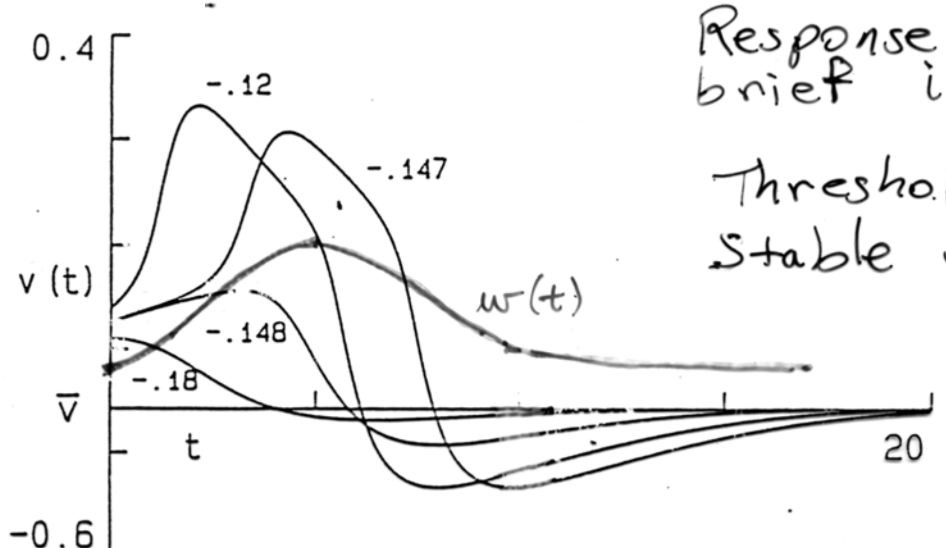
ML model
- excitable regime



V̇=0
3 Branches: "R, T, E"

Case of small φ

traj hugs V-nullcline - except for up/down jumps.



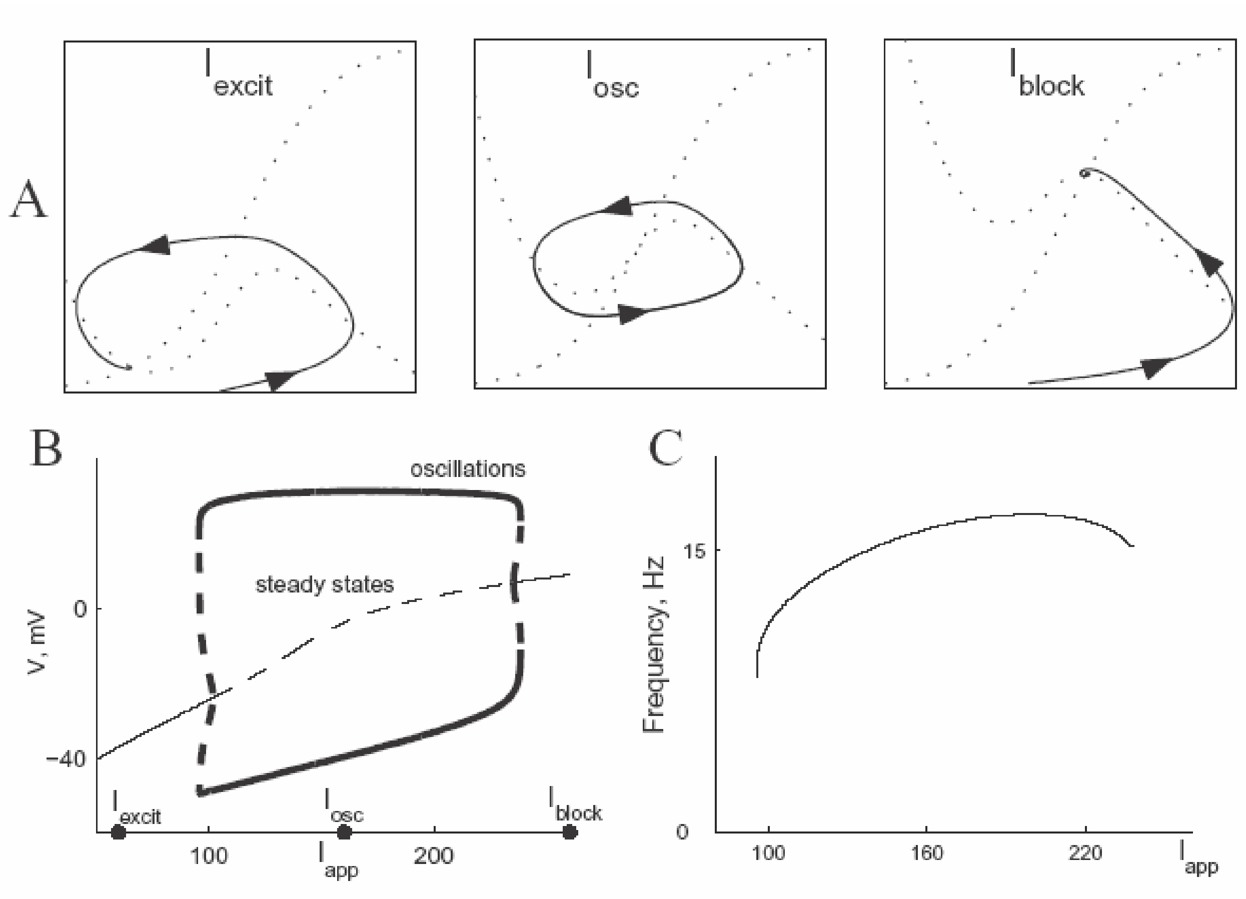
Response to brief i(t).

