Nonlinear Integrate&Fire Neuron Models: Analysis & Numerics

J. A. Carrillo

in collaboration with M.J. Cáceres (UGR), L. Tao (Pekin Univ.), J. Comp. Phys. 2010.

in collaboration with M.J. Cáceres (UGR), B. Perthame (ParisVI), to appear in J. Math. Neuroscience.

in collaboration with M.d.M. González (UPC), M.P. Gualdani (UT-Austin), M.E. Schonbek (UCSC), submitted.

ICREA - Universitat Autònoma de Barcelona

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Outline

1. Neuron Network Models
   - LIF Models
   - Conductance-based Models
2. Analytical Results
   - Stationary States
   - Linear Case
   - Blow-up & Apriori Estimates
   - Well-Posedness of Classical Solutions
3. Numerics
   - LIF Model
   - Conductance-based model
4. Conclusions

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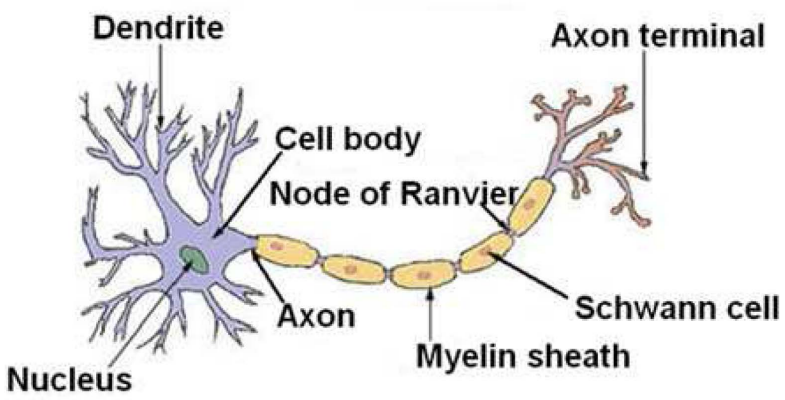
LIF Model

LIF = Leaky Integrate & Fire Model.

- Models based on the Membrane potential.
- Different concentration of ions across the membrane.
- Ion channels allow permeability.

Membrane or Action potential evolution can be simply modelled as a electric circuit - Lapicque (1907)



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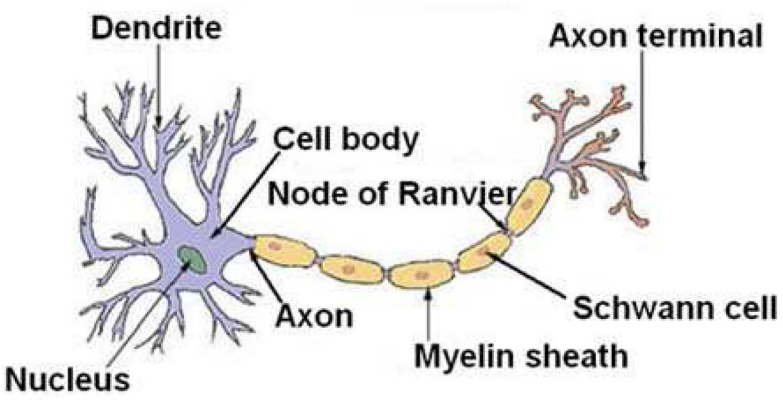

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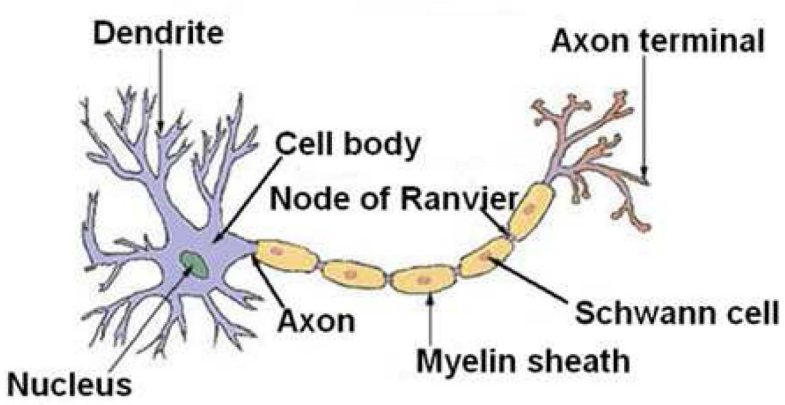

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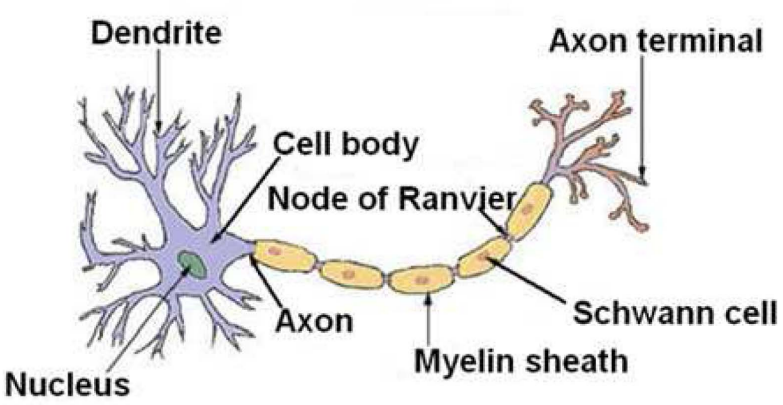

