On the Dynamics of Cortical Populations

Lawrence Sirovich

Laboratory of Applied Mathematics,

Mt. Sinai School of Medicine

Collaborators

Ehud Kaplan, Mt. Sinai School of Medicine

&

Bruce W. Knight, Rockefeller University

http://camelot.mssm.edu

Introduction

Goal is to Mathematically Model Mammalian Visual System

If done properly, modeling introduces theory.

I will report on a joint experimental & theoretical effort.
Kaplan & Sirovich Laboratories

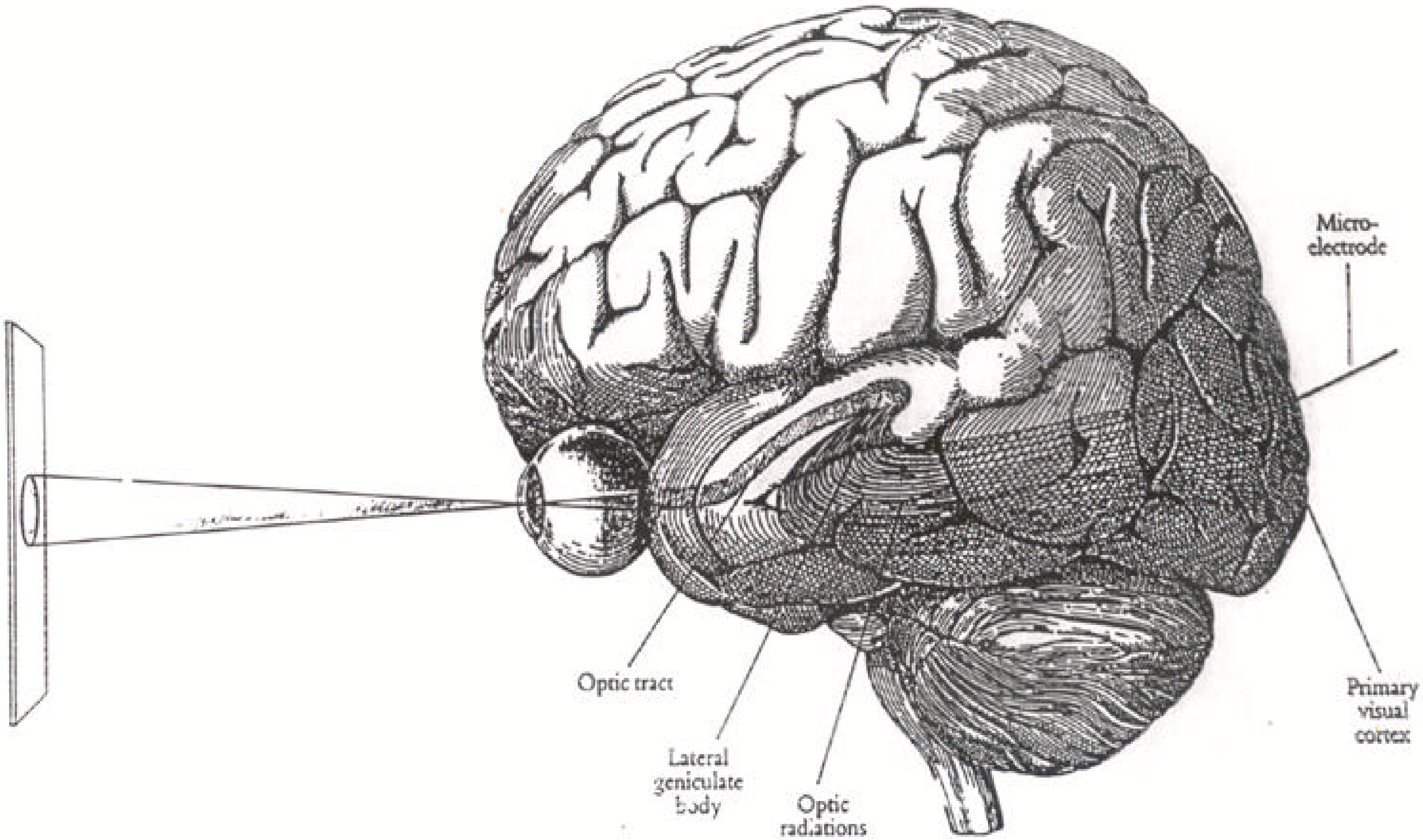
Visual system has remarkable range. We can detect as few as ~5 photons and up to O(10^{13}) that amount in daylight.

Seeing starts with encoding photon arrivals, biochemically, into electrical signals(retina).

Encoded signal travels to cortex as ‘action potentials’ *spikes*.

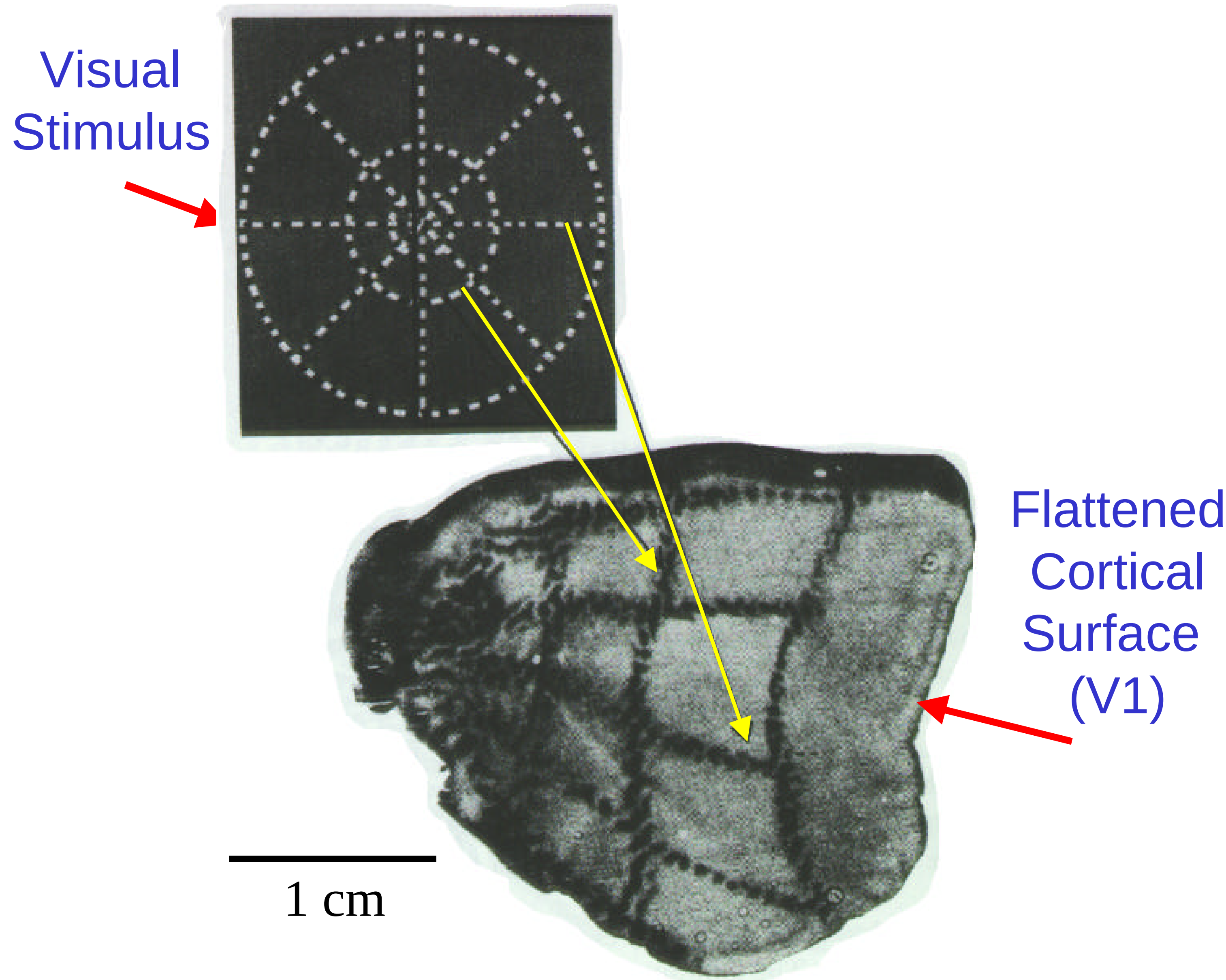
Beautiful world we see is cortical decoding of encoded photon arrivals.

Transformation of External World

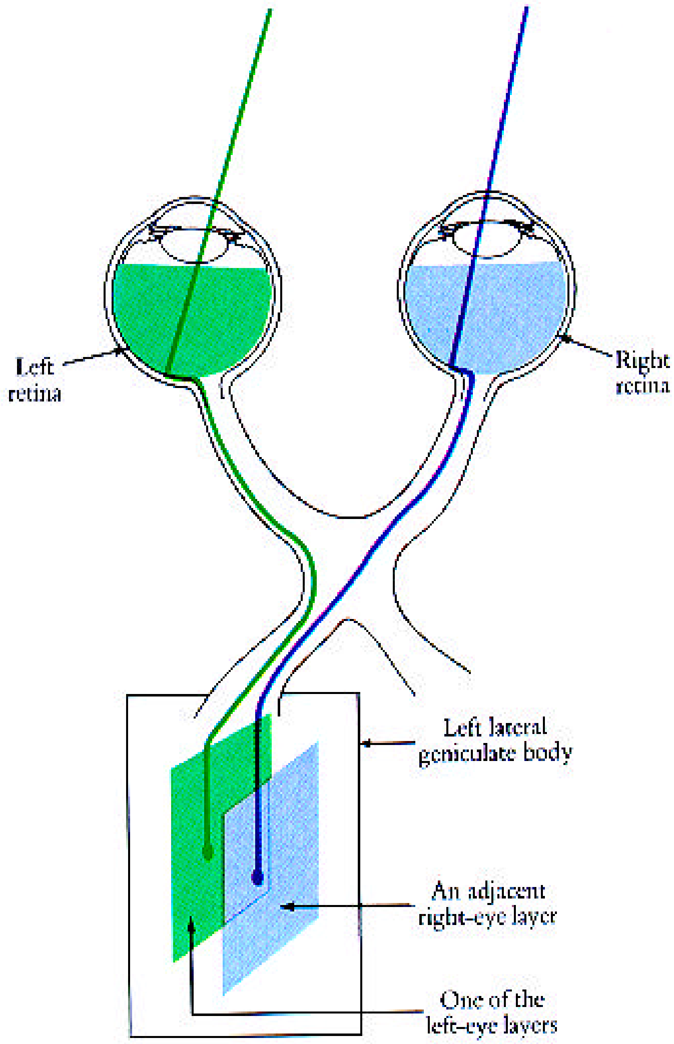


The primary visual cortex is a piece of tissue, less than 2mm thick, 15 cm^2 in area. Visual cortex contains roughly 10^9 neurons in roughly 40 areas.

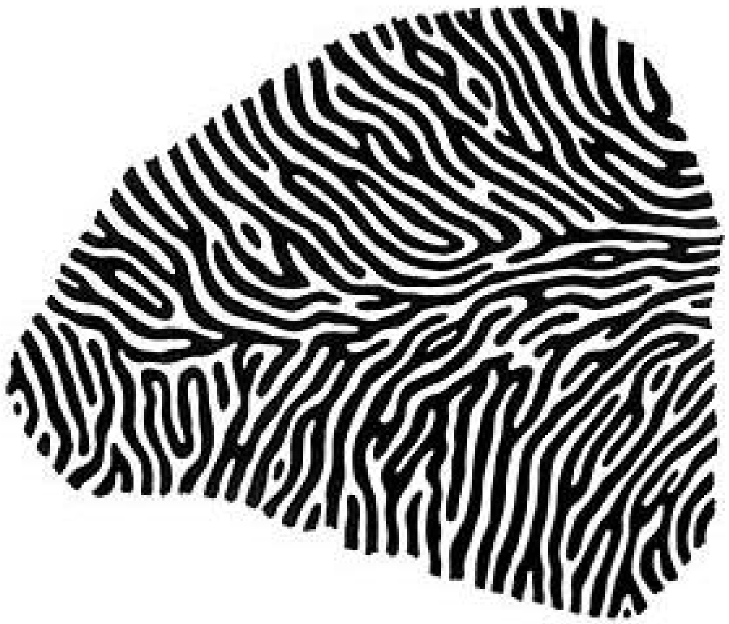
Map of Visual World onto Primate Visual Cortex, Tootel, *et al* (1988)