Threshold.

Stable rest.

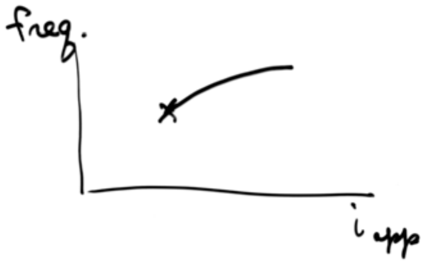
Morris-Lecar model: Repetitive firing… Type II

I_{app} ⟶



Repetitive Activity in ML (& HH)

i_{app} - adequate



"rest" — unstable

only if on middle branch (math)

Onset is via Hopf bifurcation

Condition for instability*:

damped $i < i_1$

growing $i > i_1$

(Hopf)

$$\underbrace{\frac{1}{C_m}\frac{\partial i_{ion}}{\partial v}}_{\text{"negative" resistance — destabilizing}} < -\frac{\phi}{\tau_w}$$

* near "rest"
i_{ss} – monotone

“Type II” onset

Hodgkin ‘48

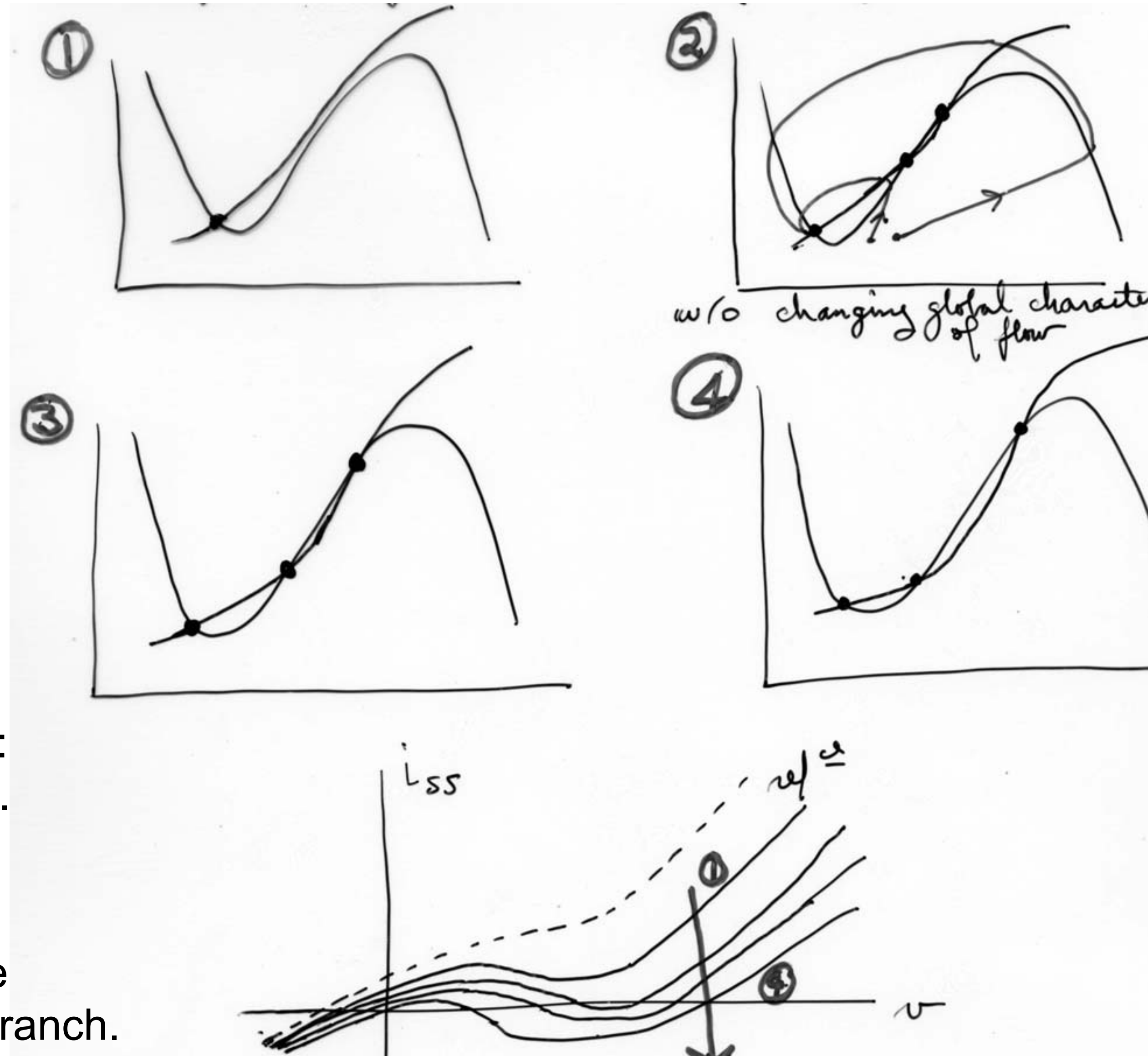
Adjust param's → changes nullclines: case of 3 "rest" states