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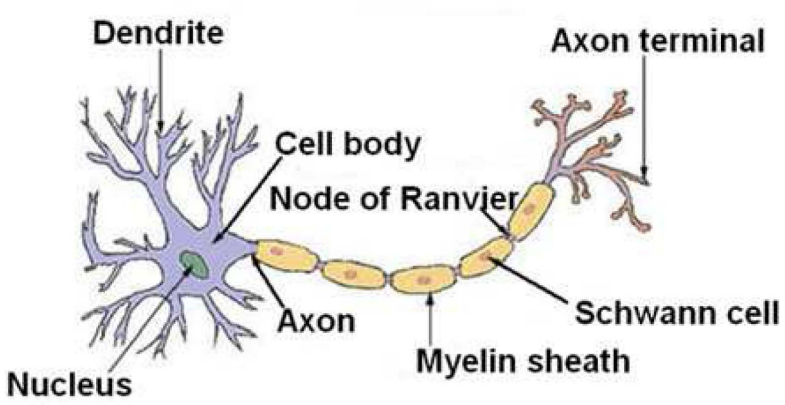
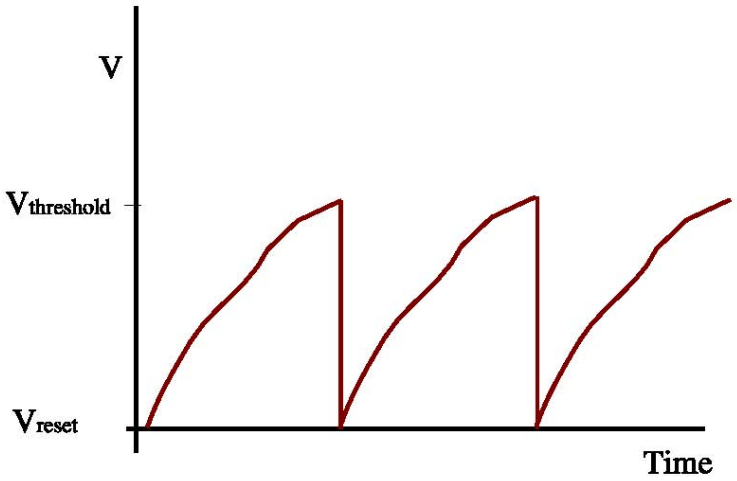


LIF Models: Potential

Basic LIF model

$$C_m \frac{dV}{dt} = -g_L(V - V_L) + I(t)$$

1. $\tau_m = C_m/g_L \approx 10ms$ and $V_L \approx -70mV$.
2. $I(t)$: the external input current.
3. Firing voltage: threshold value $V_F \approx -50mV$.
4. Reset voltage: discharged value $V_R \approx -60mV$.



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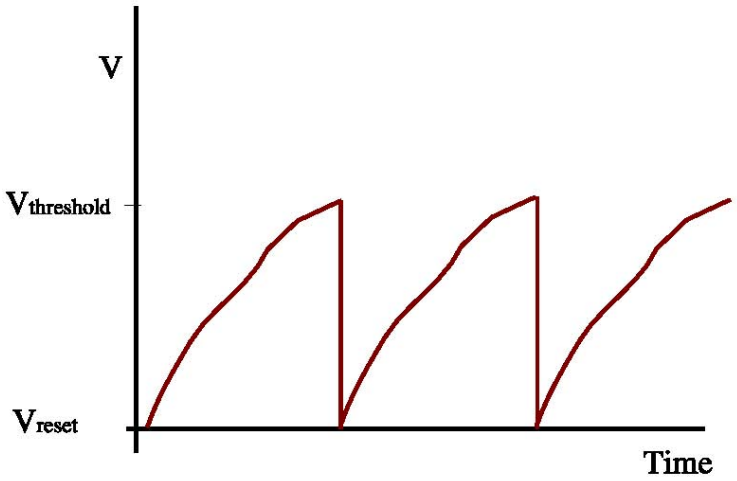

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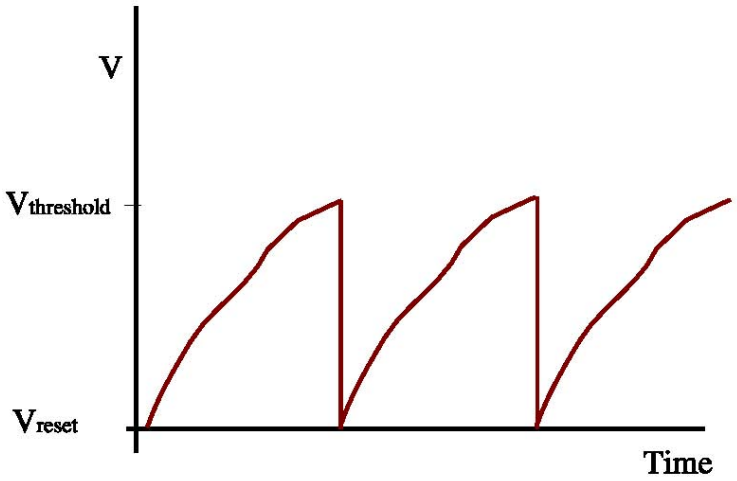

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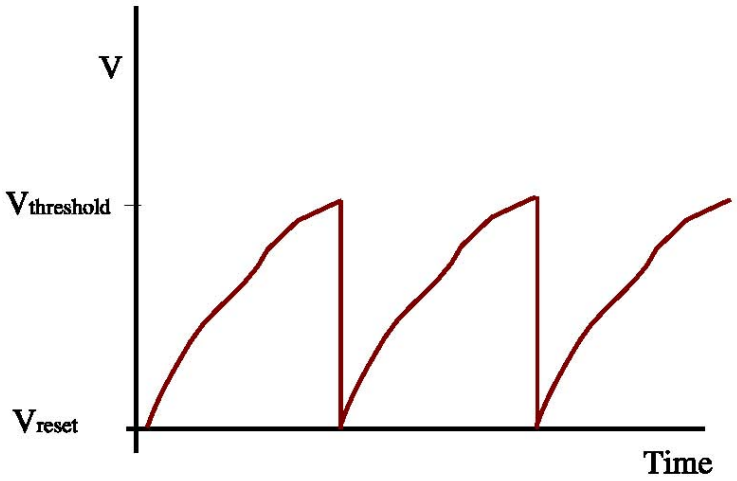