The inputs from the two eyes are segregated all the way to the visual cortex



from D. Hubel, 1988

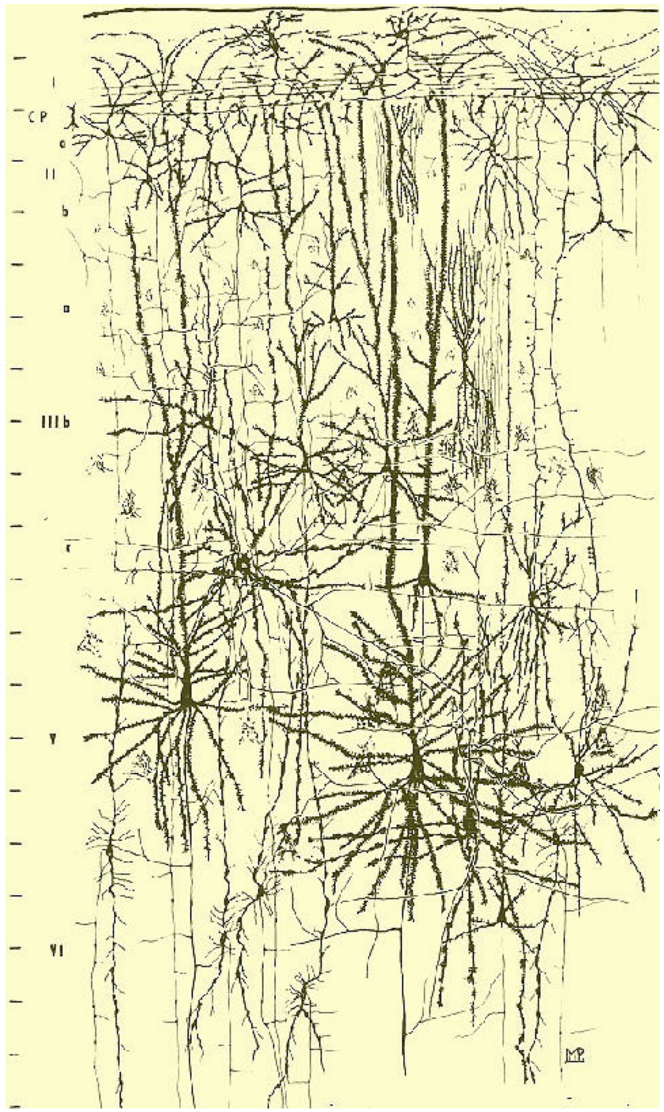


Monkey primary visual cortex

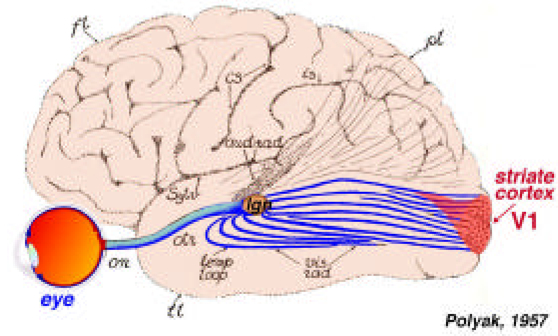
From LeVay, Hubel & Wiesel, 1975

Golgi staining of cortical cells

1.8 mm



Numbers



Retina – 10^8 photoreceptors

Optic Tract-10^6 fibers

LGN – 10^6 neurons

Primary Visual Cortex (15 cm^2) – 10^8 neurons
(full visual field)

1mm^2 : full range of modalities – 10^5 neurons

10 modalities/mm – 10^4 neurons/patch

Each neuron talks to 10^4 – 10^5 neurons

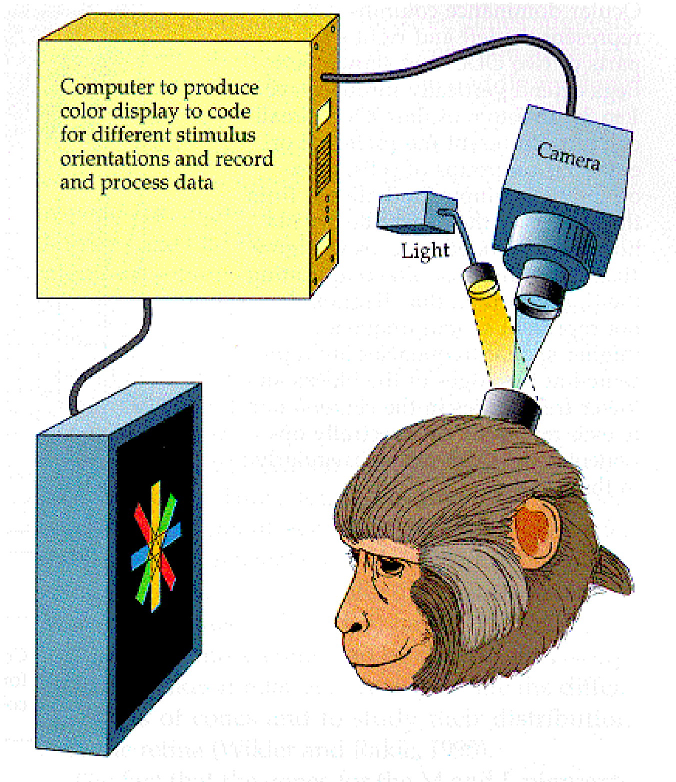
Roughly 40 areas, each covers the full field of vision

Time scales range from sub-millisec. to many seconds.

Faithful direct numerical simulation is not possible.

Long Range Goal- A Numerical Cortex

Optical Imaging

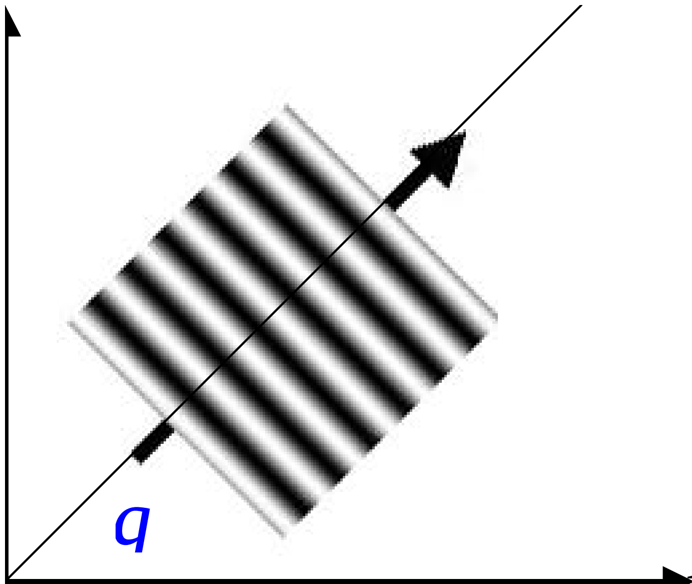


Cortical activity in response to (computer controlled) stimuli produces changes in reflectivity from cortical tissue.

Mapping of primary visual cortex under ocular dominance and orientation preference well established by optical imaging.

Optical imaging has presented us with serious signal analysis problems.

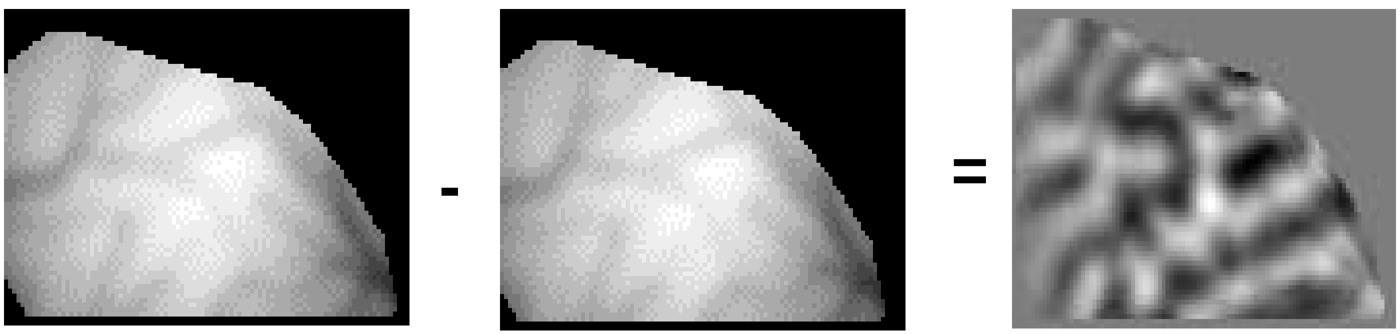
Signal / Noise ~10^{-3} – 10^{-4}



‘*Differential*’ Imaging

Ensemble of Images: $\{f(t,q,x)\}$

$$f(t,q,x) = B(t,x) + S_q(t,x), \quad \|S_q\| \div \|B\| \approx 10^{-3}$$

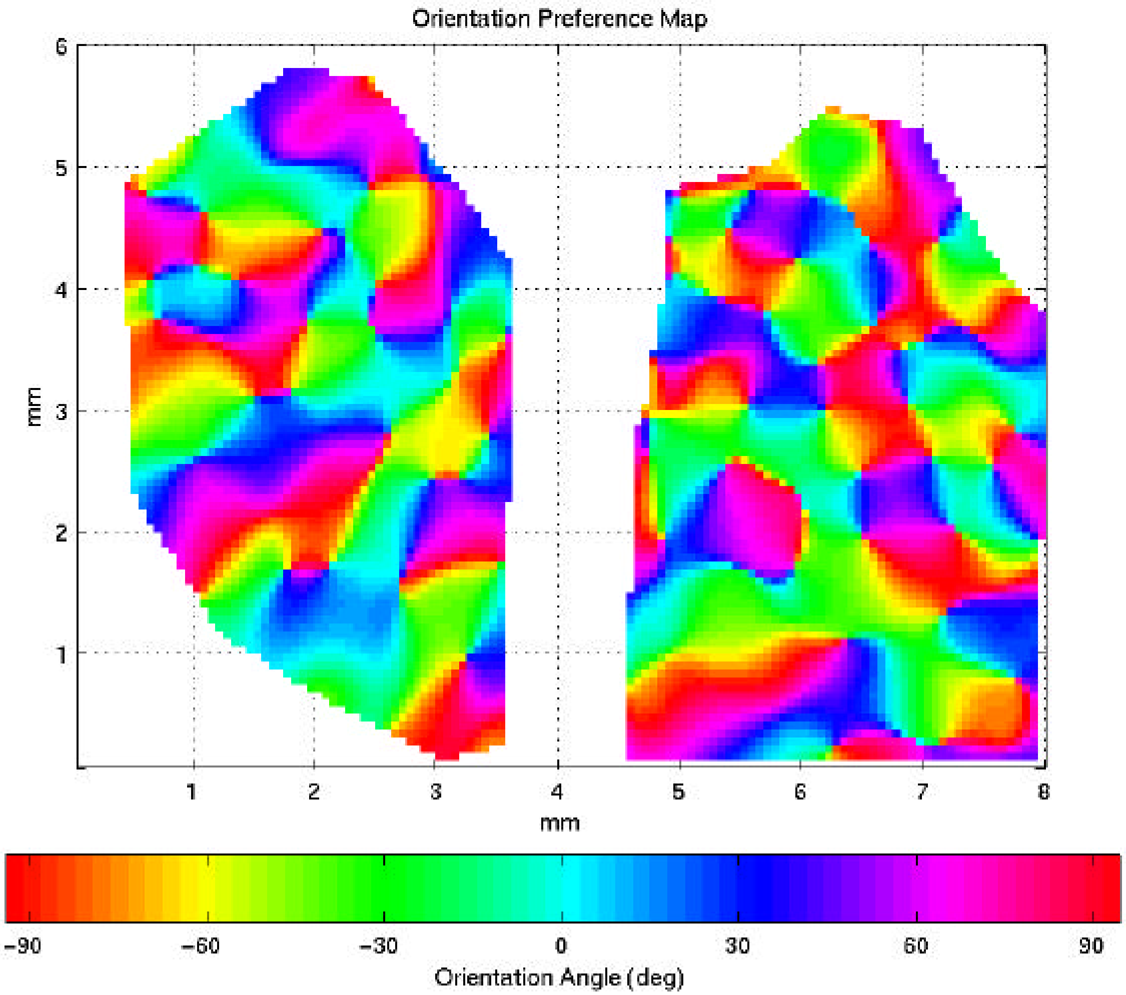


left right Ocular Dominance

$$< F(q,x) >_q = \lim_{T\uparrow\infty} < \frac{1}{T}\int_{-T/2}^{T/2} \left(f_r(t,q,x) - f_l(t,q,x) \right) dt >_q$$