3 states → I_{ss}
is N-shaped

Stable or Unstable?

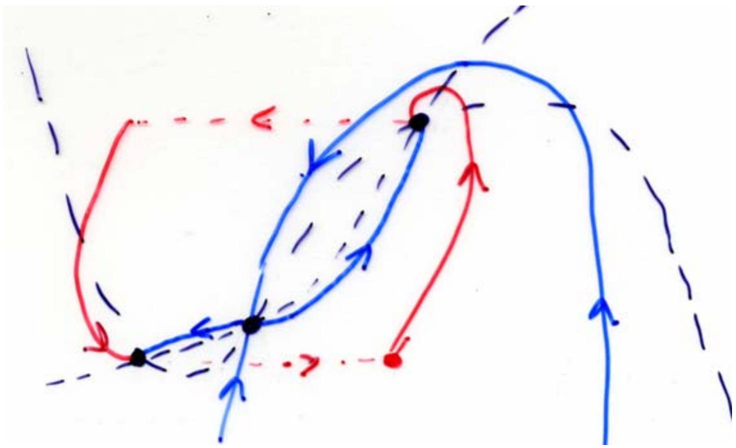
3 states – not necessarily:
stable – unstable – stable.

Φ small enough,
then both upper/middle
unstable if on middle branch.

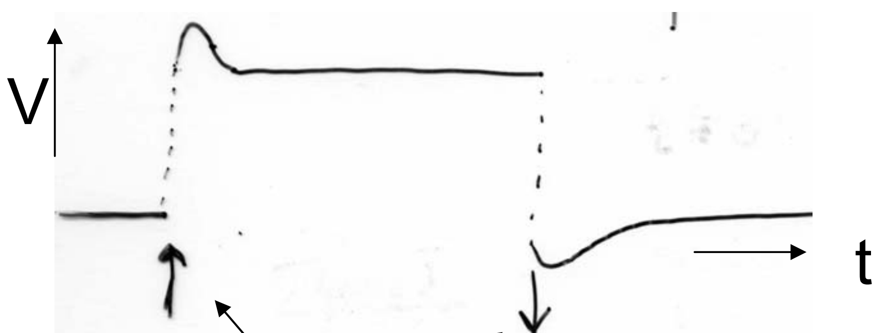


ML: φ large → 2 stable steady states

Neuron is bistable: plateau behavior.