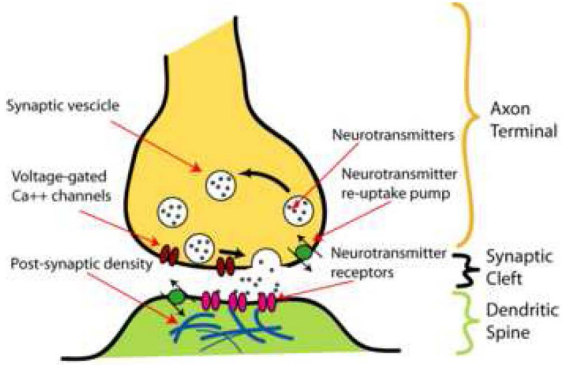
LIF Models: Synapsis

Stochastic Synapsis Model

$$I(t) = J_E \sum_{i=1}^{C_E} \sum_j \delta(t - t^i_{Ej}) - J_I \sum_{i=1}^{C_I} \sum_j \delta(t - t^i_{Ij})$$

Parameters

1. Two different Neuron-types: Inhibitory (I) or Excitatory (E).
2. Strength of the Synapses: J. Number of presynaptic neurons: C.
3. Spiking times: t^i_j = time of the jth-spike coming from the ith-presynaptic neuron.
4. Stochastic Assumption: Neurons spike according to a Poisson process with constant probability of emitting a spike per unit time ν.



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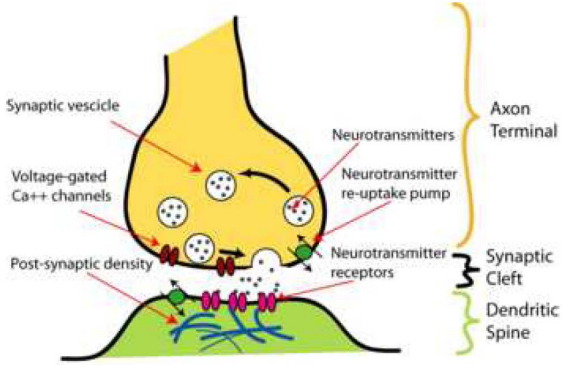

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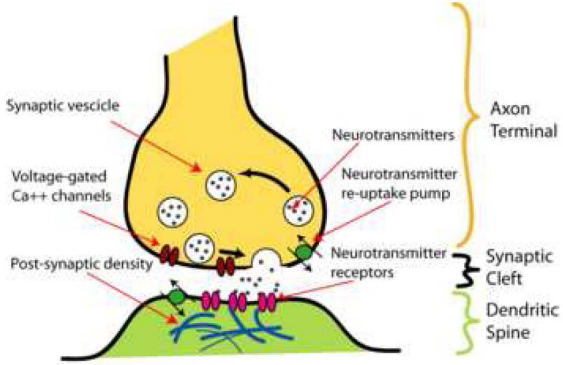

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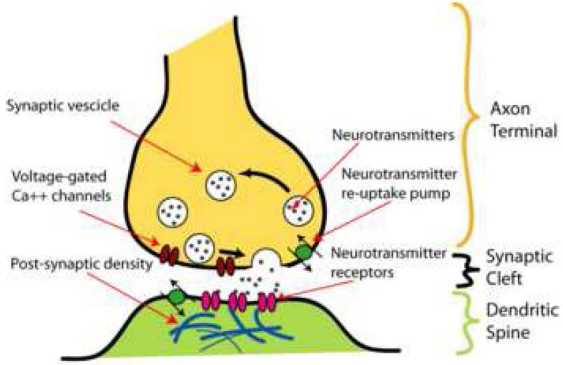

LIF Models: Diffusion Approximation

Mean and Variance of $I(t)$ are given by:

$$\mu_C = b\nu \qquad \text{with} \qquad b = C_E J_E - C_I J_I \qquad \text{and} \qquad \sigma_C^2 = (C_E J_E^2 + C_I J_I^2)\nu.$$

Diffusion Approximation

Several authors (Brunel, Hakim, Renart, Wang, Mattia, del Giudice) propose to approximate the current by

$$I(t)\,dt \approx \mu_C\,dt + \sqrt{\sigma_C}\,dB_t$$

1. Firing rate: $\nu = \nu_{ext} + N(t)$ where $N(t)$ is the mean firing rate of the network.
2. The value of $N(t)$ is then computed as the flux of probability that neurons cross the threshold voltage V_F per unit time.
3. Average-excitatory (-inhibitory resp.) if $b > 0$ ($b < 0$ resp.).

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LIF Model: PDE

Ito's rule: PDE for the evolution of the probability density $p(v,t) \geq 0$ of finding neurons at a voltage $v \in (-\infty, V_F]$ at a time $t \geq 0$.

Final PDE Model:

$$\frac{\partial p}{\partial t}(v,t) + \frac{\partial}{\partial v}\left[h(v,N(t))p(v,t)\right] - a(N(t))\frac{\partial^2 p}{\partial v^2}(v,t) = \delta(v - V_R)N(t),$$

in $v \in (-\infty, V_F]$, with $h(v,N(t)) = -V + V_L + \mu_c$ and $a(N) = \sigma_C^2/2$.

Boundary conditions: $p(V_F,t) = 0, p(-\infty,t) = 0, p(v,0) = p_0(v)$.