Orientation Preference Map

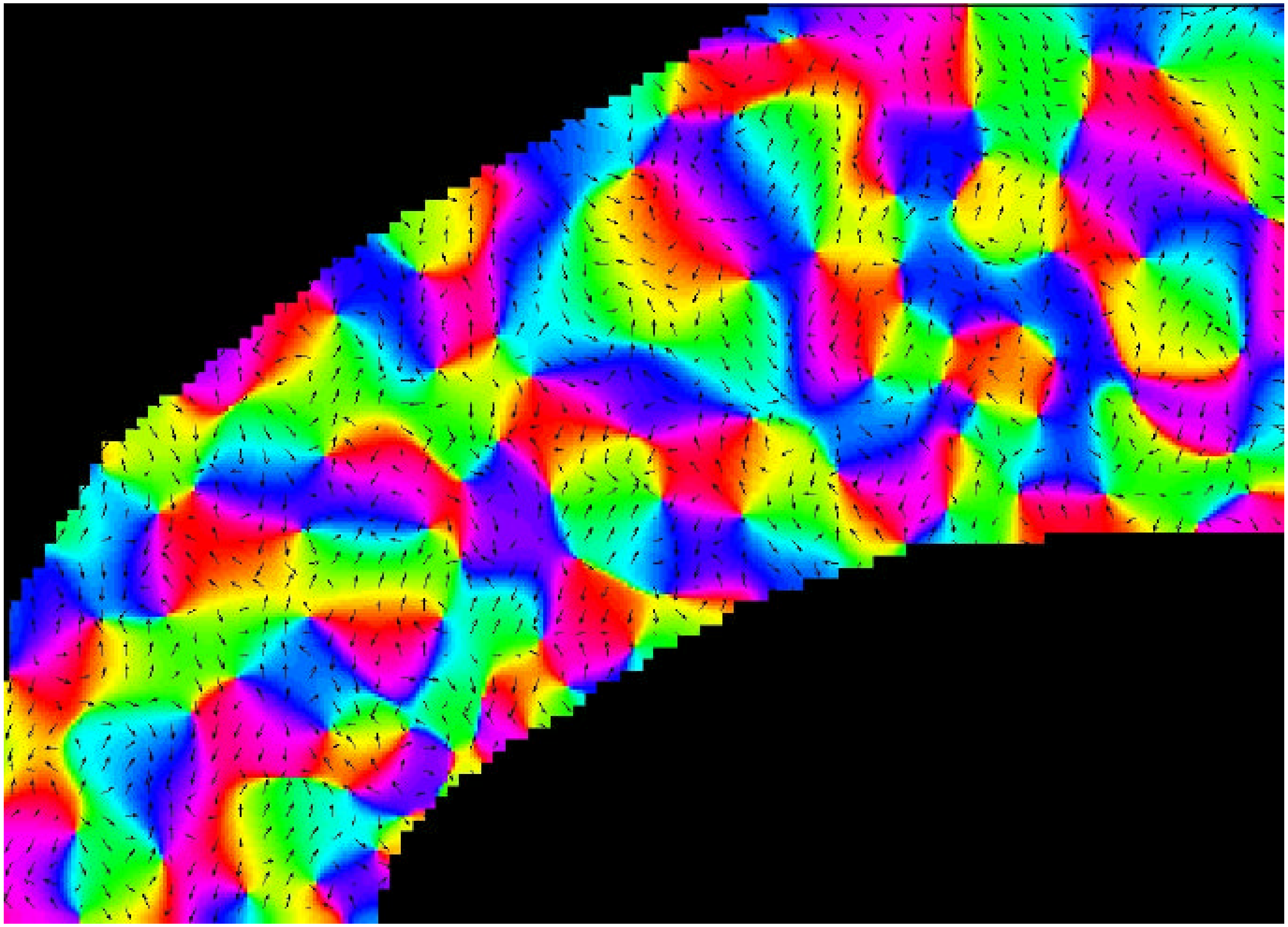
(At each pixel determine preferred orientation.)



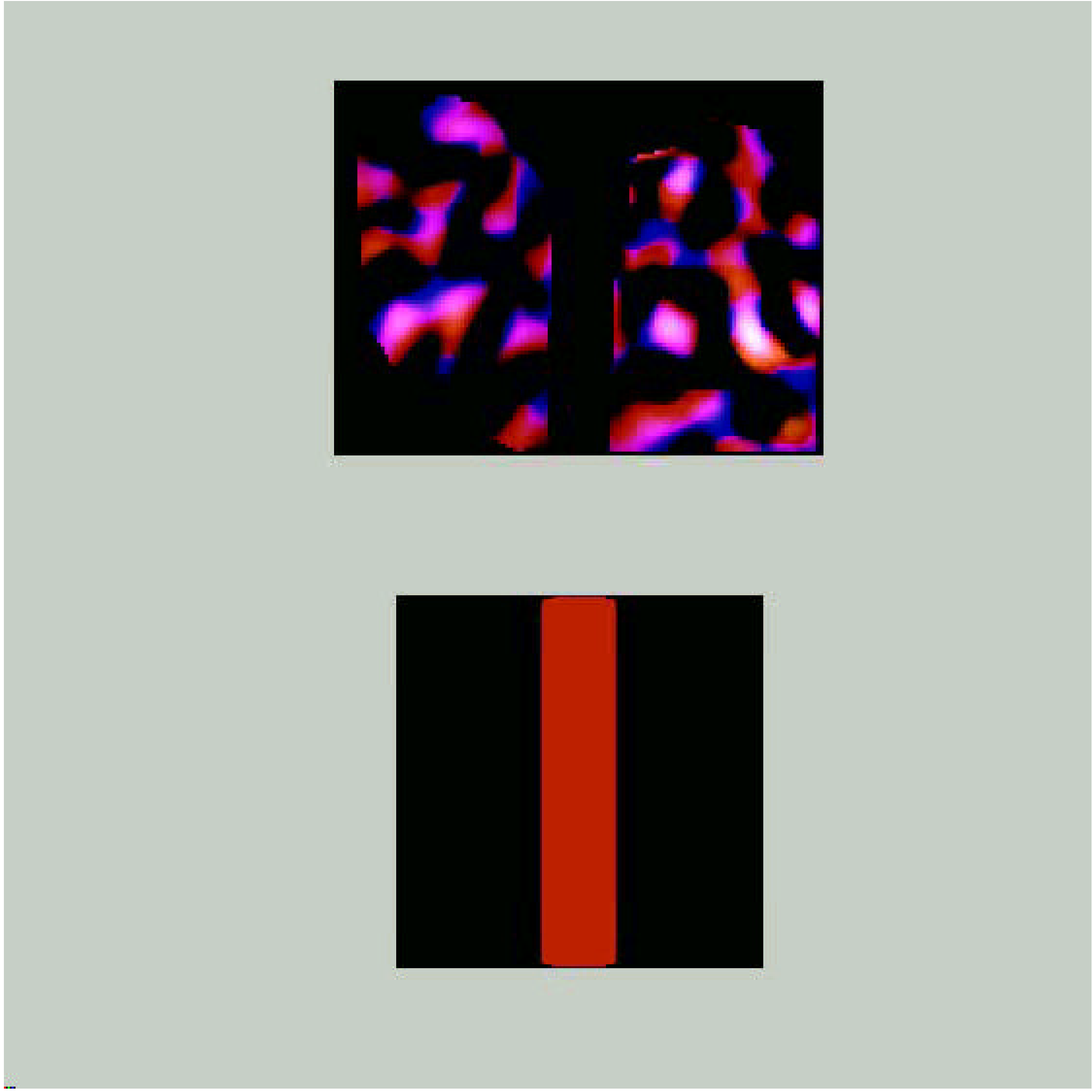
Orientation Preference Columns

G. Blasdel (1989)

Orientation & Direction



Orientation Dynamics



Modalities

Primary Visual Cortex, V1 (or area 17) is Gateway to Visual Cortex

External World is Represented in Terms of:

1. Orientation
2. Spatial Frequency

} Local Fourier Analysis

3. Temporal Frequency
4. Direction
5. Two Color Mechanisms

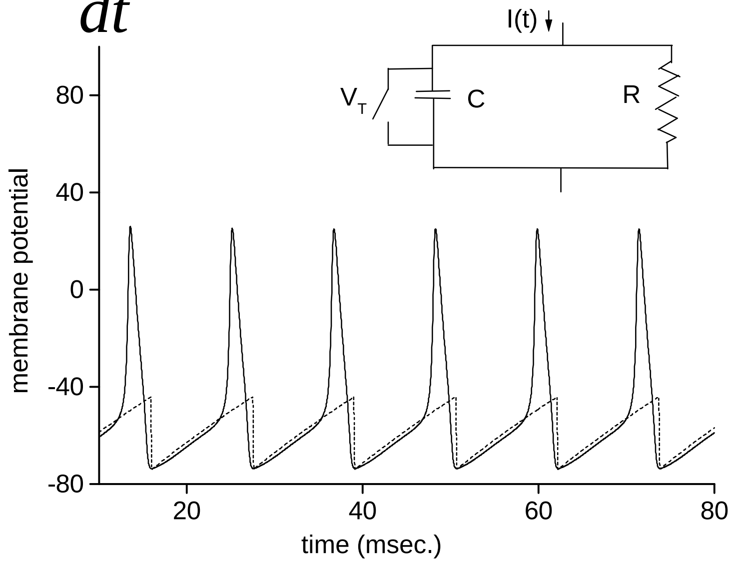
7. ?????

Single Neuron Dynamics

Integrate-and-Fire Approximation

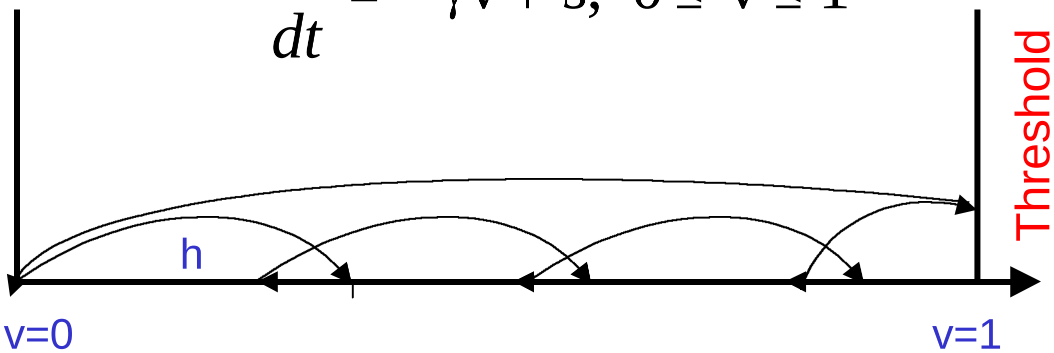
(Excellent Hodgkin-Huxley Approximation)

$$\frac{d\mathrm{v}}{dt} = -\gamma \mathrm{v} + s; \;\; 0 \le \mathrm{v} \le 1$$



Population Modeling– *A Statistical Mechanics*

$$\frac{dv}{dt} = -\gamma v + s;\ \ 0 \le v \le 1$$



Synaptic arrival rate:

s =s/h

Probability: $r\,(v,t)$; *J,* flux of r

$$\frac{\partial r}{\partial t} = -\frac{\partial}{\partial v} J$$

$$J = \left\{ -(g\, v r) + s\ (t) \int_{v-h}^{v} r\ (v)\, dv \right\}$$

Population Equation

$$\frac{\partial r}{\partial t} = g\ \frac{\partial}{\partial v}(v r) + s\ (t)\{ r\ (v-h) - r\ (v)\}$$

Additional Remarks

B.C. $J(v=1) = J(v=0)$: probability is conserved. $\rho(1)=0$, $v=1$, absorbing boundary.