Saddle point, with
stable and unstable manifolds

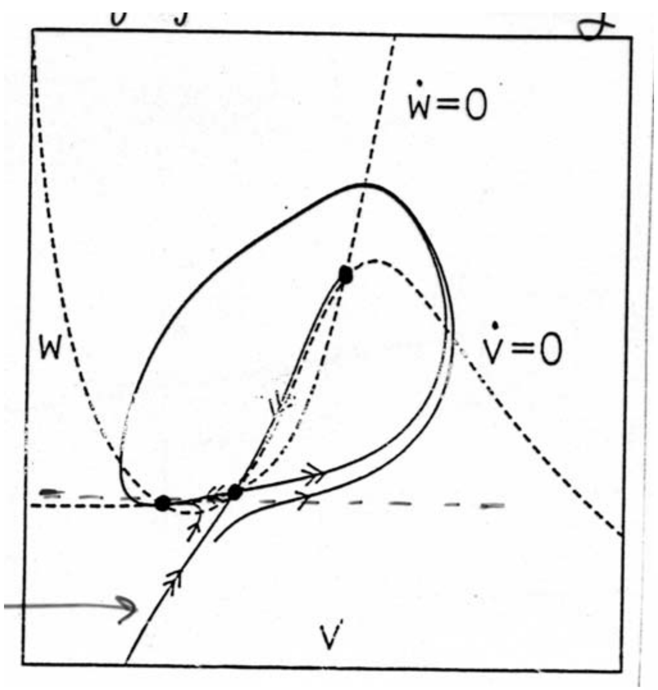


I_{app} switching pulses

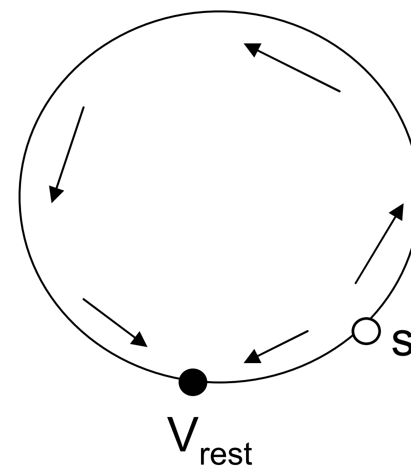
e.g., HH with
V_K = 24 mV

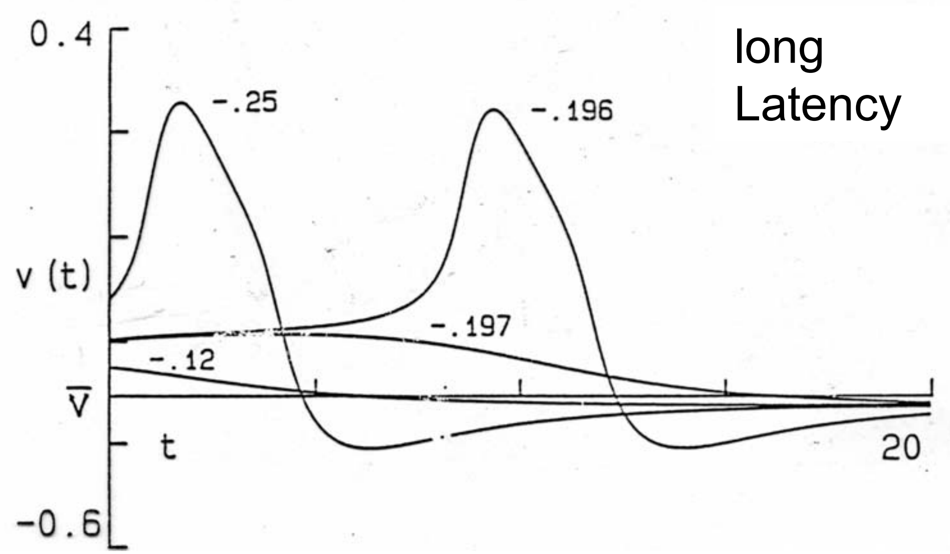
ML: φ small → both upper states are unstable

Neuron is excitable with strict threshold.



threshold separatrix





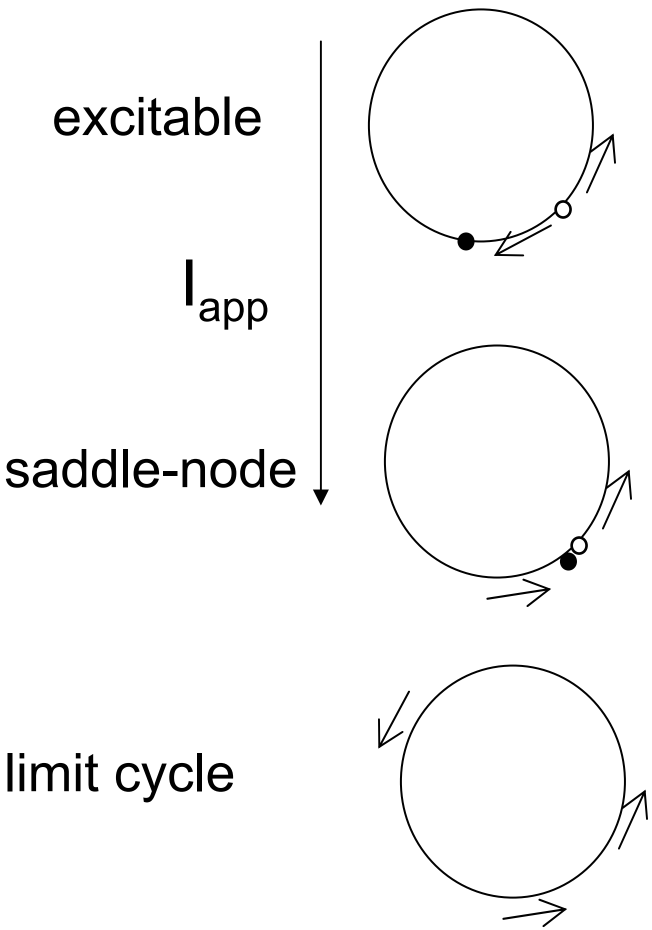
long Latency

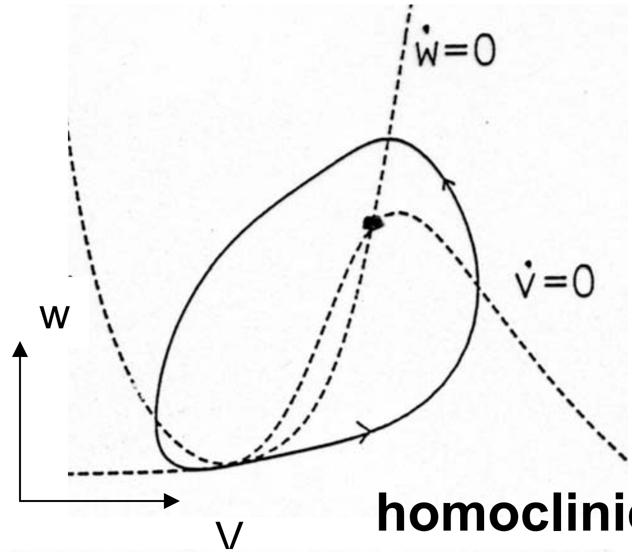
I_{ss} must be N-shaped.