Source by the Mean Firing Rate:

$$N(t) := -a(N(t))\frac{\partial p}{\partial v}(V_F,t) \geq 0\,.$$

Translating the voltage origin:

$$h(v,N) = -v + bN, \qquad a(N) = a_0 + a_1 N\,.$$

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Neuron Network Model

Conductance IF model

$$\frac{dV_i}{dt} = -(V_i - V_R) - G_i(V_i - V_E)$$
$$\frac{dG_i}{dt} = -G_i + I(t)$$

1. τ_m typical leak time.
2. $I(t)$: the external input current.

Diffusion approximation in Cai-Tao-Rangan-McLaughlin (Commun. Math. Sci. 2006): PDE for the evolution of the probability density $\rho(t, v, g) \geq 0$ of finding neurons at a voltage $v \in [V_R, V_F]$ with conductance $g \in [0, \infty)$ at a time $t \geq 0$.

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Conductance-based Model

Final PDE Model:

$$\partial_t \rho(t,v,g) + \partial_v J_V(t,v,g) + \partial_g J_G(t,v,g) = 0,$$

where the fluxes are

$$J_V(t,v,g) = \left[(V_R - v) + g\,(V_E - v)\right]\rho(t,v,g)$$

$$J_G(t,v,g) = (\bar{g}_E(t) - g)\rho(t,v,g) - \sigma_g^2(t)\partial_g \rho(t,v,g)\,.$$

Boundary conditions:

$$J_V(t,V_T,g) = J_V(t,V_R,g) \quad \text{and} \quad J_G(t,v,0) = J_G(t,v,\infty) = 0$$

Mean Firing Rate: $\bar{g}_E(t)$ and $\sigma_g^2(t)$ are affine functions of

$$m_E(t) = \int_0^\infty J_V(t,V_T,g)\,dg\,.$$

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$$J_G(t,v,g) = (\bar{g}_E(t) - g)\rho(t,v,g) - \sigma_g^2(t)\partial_g \rho(t,v,g)\,.$$

Boundary conditions:

$$J_V(t,V_T,g) = J_V(t,V_R,g) \quad \text{and} \quad J_G(t,v,0) = J_G(t,v,\infty) = 0$$

Mean Firing Rate: $\bar{g}_E(t)$ and $\sigma_g^2(t)$ are affine functions of

$$m_E(t) = \int_0^\infty J_V(t,V_T,g)\,dg\,.$$

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Integrating the PDE

Stationary solutions satisfy

$$\frac{\partial}{\partial v}\left[(v-bN)p + a(N)\frac{\partial}{\partial v}p(v) + NH(v-V_R)\right] = 0$$

Using the BC's:

$$(v-bN)p + a(N)\frac{\partial p}{\partial v} + NH(v-V_R) = 0$$

Integrating we conclude

$$p(v) = \frac{N}{a(N)}e^{-\frac{(v-bN)^2}{2a}}\int_v^{V_F} e^{\frac{(w-bN)^2}{2a}}H[w-V_R]dw$$

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Set-up of the Quest of Stationary States

Summarizing all solutions of the stationary problem are of that form with N being any positive solution to

$$\frac{a(N)}{N} = \int_{-\infty}^{V_F} \left[e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v,V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw \right] dv \,.$$

Changing variables, this condition is equivalent to

$$\begin{cases} \dfrac{1}{N} = I(N), \\ I(N) := \displaystyle\int_{-\infty}^{w_F} \left[e^{-\frac{z^2}{2}} \int_{\max(z,w_R)}^{w_F} e^{\frac{u^2}{2}} du \right] dz \end{cases} \quad \text{with } w_{F/R} = \frac{V_{F/R} - bN}{\sqrt{a(N)}}$$

$I(N)$ can also be expressed as

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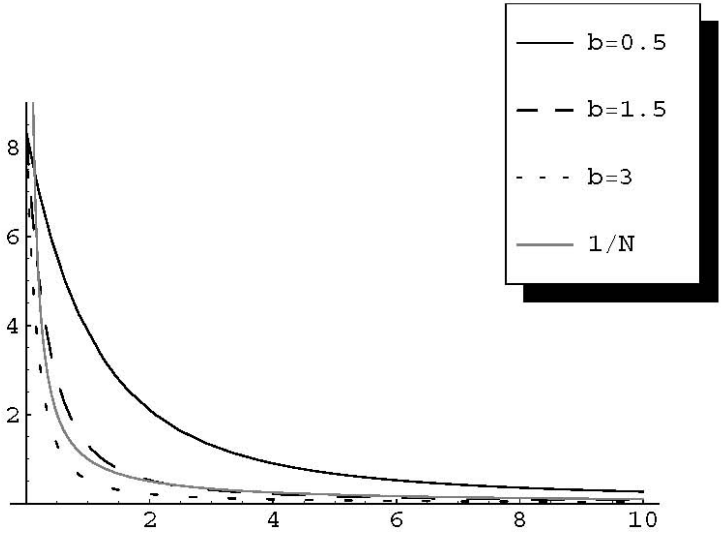
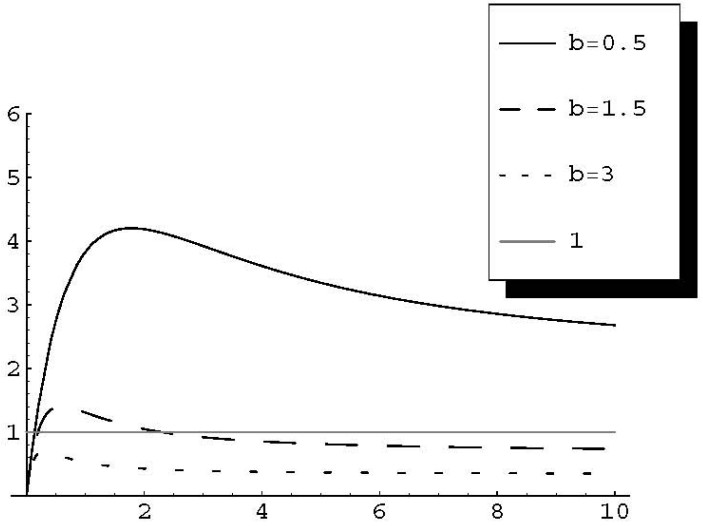
Shape of I(N)