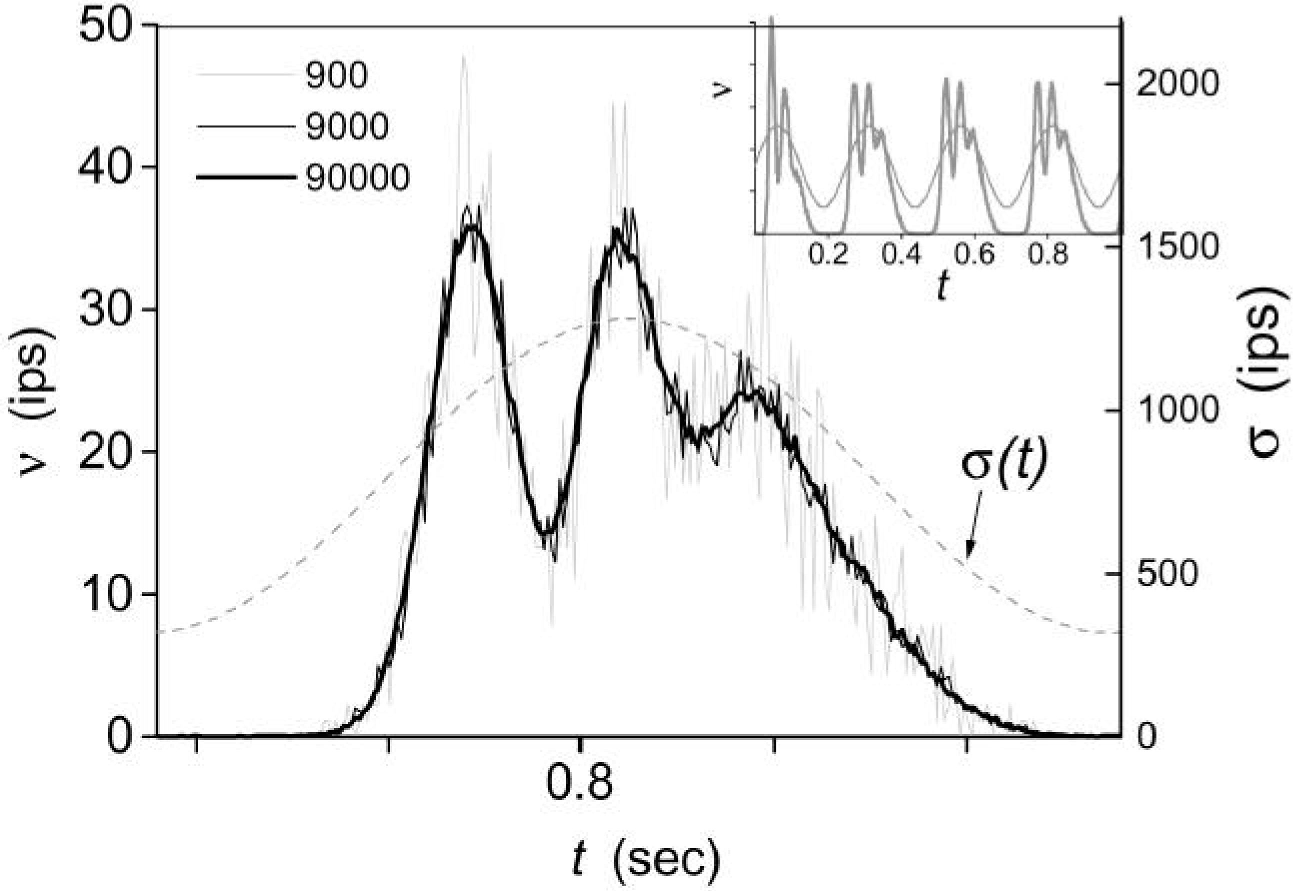
Another form:

$$\frac{\partial \rho}{\partial t} = \gamma \frac{\partial}{\partial v}(v\rho) + \sigma(t)\{\rho(v-h) - \rho(v)\} + \sigma(t)\int_{1-h}^{1} \rho(v')dv'\delta(v)$$

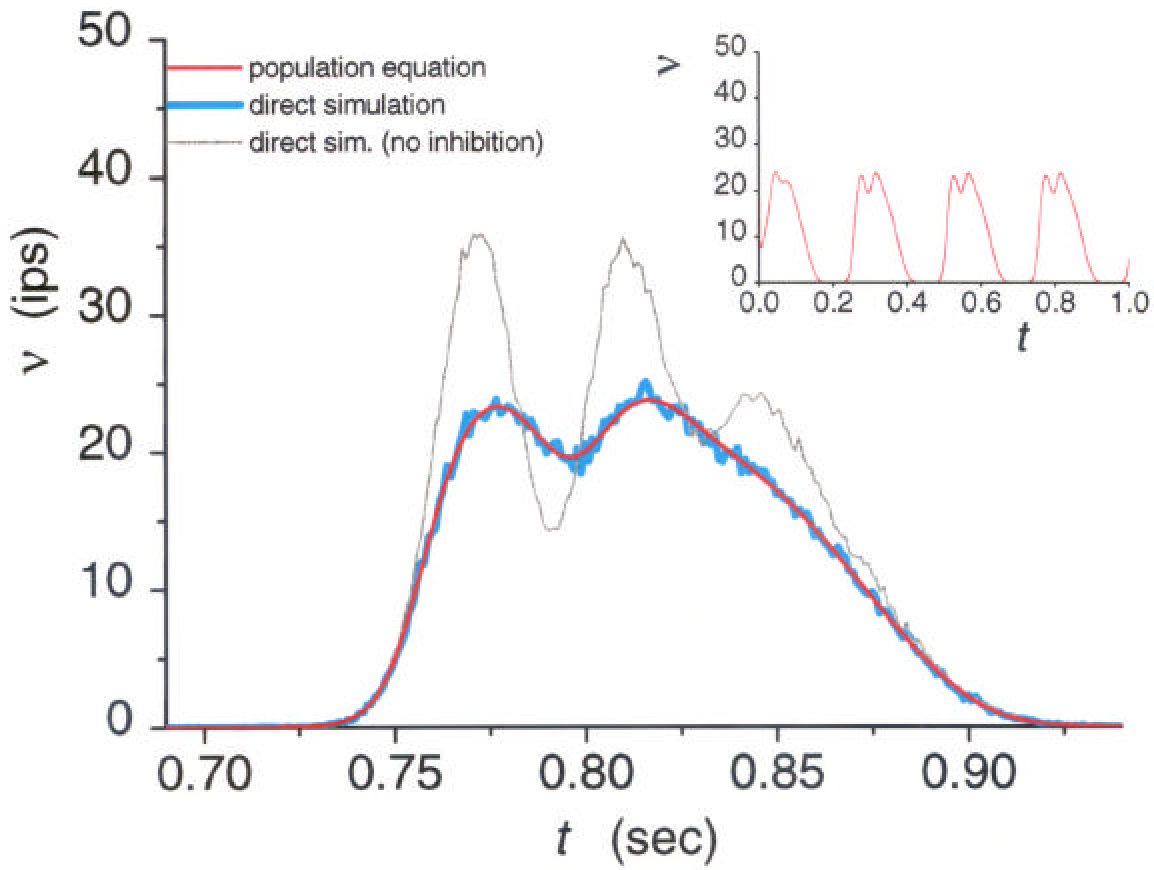
Per neuron firing rate:

$$r(t) = J(v=1) = \sigma(t)\int_{1-h}^{1} \rho(v')dv' = \sigma(t)A$$

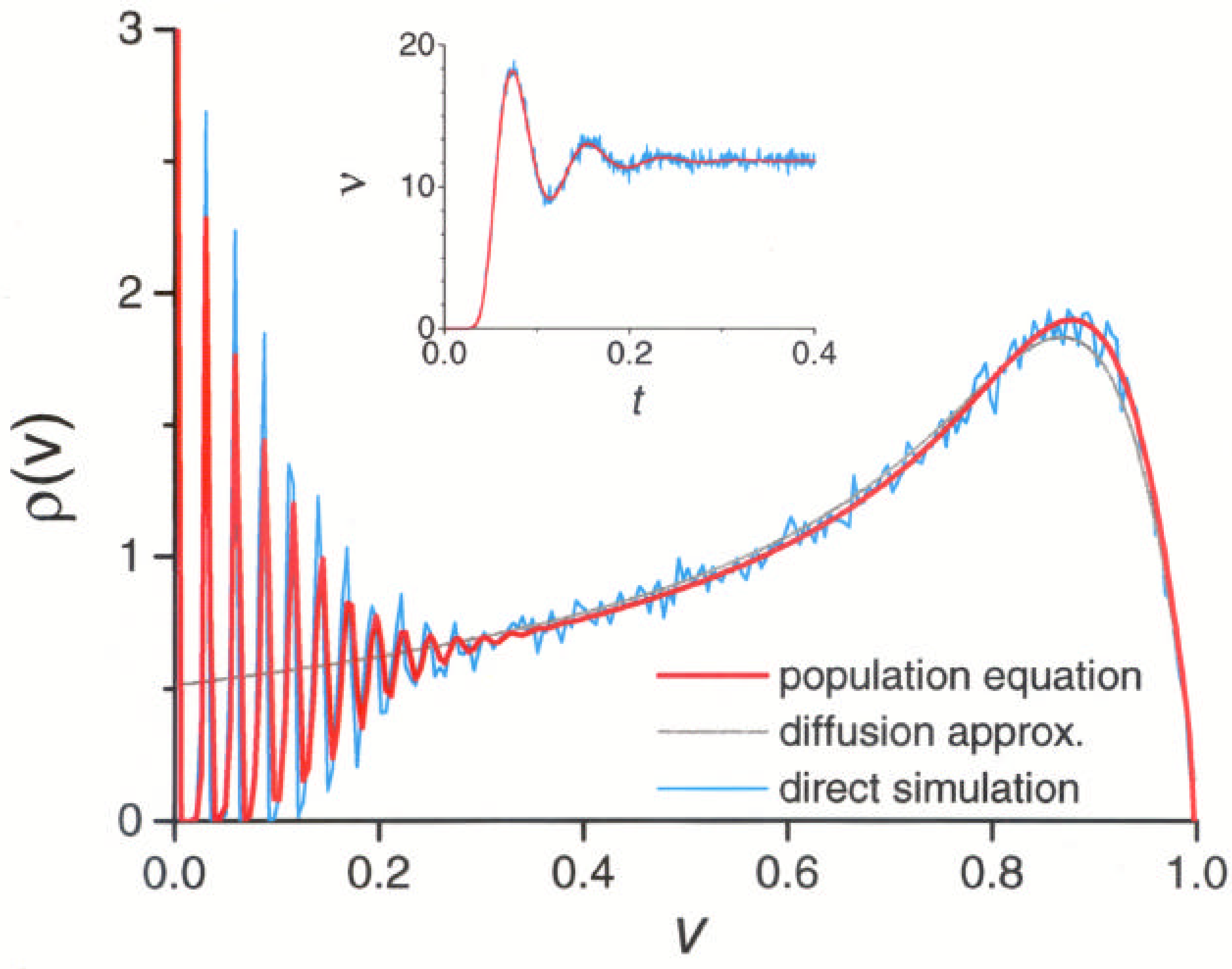
Direct Simulation vs Population Calculation: Sinusoidal Driving: No Free Parameters



Excitation & Inhibition



Equilibrium Density, $\theta=100$, h$=.03$
Direct Simulation, $O(10^5)$ Neurons, vs. Population Calculation



The Eigenfunction Problem

Normalize

$$\partial_t r = L r = \frac{1}{q}\frac{\partial}{\partial \mathrm{v}}(\mathrm{v} r) + \{ r(\mathrm{v}-h) - r(\mathrm{v}) \} + \int_{1-h}^{1} r(\mathrm{v}')\, d\mathrm{v}' d(\mathrm{v}); \quad q = \frac{s}{g}$$

Eigenfunction Problem

$$Lf = l f;\ J(f)_{\mathrm{v}=0} = J(f)_{\mathrm{v}=1};\ f(\mathrm{v}=1) = 0$$

Adjoint Problem

$$L^{\dagger}\widehat{\phi} = \begin{cases} -\frac{v}{\theta}\frac{\partial}{\partial v}\widehat{\phi} - \left\{ \widehat{\phi}(v) - \widehat{\phi}(v+h) \right\}; 0 \le v \le 1-h \\ -\frac{v}{\theta}\frac{\partial}{\partial v}\widehat{\phi} - \left\{ \widehat{\phi}(v) - \widehat{\phi}(0) \right\}; 1-h \le v \le 1 \end{cases} .$$

$$\widehat{\phi}(0) = \widehat{\phi}(1)$$

$l=0$ corresponds to equilibrium (f =1 for adjoint problem)

Zero Leak ($g=0$)

$$\frac{\partial r}{\partial t} = Lr = \{r(\mathrm{v}-h) - r(\mathrm{v})\} + \int_{1-h}^{1} r(\mathrm{v}')\,d\mathrm{v}'\,\delta(\mathrm{v})$$

$$\rho(v,t) = \sum_{k=1}^{N} \rho_k(v,t)$$

$$\rho_k(v,\tau) = \widehat{\rho}_k(v,\tau) + D_k(\tau)\delta(v-(k-1)h)$$

$$\frac{d}{dt}\widehat{\boldsymbol{\rho}} = \mathbf{L}\widehat{\boldsymbol{\rho}}.$$

$$\mathbf{L} = \begin{pmatrix} -1 & 0 & 0 & \dots & \dots & 0 \\ T_h & -1 & & & & \\ 0 & T_h & -1 & 0 & \dots & 0 \\ 0 & 0 & T_h & & & \vdots \\ \vdots & & & & & \\ 0 & 0\dots & & 0 & T_h & -1 \end{pmatrix}$$

$$T_h f(v) = f(v-h)$$

Zero Leak ($g=0$) ,continued

$$\widehat{\rho}_N(v,t) = e^{-\tau}\sum_{k=1}^{N}\frac{(\tau T_h)^{N-k}}{(N-k)!}\rho_k^0(v) = e^{-\tau}\sum_{k=1}^{N}\frac{\tau^{N-k}}{(N-k)!}\rho_k^0(v-(N-k)h)$$