$I_{K\text{-}A}$ can give long latency but not necessary.

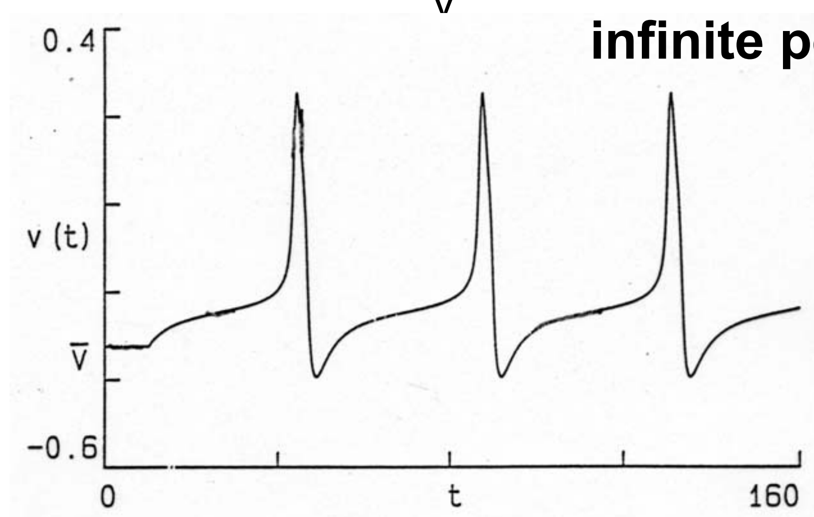
Onset of Repetitive Firing – 3 rest states