Result

Stationary States

Assume $h(v, N) = bN - v$, $a(N) = a$ is constant.

i) For $b < 0$ and $b > 0$ small enough there is a unique steady state.

ii) Under either $0 < b < V_F - V_R$ or $0 < 2ab < (V_F - V_R)^2 V_R$, then there exists at least one steady state solution.

iii) If both $2ab < (V_F - V_R)^2 V_R$ and $b > V_F - V_R$ hold, then there are at least two steady states.

iv) There is no steady state under the high connectivity condition

$$b > \max(2(V_F - V_R), 2V_F I(0)).$$

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General Relative Entropy Principle

Result for $b = 0$

Solutions to the linear equation satisfy, for any smooth convex function $G : \mathbb{R}^+ \longrightarrow \mathbb{R}$, the inequality

$$-\frac{\partial}{\partial t}\int_{-\infty}^{V_F} p_\infty(v) G\left(\frac{p(v,t)}{p_\infty(v)}\right) =$$

$$N_\infty\left[G\left(\frac{N(t)}{N_\infty}\right) - G\left(\frac{p(v,t)}{p_\infty(v)}\right) - \left(\frac{N(t)}{N_\infty} - \frac{p(v,t)}{p_\infty(v)}\right) G'\left(\frac{p(v,t)}{p_\infty(v)}\right)\right]\Big|_{V_R}$$

$$+ a\int_{-\infty}^{V_F} p_\infty(v)\, G''\left(\frac{p(v,t)}{p_\infty(v)}\right)\left[\frac{\partial}{\partial v}\left(\frac{p(v,t)}{p_\infty(v)}\right)\right]^2 dv \geq 0.$$

Consequences of GRE

Poincaré Inequality

There exists $\gamma > 0$ such that

$$\gamma \int_{-\infty}^{V_F} p_\infty(v) \left(\frac{q(v)}{p_\infty(v)} \right)^2 dv \leq \int_{-\infty}^{V_F} p_\infty(v) \left[\frac{\partial}{\partial v} \left(\frac{q(v)}{p_\infty(v)} \right) \right]^2 dv$$

for all functions q such $\frac{q}{p_\infty} \in H^1\left(p_\infty(v)dv\right)$.

Exponential decay

Solutions to the linear equation satisfy

$$\int_{-\infty}^{V_F} \frac{(p(v,t) - p_\infty(v))^2}{p_\infty(v)} dv \leq e^{-2a\gamma t} \int_{-\infty}^{V_F} \frac{(p_0(v) - p_\infty(v))^2}{p_\infty(v)} dv \,.$$

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Definition of Weak Solution

Weak Solutions

We say that a pair of nonnegative functions (p, N) with

$$p \in L^\infty\left(\mathbb{R}^+; L^1_+(-\infty, V_F)\right) \qquad N \in L^1_{\text{loc},+}(\mathbb{R}^+)$$

is a weak solution of the LIF model if for any test function $\phi(v,t) \in C^\infty((-\infty, V_F] \times [0,T])$ such that $v\frac{\partial \phi}{\partial v} \in L^\infty((-\infty, V_F) \times (0,T))$, we have

$$\frac{d}{dt}\int_{-\infty}^{V_F} \phi(v)p(v,t)dv = \int_{-\infty}^{V_F}\left[\frac{\partial \phi}{\partial v}h(v,N) + a\frac{\partial^2 \phi}{\partial v^2}\right] p(v,t)dv + N(t)[\phi(V_R,t) - \phi(V_F,t)]$$

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Blow-up Result

Conservation of Mass:

$$\int_{-\infty}^{V_F} p(v,t)\,dv = \int_{-\infty}^{V_F} p_0(v)\,dv = 1\,.$$

BU for suitable initial data and any $b > 0$

Assume that the drift and diffusion coefficients satisfy

$$h(v,N) = bN - v \qquad \text{and} \qquad 0 < a_m \leq a(N)\,.$$

If the initial data is concentrated enough around $v = V_F$, in the sense that

$$\int_{-\infty}^{V_F} e^{\mu v} p_0(v)\,dv \text{ is large enough with } \mu > \max\left(\frac{V_F}{a_m}, \frac{2}{b}\right),$$

then no global-in-time weak solutions exist.

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From Fokker-Planck to Heat

- Change of variables: Fokker-Plank to heat equation
  $y = e^t v, \quad \tau = \frac{1}{2}(e^{2t} - 1), \quad p(v,t) = e^t w\left(e^t v, \frac{1}{2}(e^{2t} - 1)\right)$ yields

$$\boxed{w_\tau = w_{yy} - bM(\tau)\alpha^{-1}(\tau)w_y + M(\tau)\delta_{\{y=\frac{v_R}{\alpha(\tau)}\}}}$$

  where $\alpha(\tau) = (2\tau + 1)^{-1/2} = e^{-t}, \quad M(\tau) = -\left.\frac{\partial w}{\partial y}\right|_{y=0}.$

- Change of variables: Get rid of w_y term:

$$u(x,\tau) = w(y,\tau), \quad x = y - b\int_0^\tau M(s)\alpha^{-1}(s)\,ds.$$

- Get a free boundary Stefan problem with source
- Related to a price formation equation (Lasry-Lions,González-Gualdani, Chayes-González-Gualdani-Kim, Caffarelli-Markowich-Pietschmann)