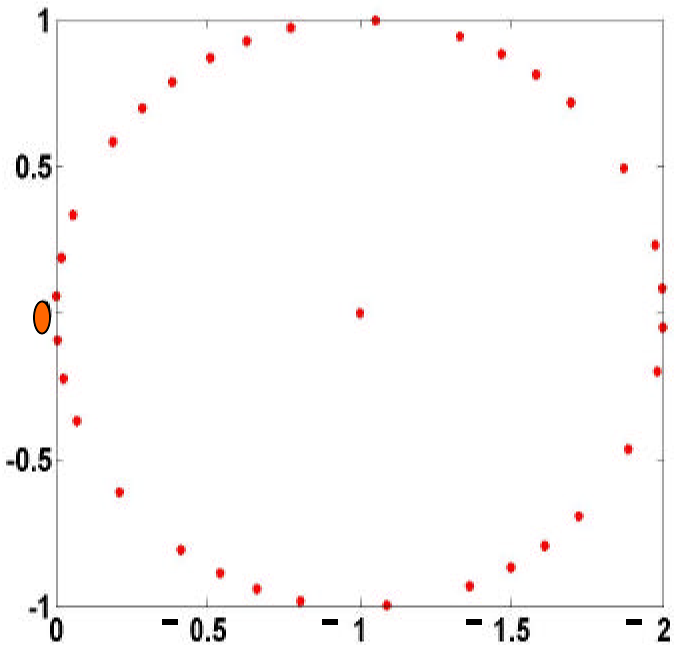
$$\frac{d}{d\tau}\mathbf{D} = \mathbf{C}\mathbf{D} + \mathbf{g}$$

$$\mathbf{C} = \begin{pmatrix} -1 & 0 & 0 & 0\dots & & 1 \\ 1 & -1 & 0 & & & \vdots \\ 0 & 1 & -1 & & & \vdots \\ \vdots & & & & & 0 \\ 0 & \dots\dots\dots & & & 1 & -1 \end{pmatrix}$$

$$\mathbf{g}^\dagger = [\int_{1-h}^{1}\widehat{\rho}_N(w,\tau)dw, 0, ..., 0]$$

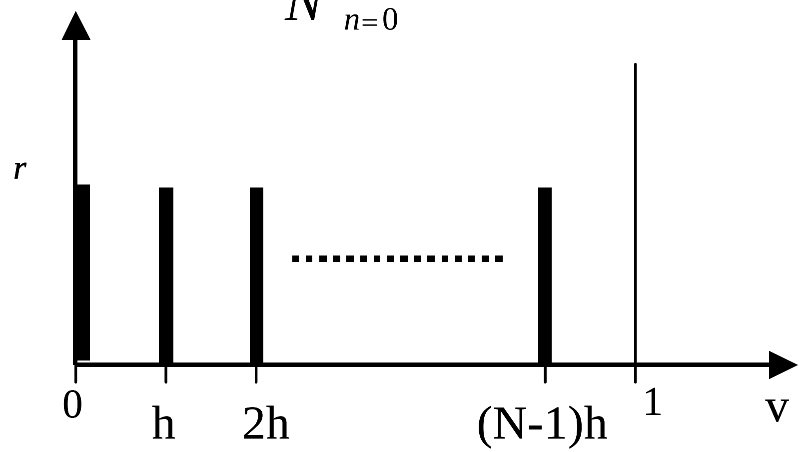
Zero Leak ($g = 0$) ,continued

Eigenvalues $, Lf = l\, f$



Equilibrium $, l = 0$

$$f_o = \frac{1}{N}\sum_{n=0}^{N-1} d\,(\mathrm{v - nh})$$



$l = -1$: Algebraic multiplicity N; Geometric multiplicity one.

Eigenvalues of C: $\lambda_j = -1 + e^{2\pi i j/N} \quad j = 0, \ldots N-1$

Finite Leak, $\gamma \neq 0$; h=1/2: Two Compartments

$$\frac{\partial \rho}{\partial \tau} = \frac{\rho}{\theta} + \frac{v}{\theta}\frac{\partial \rho}{\partial v} - \rho(v) + \rho(v - \frac{1}{2}) + A\delta(v) \quad \theta = \frac{\sigma}{\gamma}$$

$$A = \int_{\frac{1}{2}}^{1} \rho(w)dw$$

$$\rho_1 = D(\tau)\delta(v) + \widehat{\rho}_1(v,\tau),$$

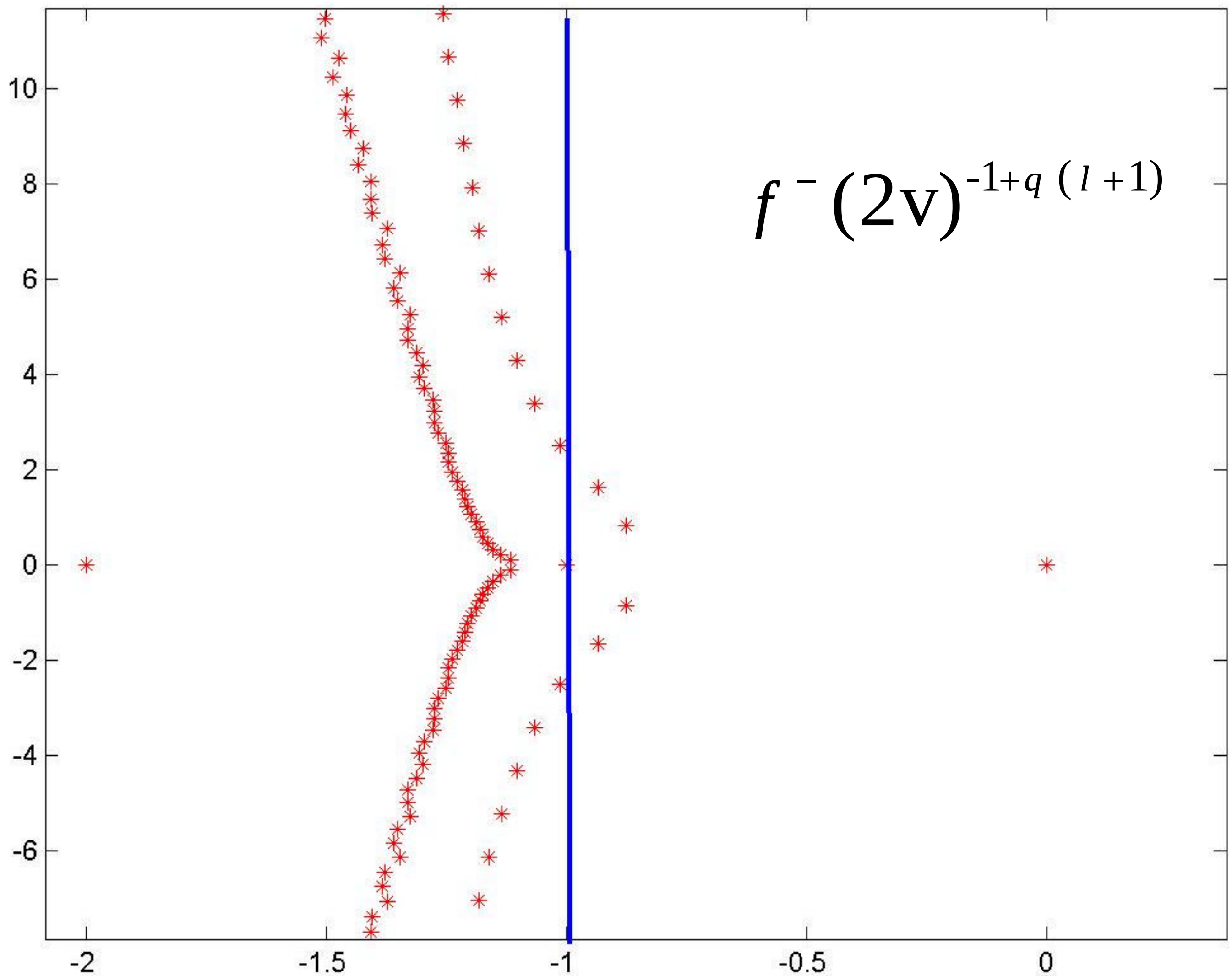
$$\dot{D} = -D + A$$

$$\frac{\partial \widehat{\rho}_1}{\partial \tau} = \frac{1}{\theta}\frac{\partial (v\widehat{\rho}_1)}{\partial v} - \widehat{\rho}_1$$

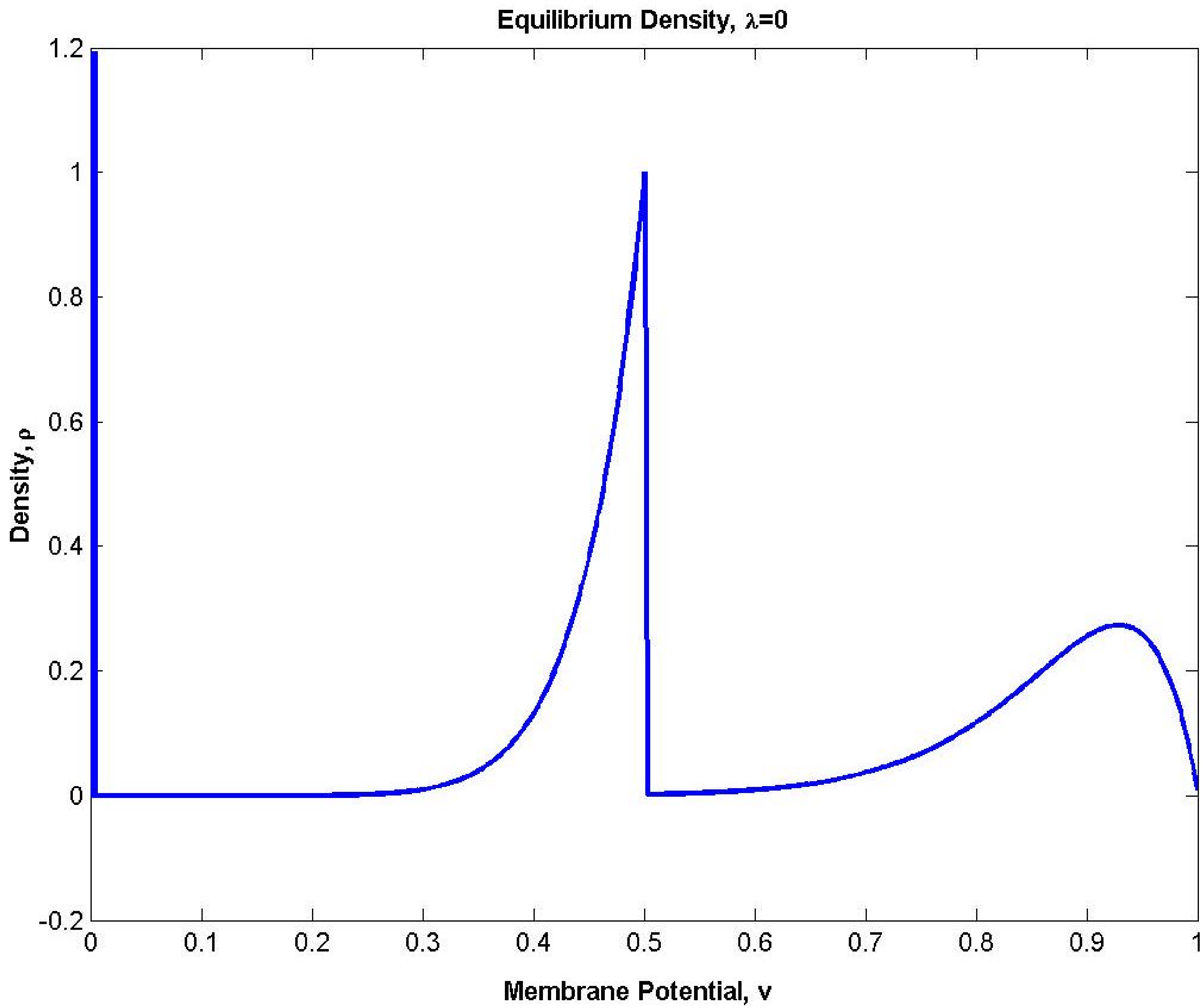
$$\frac{\partial}{\partial \tau}\rho_2 - \frac{v}{\theta}\frac{\partial}{\partial v}\rho_2 = (\frac{1}{\theta} - 1)\rho_2 + D\delta(v - \frac{1}{2}) + \widehat{\rho}_1(v - \frac{1}{2}, \tau)$$