SNIC- saddle-node on invariant circle





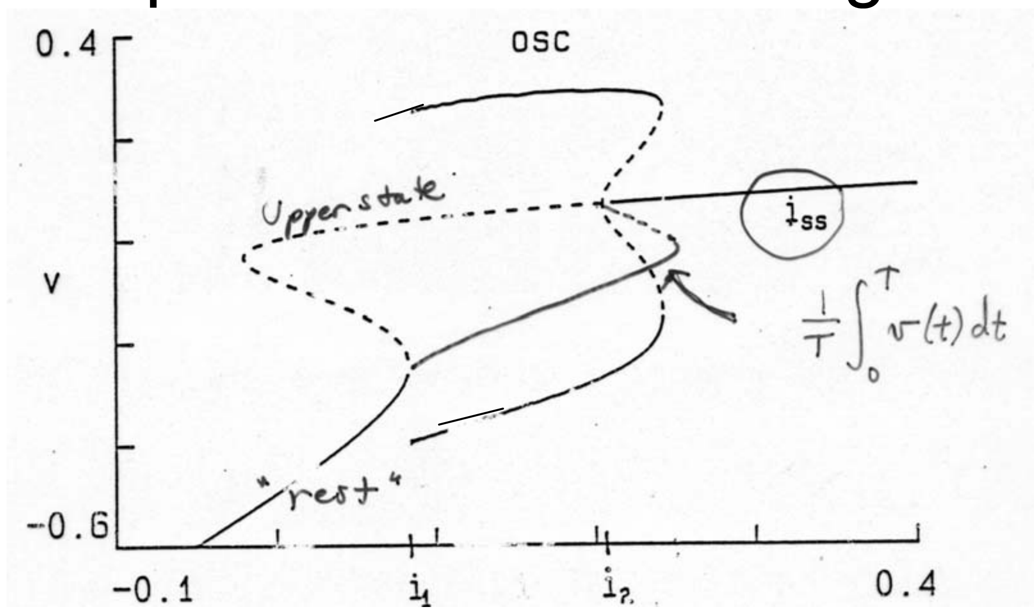
homoclinic orbit; infinite period



emerge w/ large amplitude – zero frequency

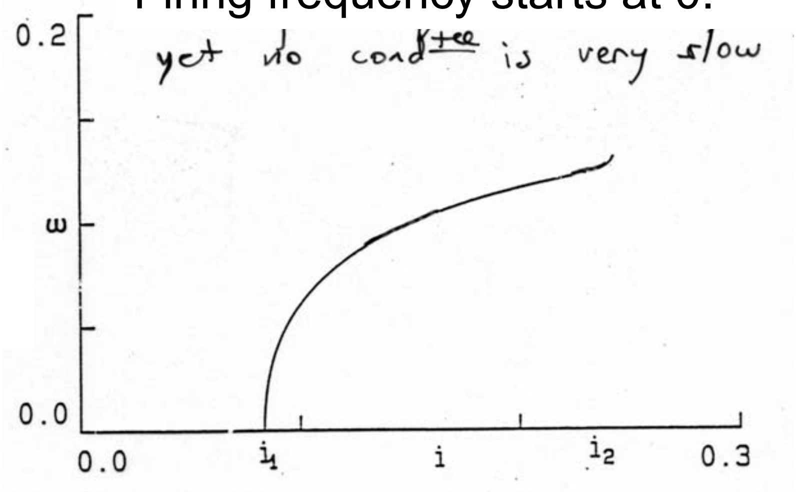
Response/Bifurcation diagram

ML: φ small



freq $\sim\sqrt{I - I_1}$

Firing frequency starts at 0.



low freq but no conductances very slow

$I_{K\text{-}A}$? (Connor et al '77)

"Type I" onset

Hodgkin '48

Transition from Excitable to Oscillatory

Same for W-C network models.

Type II, min freq ≠ 0

- I_{ss} monotonic
- subthreshold oscill'ns
- excitable w/o distinct threshold
- excitable w/ finite latency

Type I, min freq = 0

- I_{SS} N-shaped – 3 steady states
- w/o subthreshold oscillations
- excitable w/ "all or none" (saddle) threshold
- excitable w/ infinite latency

Hodgkin '48 – 2 classes of repetiitive firing;
Also - Class I less regular ISI near threshold

J Neurophysiol 92: 2283–2294, 2004;
10.1152/jn.00109.2004.

Threshold Firing Frequency–Current Relationships of Neurons in Rat Somatosensory Cortex: Type 1 and Type 2 Dynamics

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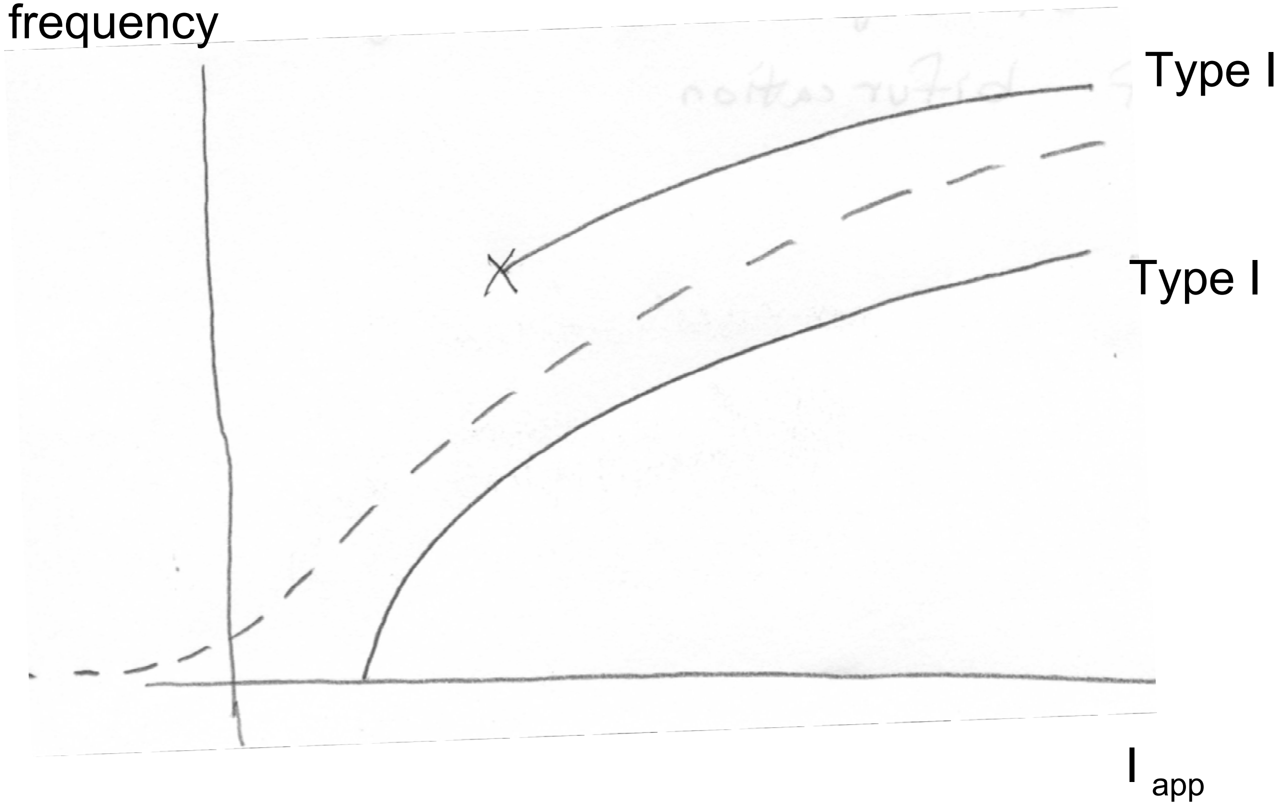
Tateno, T., A. Harsch, and H.P.C. Robinson. Threshold firing frequency–current relationships of neurons in rat somatosensory cortex: type 1 and type 2 dynamics. *J Neurophysiol* 92: 2283–2294, 2004; 10.1152/jn.00109.2004. Neurons and dynamical models of spike generation display two different types of threshold behavior, with steady current stimulation: type 