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$$(P)\quad \begin{cases} u_t = u_{xx} + M(t)\delta_{x=s_1(t)}, & x < s(t), t > 0, \\ s(t) = -b\displaystyle\int_0^t M(s)\alpha^{-1}(s)\,ds, & t > 0, \\ M(t) = -\left.\dfrac{\partial u}{\partial x}\right|_{x=s(t)}, & t > 0, \\ s_1(t) = s(t) + \dfrac{v_R}{\alpha(t)}, & t > 0, \\ u(-\infty, t) = 0, \quad u(s(t), t) = 0, & t > 0, \\ u(x, 0) = u_I(x), & x < 0. \end{cases}$$

1. Conservation of mass: $\int_{-\infty}^{s(t)} u(x,t)\,dx = \int_{-\infty}^{0} u_I(x)dx$
2. The flux across the free boundary s_1 is the jump of the δ: $M(t) := -u_x(s(t),t) = u_x(s_1(t)^-,t) - u_x(s_1(t)^+,t)$
3. If $b < 0$ resp. $b > 0$, the free boundary $s(t)$ is an increasing resp. decreasing function of time, and $s(t)$, $s_1(t)$ never cross.

Integral formulation *a la Friedman*

- Green's function: $G(x,t,\xi,\tau) = \frac{1}{[4\pi(t-\tau)]^{1/2}} \exp\left\{-\frac{|x-\xi|^2}{4(t-\tau)}\right\}$
- Duhamel's formula:

$$u(x,t) = \underbrace{\int_{-\infty}^{0} G(x,t,\xi,0)u_I(\xi)d\xi}_{\text{homogeneous heat equation}}$$

$$\underbrace{-\int_0^t M(\tau)G(x,t,s(\tau),\tau)d\tau}_{\text{Takes care of free boundary}} + \underbrace{\int_0^t M(\tau)G(x,t,s_1(\tau),\tau)d\tau}_{\text{Delta function at } s_1(t)}$$

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Integral formula for M

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\begin{aligned}
M(t) &= \partial_x u(s(t),t) \\
&= -2\int_{-\infty}^{0} G(s(t),t,\xi,0)u_I'(\xi)\,d\xi \\
&\quad + 2\int_0^t M(\tau)G_x(s(t),t,s(\tau),\tau)d\tau \\
&\quad - 2\int_0^t M(\tau)G_x(s(t),t,s_1(\tau),\tau)d\tau \\
&=: \Theta(M)(t)
\end{aligned}
$$

Fixed point argument: $\Theta : C_{\sigma,m} \to C_{\sigma,m}$, where
$C_{\sigma,m} := \{M \in \mathcal{C}([0,\sigma]) : \|M\| \le m\}$
$\|M\| := \sup_{0\le t\le\sigma} |M(t)|$
Contraction for σ small, where $\sigma = \sigma\left(\|u_I'\|\right)$

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Global existence ($b < 0$) & Blow up when $b > 0$

Criterium

Solution exists up to time T^*, where $T^* = \sup\{t > 0 : M(t) < \infty\}$.

Lemma - no break up time for $b < 0$

$\exists \varepsilon > 0$ small enough such that, for any $t_0 > 0$, if

$$\sup_{x \in (-\infty, s(t_0-\varepsilon)]} |u_x(x, t_0 - \varepsilon)| < \infty,$$

then also

$$\sup_{t_0-\varepsilon < t < t_0} M(t) < \infty.$$

Here ε is independent of t_0.

Theorem ($b < 0$)

There exists a unique regular solution u for all $t > 0$.

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1 Neuron Network Models
- LIF Models
- Conductance-based Models

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- Linear Case
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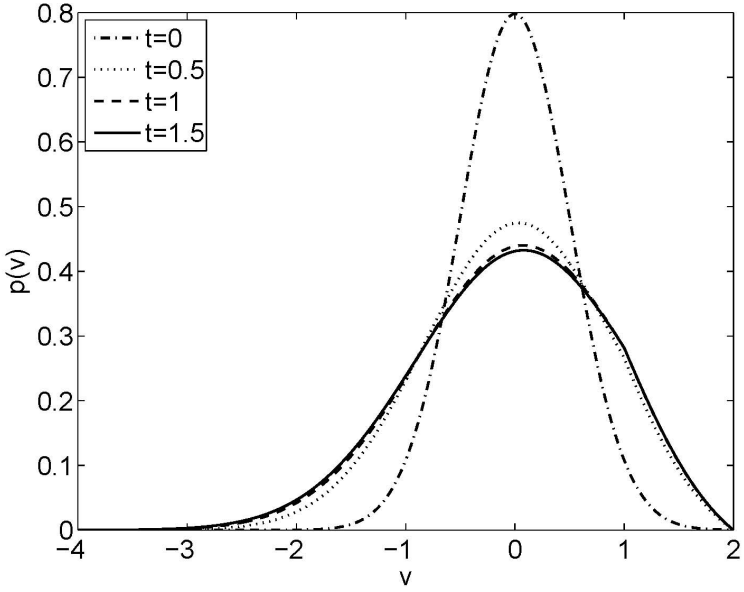
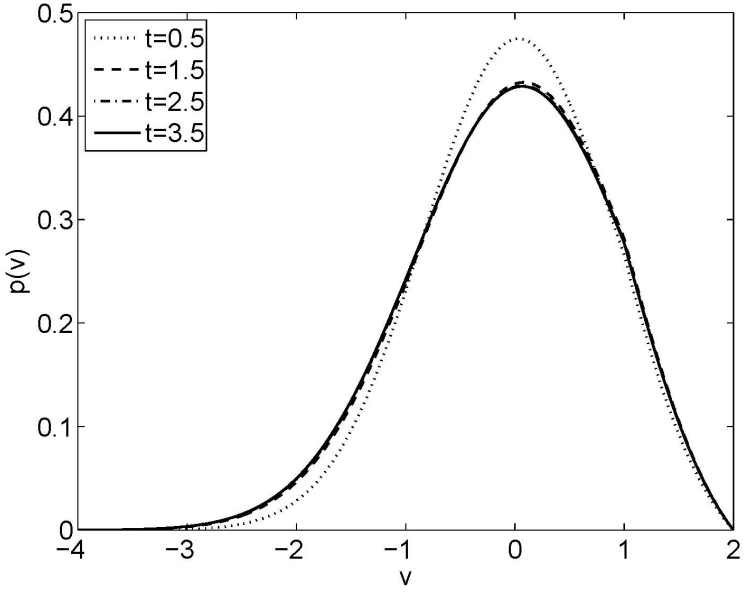
- Well-Posedness of Classical Solutions