$$\frac{1}{2\theta}(\rho^+(\tau) - \rho^-(\tau)) + D = 0$$

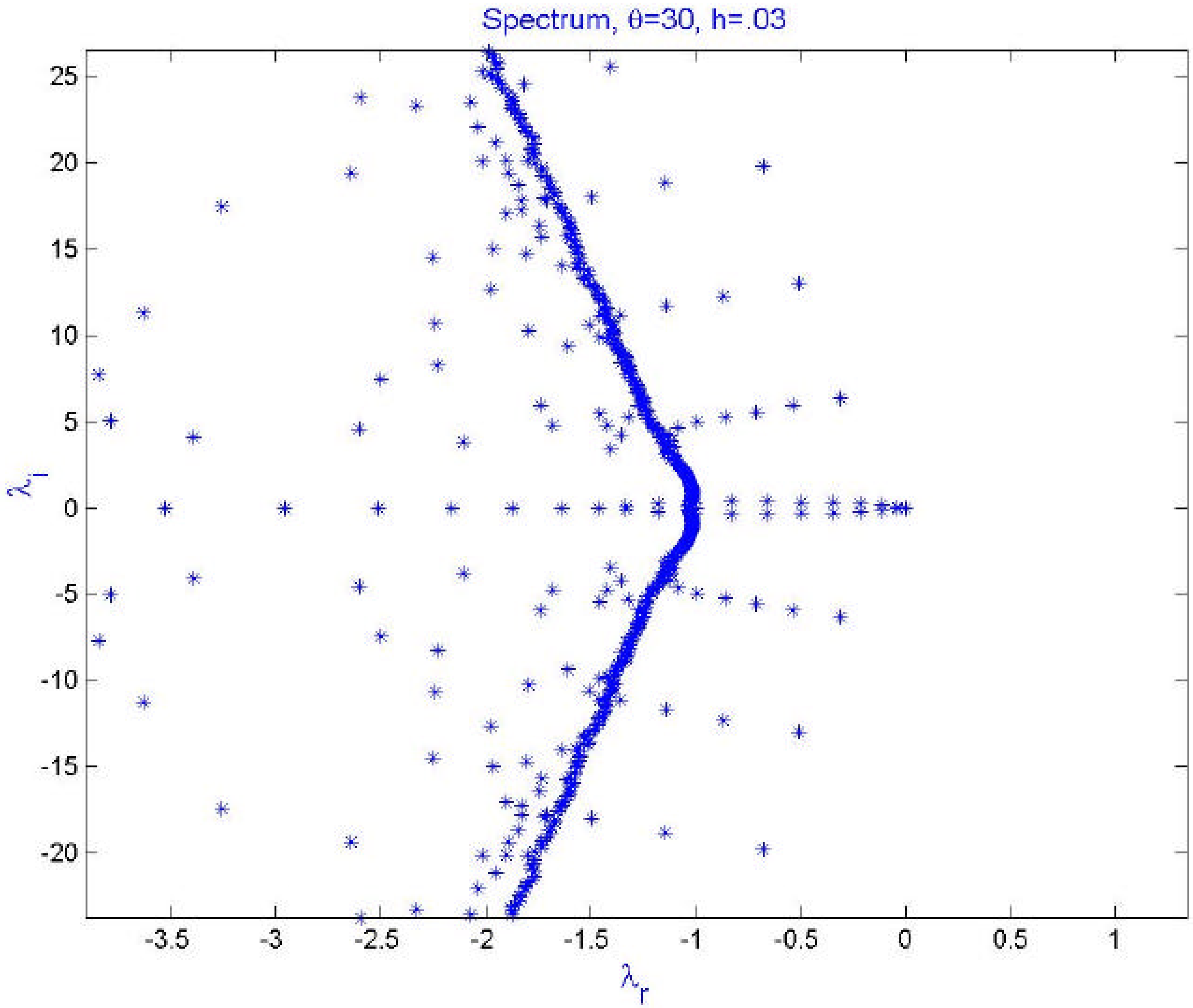
Spectrum, q=10



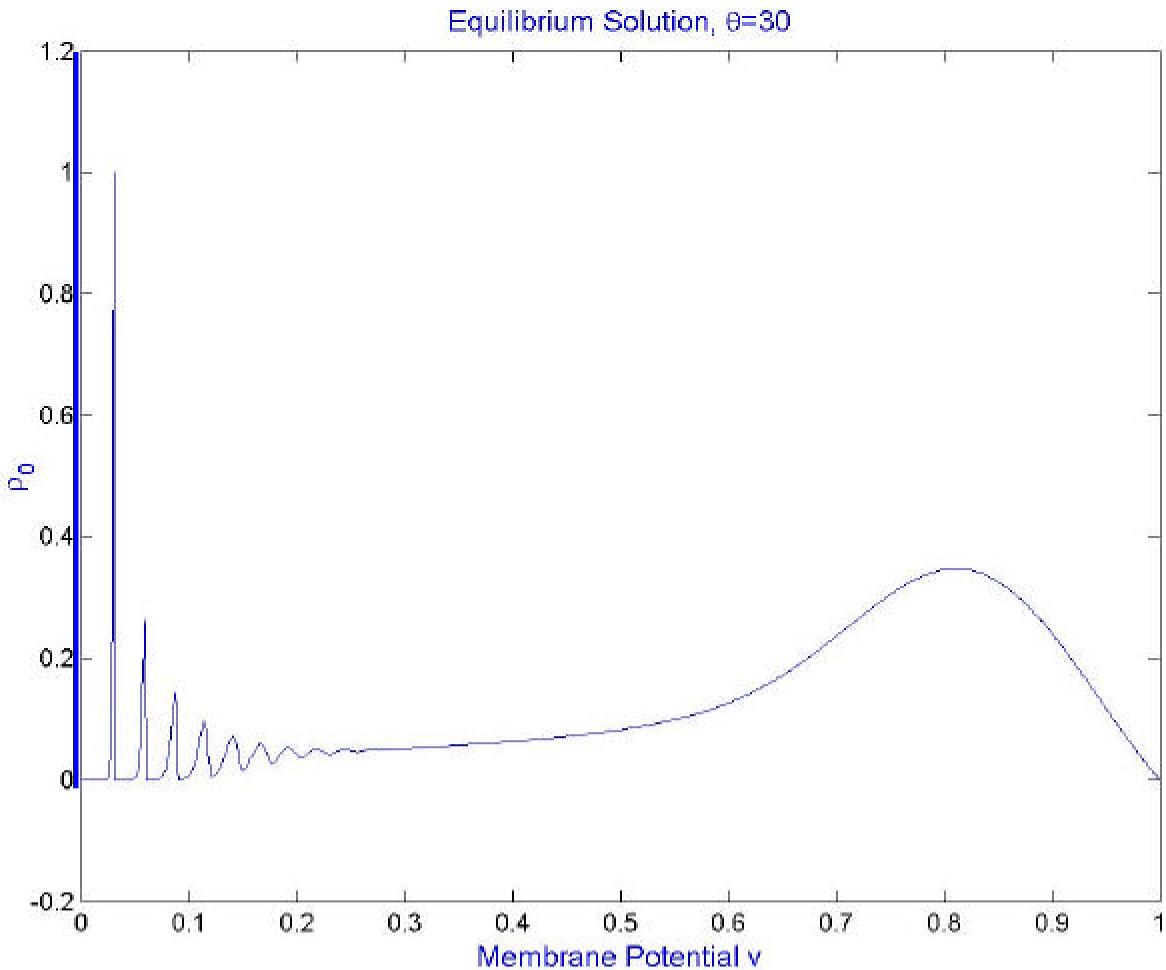
Equilibrium Density, $Q=10$



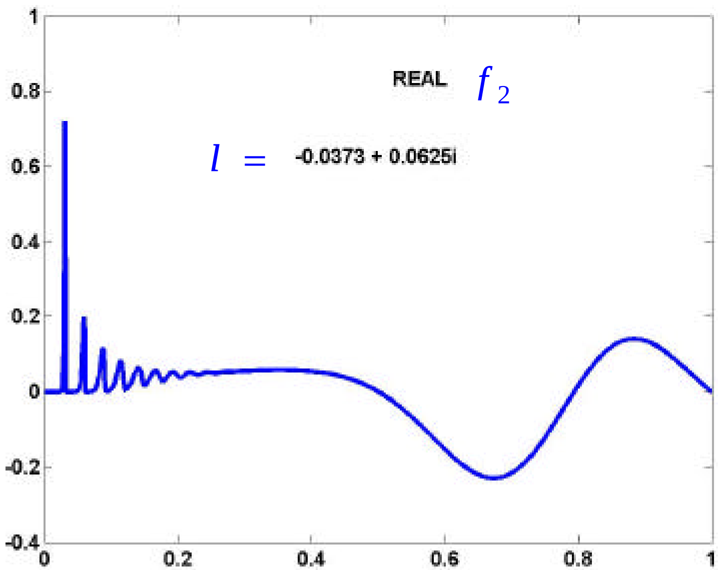
Spectra (non-zero leak) q=30, h=.03

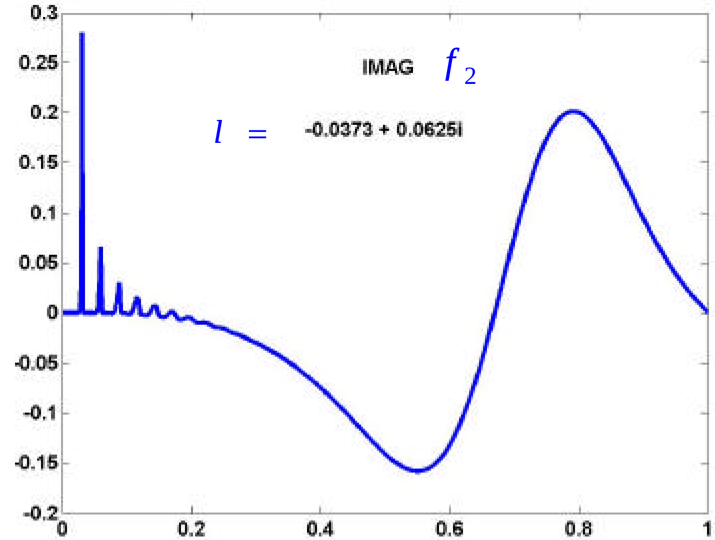


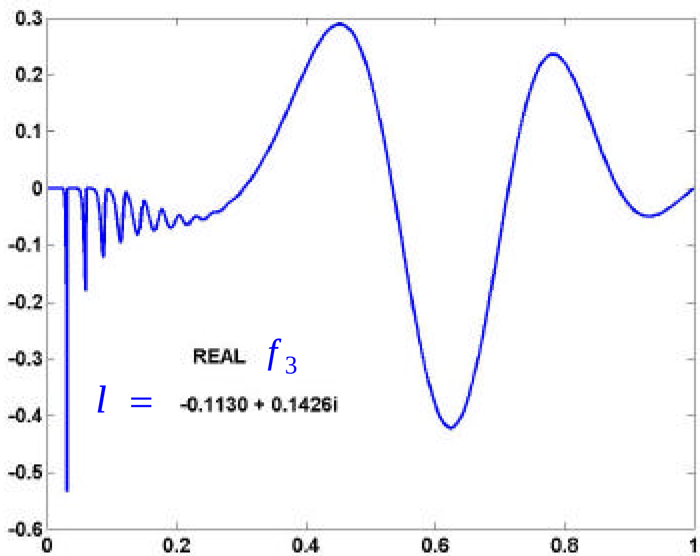
Equilibrium Density, first eigenfunction, $\theta=30$, h$=.03$