1 [the firing frequency vs. current (*f–I*) relationship is continuous at threshold) and type 2 (discontinuous *f–I*)]. The dynamics at threshold can have profound effects on the encoding of input as spikes, the sensitivity of spike generation to input noise, and the coherence of population firing. We have examined the *f–I* and frequency–conductance (*f–g*) relationships of cells in layer 2/3 of slices of young (15–21 DIV) rat somatosensory cortex, focusing in detail on the nature of the threshold. Using white-noise stimulation, we also measured firing frequency and inter-spike interval variability as a function of noise amplitude. Regular-spiking (RS) pyramidal neurons show a type 1 threshold, consistent with their well-known ability to fire regularly at very low frequencies. In fast-spiking (FS) inhibitory interneurons, although regular firing is supported over a wide range of frequencies, there is a clear discontinuity in their *f–I* relationship at threshold (type 2), which has not previously been highlighted. FS neurons are unable to support maintained periodic firing below a critical frequency f_c, in the range of 10 to 30 Hz. Very close to threshold, FS cells switch irregularly between bursts of periodic firing and subthreshold oscillations. These characteristics mean that the dynamics of RS neurons are well suited to encoding inputs into low-frequency firing rates, whereas the dynamics of FS neurons are suited to maintaining and quickly synchronizing to gamma and higher-frequency input.