3 Numerics
- LIF Model
- Conductance-based model

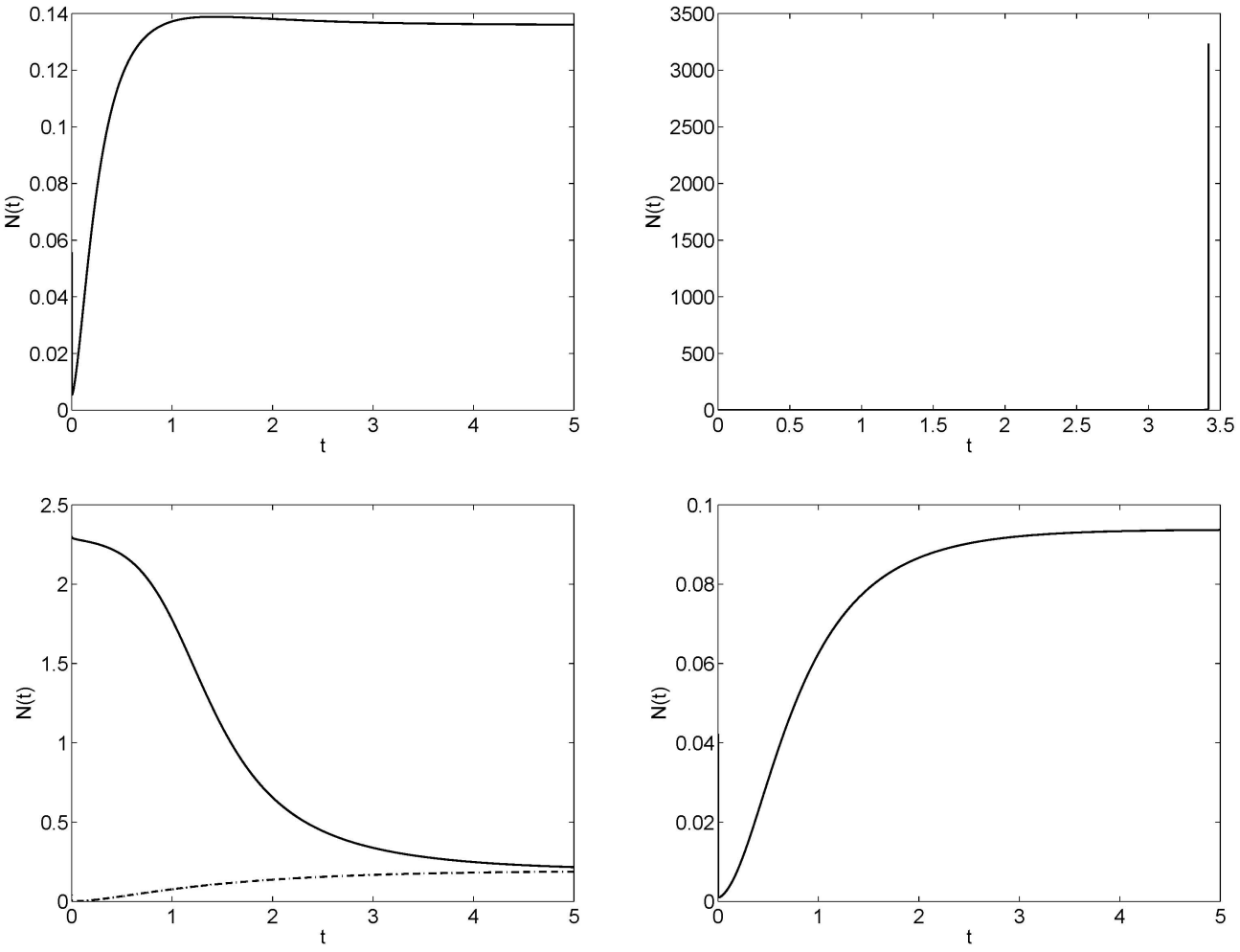
4 Conclusions

One Stationary State

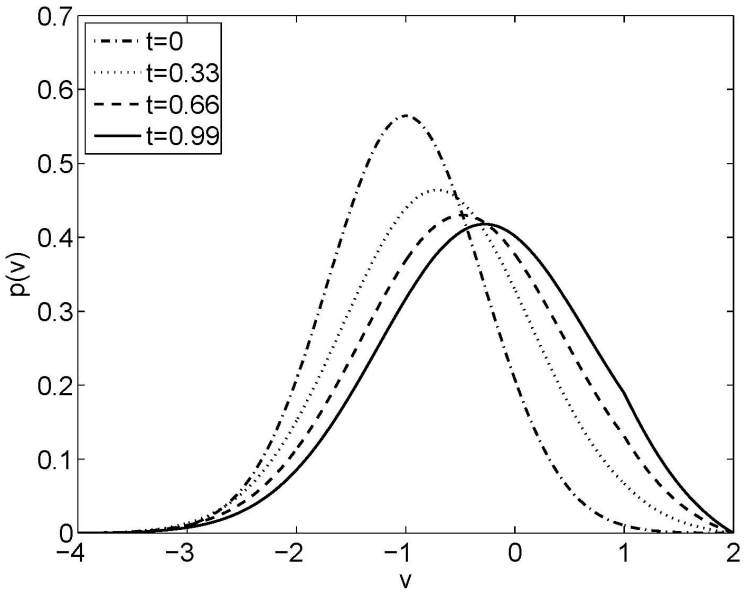


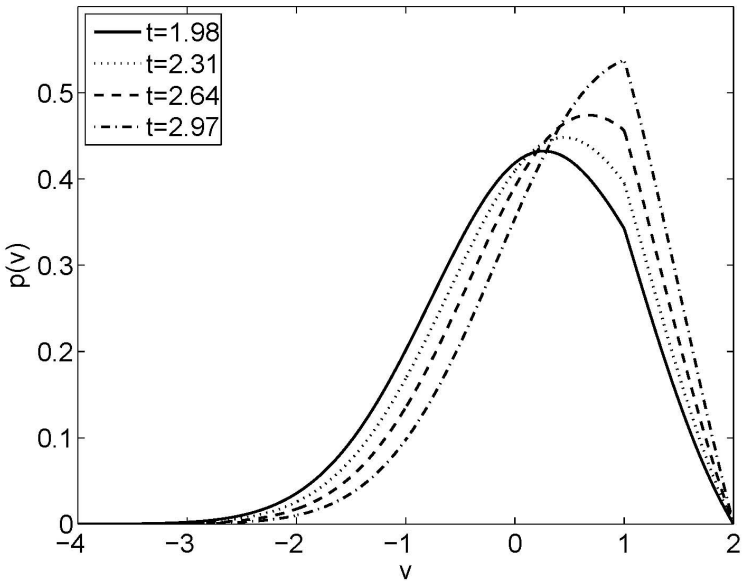


Firing Rates

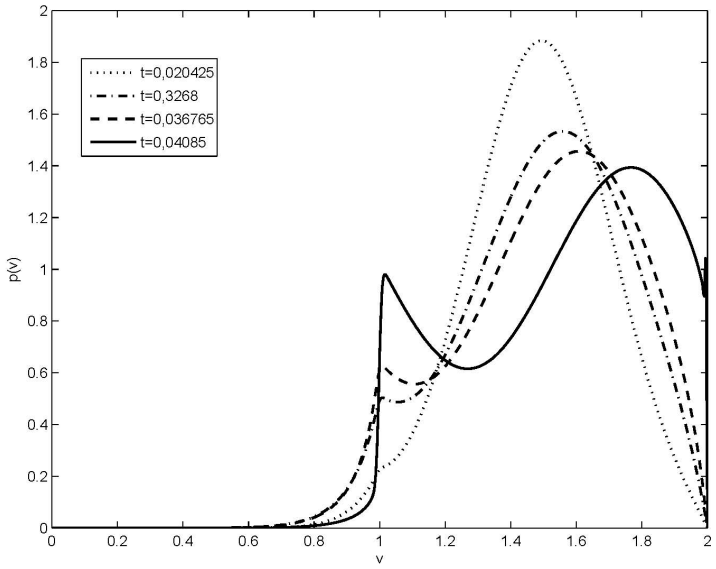


No Steady State, $b = 3$





Blow-up, $b = 1.5$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t=0,3268