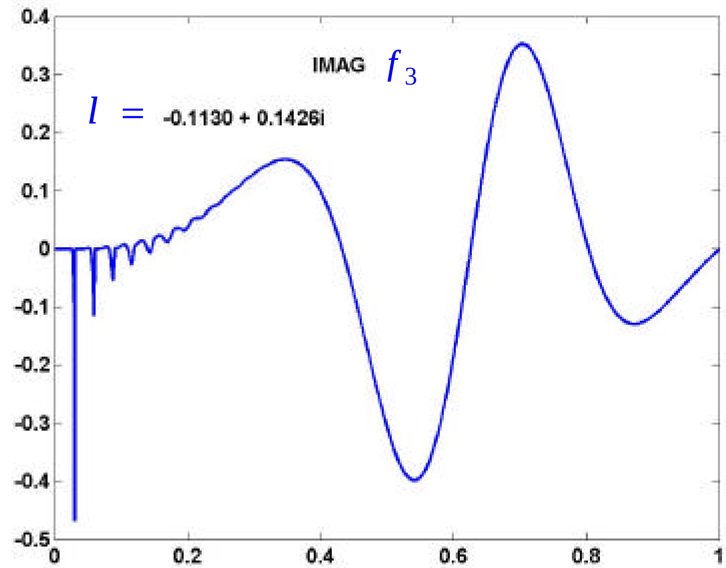


Next Four Eigenfunctions, $\theta=30$, h=.03









Solution by Eigenfunctions

$$\{f_n\} : L f_n = l_n f_n$$

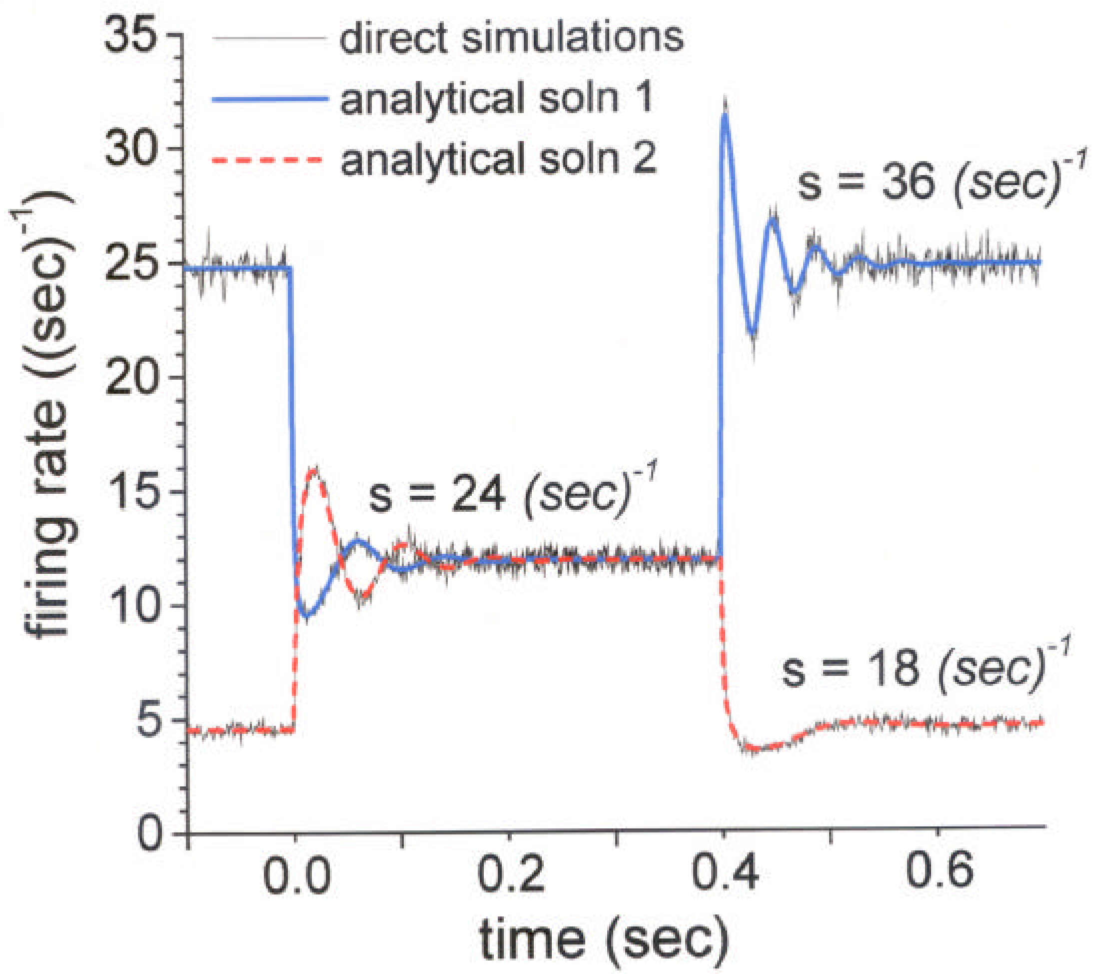
$$\{\widehat{f_n}\} : L^{\dagger} \widehat{f_n} = l_n \widehat{f_n}$$

$$(f_n, \widehat{f_m})_{\mathrm{v}} = d_{m,n}$$

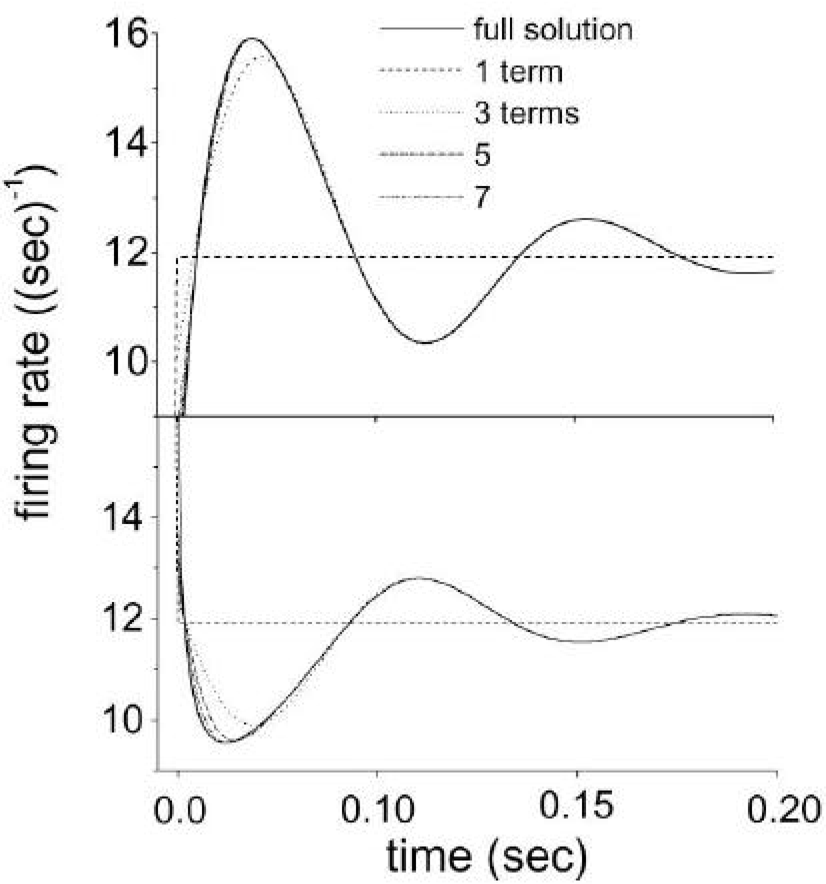
$$\frac{\partial r}{\partial t} = L r \,, \; r(\mathrm{v}, 0) = r^{0}(\mathrm{v})$$

$$r(\mathrm{v}, t) = \sum_{n} (\widehat{f_n}, r^{0})_{v} f_n(\mathrm{v}) e^{l_n t}$$

An Exact Solution: Equilibrium Jumping



Truncated Approximations



Equilibrium Solutions

Feedback (Gain) G:

$$\sigma(t) = \frac{s(t)}{h} = \sigma^0(t) + Gr(t).$$

Then

$$\frac{\partial \rho}{\partial t} = \gamma \frac{\partial}{\partial v}(v\rho) + \frac{\sigma^0}{1 - G\int_{1-h}^{1} \rho(v')dv'} \{\rho(v-h) - \rho(v)\}$$

Equilibrium

$$0 = \gamma \frac{\partial}{\partial v}(vU) + \sigma_0 \{U(v-h) - U(v)\}$$

with

$$\sigma_0 = \sigma^0 \left(1 + \frac{kG}{1-kG}\right) = \frac{\sigma^0}{1-kG}$$

&

$$A_0 = \int_{1-h}^{1} U(v, \sigma_0)\, dv = k(\sigma_0).$$

Open loop, $k=0$, yields closed loop, $k \neq 0$, family of solutions.

Stability of Equilibrium

Linearize

$$\rho = U + \epsilon u\left(v,t\right)$$

$$\frac{\partial u}{\partial t} = \gamma \frac{\partial}{\partial v} vu - \sigma_0 \left\{ u\left(v\right) - u\left(v-h\right)\right\} + G r_1 \left\{ U\left(v-h;\sigma_0\right) - U\left(v;\sigma_0\right)\right\}$$

with

$$r_1 = \frac{\sigma_0 \int_{1-h}^{1} u\left(v\right) dv}{1-kG}.$$

This is a one-dimensional perturbation of the linear operator.

Stability of Equilibrium

$$H = \begin{cases} 0; & 0 \le v \le 1 - h \\ 1; & 1 - h < v \le 1 \end{cases}$$

$$\Phi(v) = \sigma_0 \{U(v - h) - U(v)\}$$

$$\mu u = Lu + \Phi(v) \frac{G}{1 - kG} (H, u)$$

$$1 = \frac{G}{1 - kG} \sum_l \frac{(H, \phi_l)\left(\widehat{\phi}_l, \Phi\right)}{\mu - \lambda_l}$$

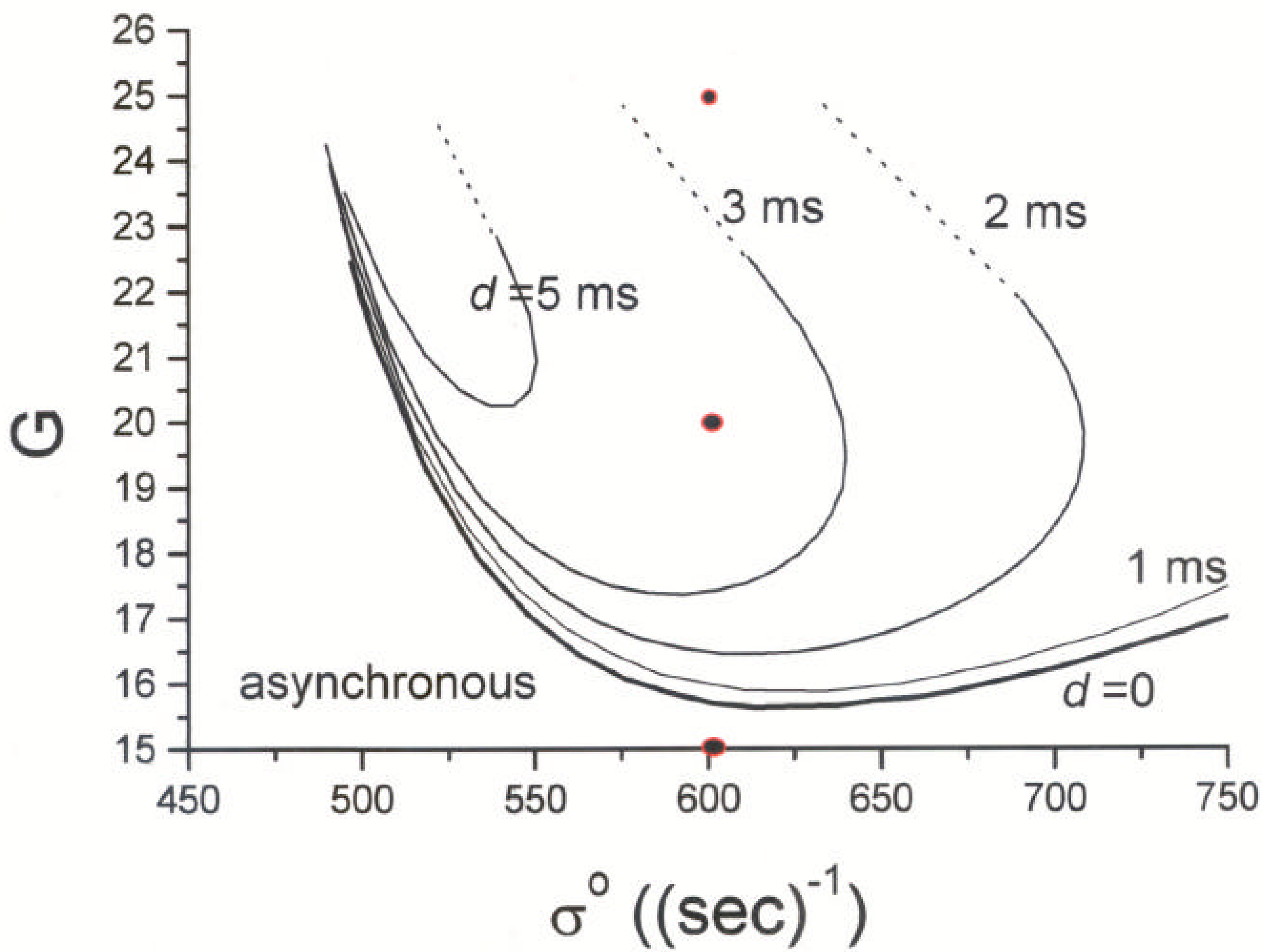
$$u = \frac{G}{1 - kG} (H, u) \sum_l \frac{\left(\widehat{\phi}_l, \Phi\right)}{\mu - \lambda_l} \phi_l$$