of these 2 types, which thus represent the behavior of a wide range of excitable membranes.

Even simple dynamical models of spike generation can exhibit both kinds of behavior, depending on their parameters (Morris and Lecar 1981; Rinzel and Ermentrout 1998). In these models, because of the different natures of dynamical bifurcation at threshold, type 1 behavior is associated with all-or-nothing spikes, whereas type 2 behavior is associated with graded spike amplitude and subthreshold oscillations. Recently, modeling studies have shown that the threshold type of the neuron profoundly affects the reliability of spike generation in the presence of noise (Gutkin and Ermentrout 1998; Robinson and Harsch 2002). Experimental classification of the responses of neurons in the cortex, however, has focused mostly on the form of the frequency vs. current (*f–I*) relationship in responses that are well above threshold (Connors and Gutnick 1990; Kawaguchi and Kubota 1997; Nowak et al. 2003); a clear classification of the continuity or discontinuity of the *f–I* relationship at threshold is lacking. Therefore in this paper we study the thresholds of 2 well-characterized types of cell—regular-spiking and fast-spiking neurons—and show that they follow type 1 and type 2 behaviors, respectively. We discuss what impact this could have on the roles of these 2 cell types in the cortical network.

METHODS

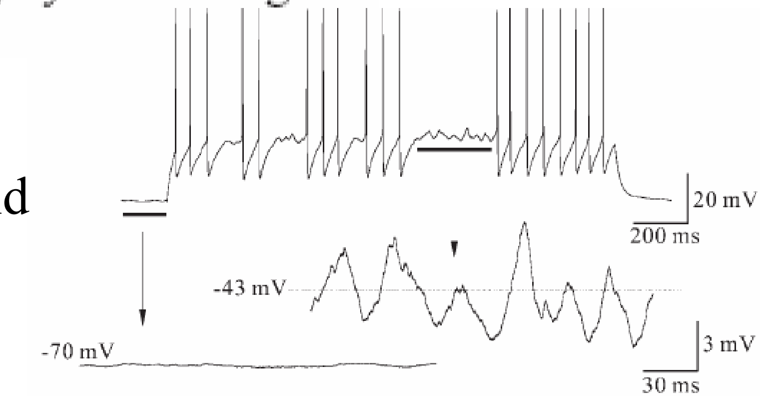
Noise smooths the f-I relation



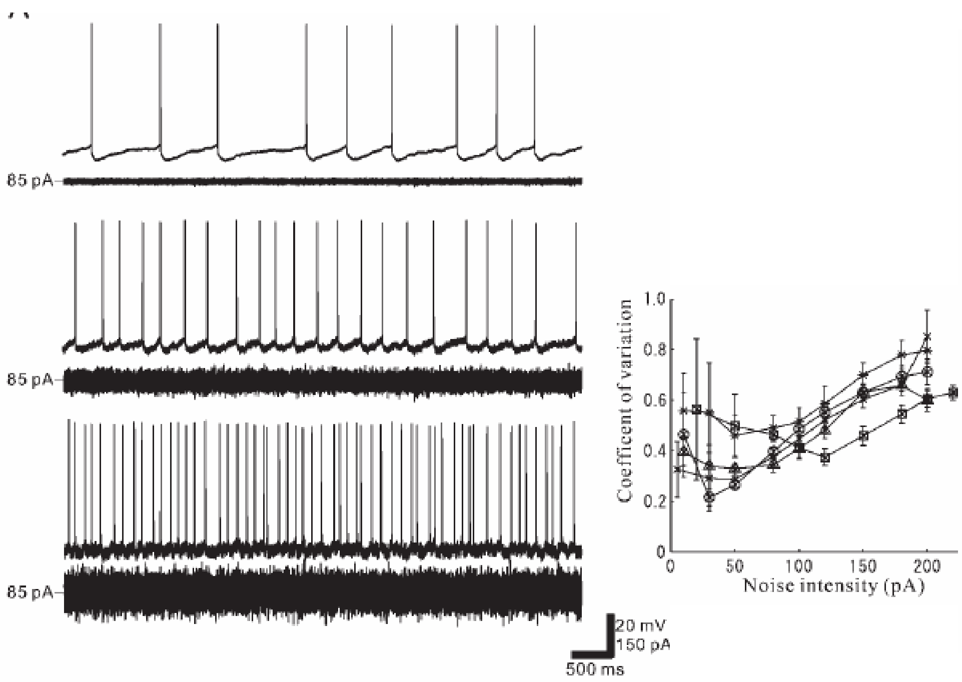
Analogy for firing rate network models?

to 30 Hz. Very close to threshold, FS cells switch irregularly between bursts of periodic firing and subthreshold oscillations. These characteristics mean that the dynamics of RS neurons are well suited to encoding inputs into low-frequency firing rates, whereas the dynamics of FS neurons are suited to maintaining and quickly synchronizing to gamma and higher-frequency input.

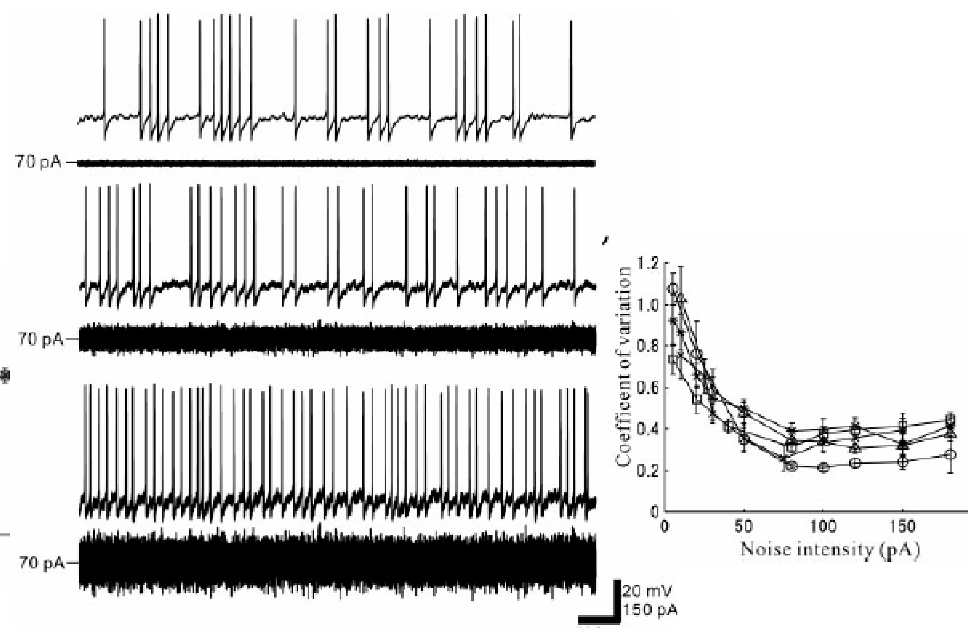
FS cell
near threshold



RS cell, w/ noise



FS cell, w/ noise



Electrical Activity of Cells

- $V = V(x,t)$, distribution within cell
  - uniform or not?, propagation?
- Coupling to other cells
- Nonlinearities
- Time scales

Current balance equation for membrane:

$$\underbrace{C_m \frac{\partial V}{\partial t}}_{\text{capacitive}} + \underbrace{I_{ion}(V)}_{\text{channels}} = \underbrace{\frac{d}{4R_i} \frac{\partial^2 V}{\partial x^2}}_{\text{cable properties}} + I_{app} + \underbrace{\text{coupling}}_{\text{other cells}}$$

Coupling: $\sum_{\mathbf{j}} g_{c,j}(V_j - V)$ "electrical" - gap junctions

other cells

$\sum_{\mathbf{j}} g_{syn,j}(V_j(t))\,(V_{syn} - V)$ chemical synapses

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$I_{ion} = I_{ion}(V,\mathbf{W})$ generally nonlinear

$= \sum_{\mathbf{k}} g_k(V,\mathbf{W})\,(V - V_k)$

channel types

$\partial \mathbf{W}/\partial t = \mathbf{G}(V,\mathbf{W})$

gating dynamics