Time Delay

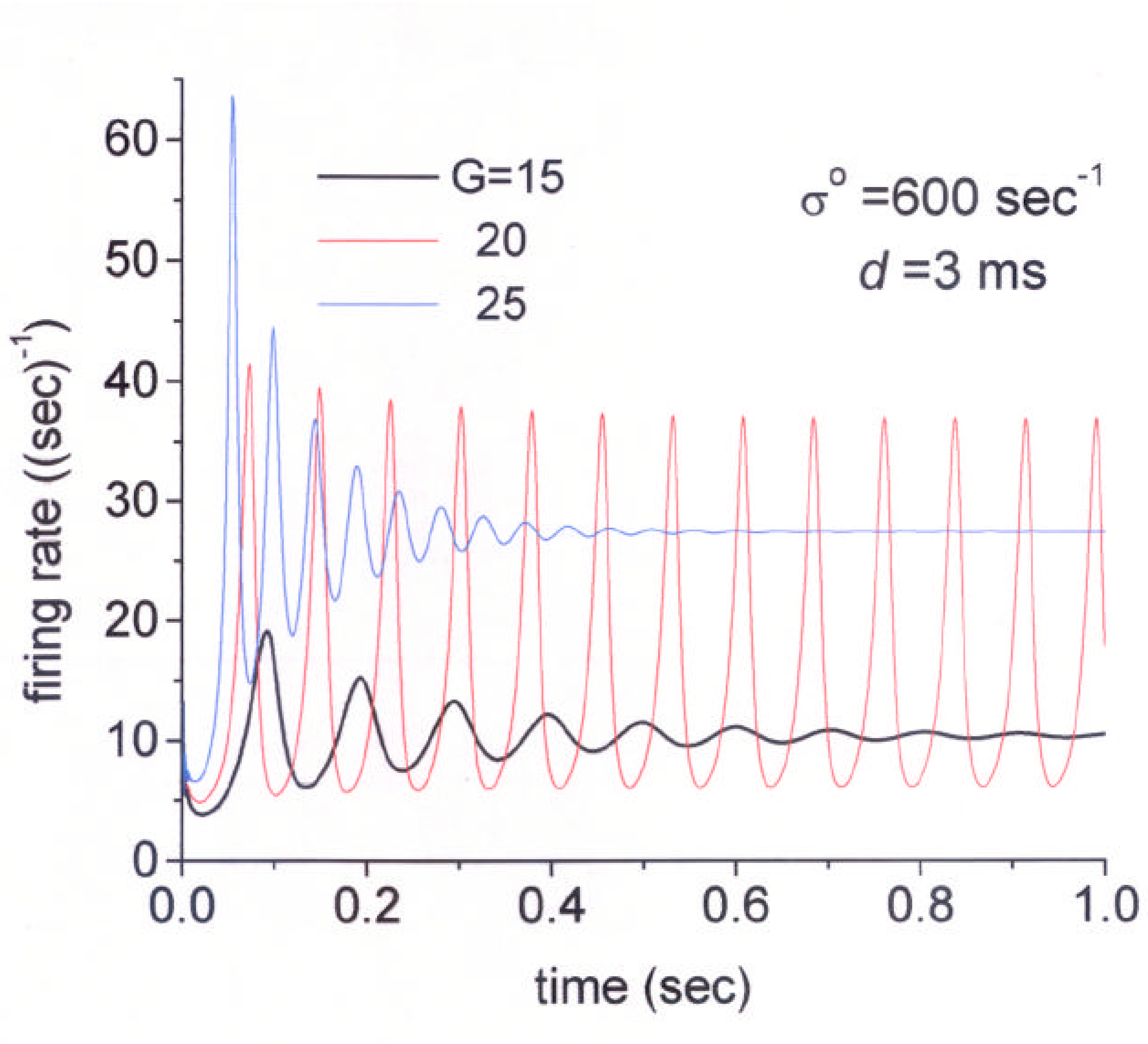
$$\sigma(t) = \sigma^0(t) + Gr(t - t_d) = \sigma^0 + GT_d r$$

$$\mu u = Lu + \Phi(v)\frac{Ge^{-\mu t_d}}{1 - A_0 G e^{-\mu t_d}}(H, u)$$

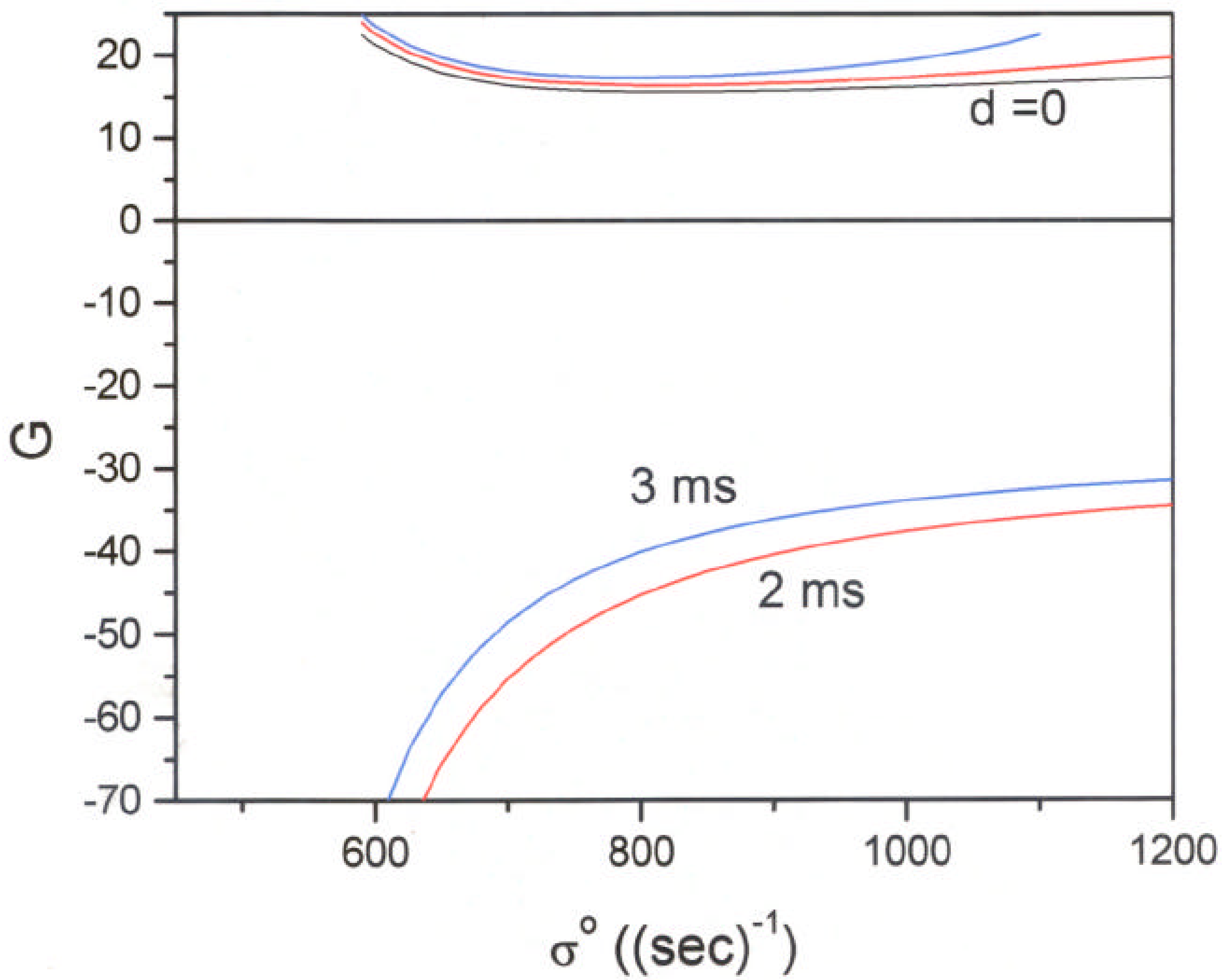
Stability Diagram



Behavior at Three Gains

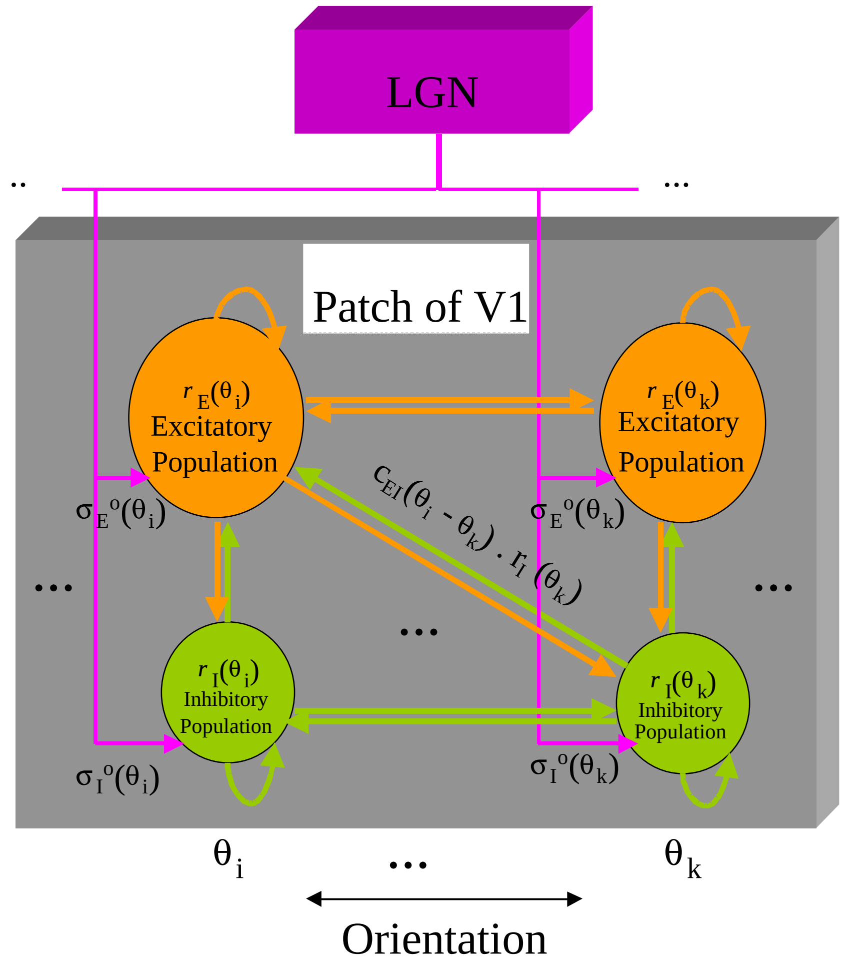


Inhibition, *G<0*



Model of an Orientation Hypercolumn

via the Kinetic Equation



INTERACTING POPULATIONS

Sub-population Densities

$$\rho_k = \rho_k(\mathbf{v}, t), k = 1, 2, \ldots, M$$

Fluxes

$$\mathbf{J}_k = \mathbf{C}\left(s_k^0, r_1, \ldots r_M\right) r_k$$

Population Firing Rate

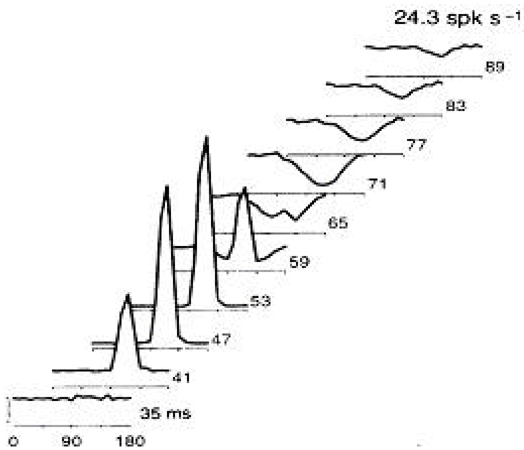
$$r_k = R[\mathbf{J}_k]$$

Continuity Equations

$$\frac{\partial \rho_k}{\partial t} = -\frac{\partial}{\partial \mathbf{v}} \cdot \mathbf{J}_k$$

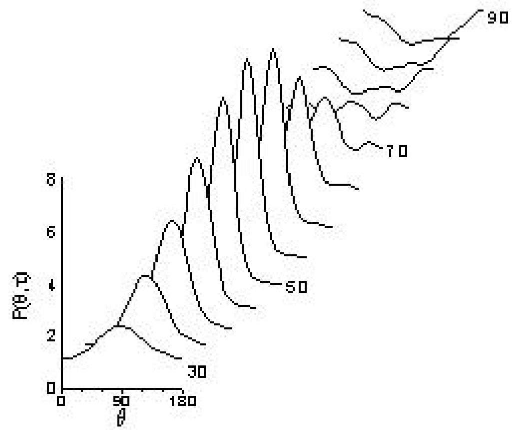
Reverse Correlation Experiment

experiment



Ringach et al ‘97

population model



Omurtag et al ‘00

Remarks

Anatomy and physiology tell us that there are a relative small number neuron types. Each may require its own model.

E.g., there exist cells, having calcium channels, which can fire in bursts as well as tonically. This has been modeled as part of a study of the LGN & V1

Typical cortical neurons synapse with $O(10^4)$ cells. This certainly justifies the use of Poisson arrivals. However there are highly correlated cells, e.g., RGC & LGN cells. This has led to an interesting new model.

Estimate that the external world is mapped to a *mosaic* of $O(10^3)$ elements on V1.

If *10* modalities/element then $O(10^4)$ populations in primary visual cortex.

Presently this would be an excessive calculation. But not for long. Nevertheless substantial portions of tissue can now be simulated.

Problem is that we know very little about cortical interactions.

The present objective is to use simulation as an exploratory tool, in conjunction with experiment, to leverage both theory & experiment.

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