t=0,036765
t=0,04085
p(v)
v
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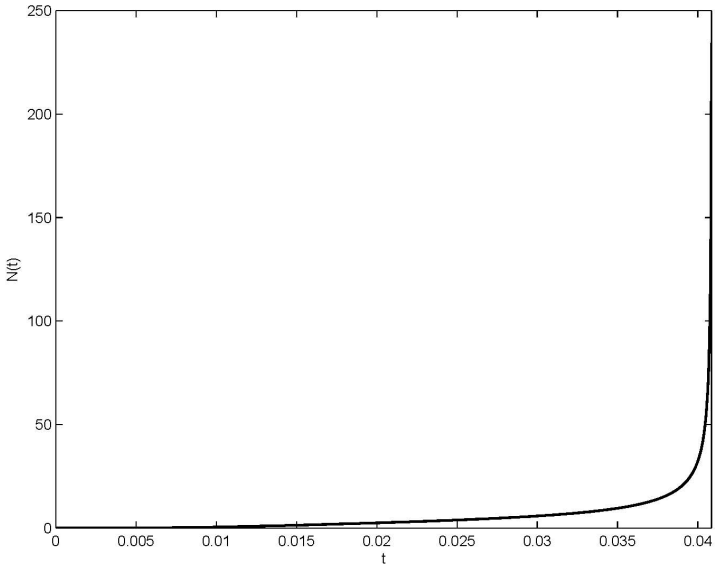
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2


N(t)
t
0
50
100
150
200
250
0.005
0.01
0.015
0.02
0.025
0.03
0.035
0.04

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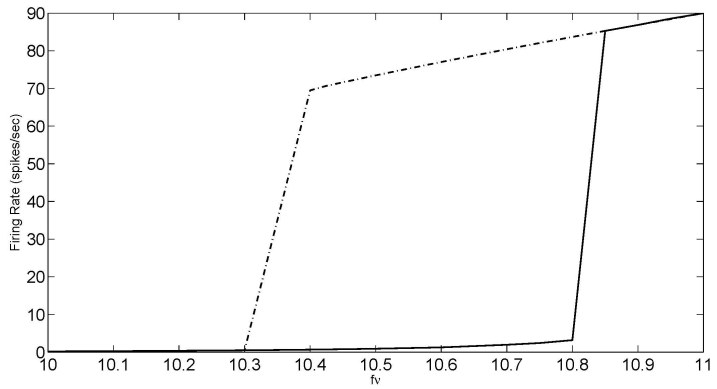
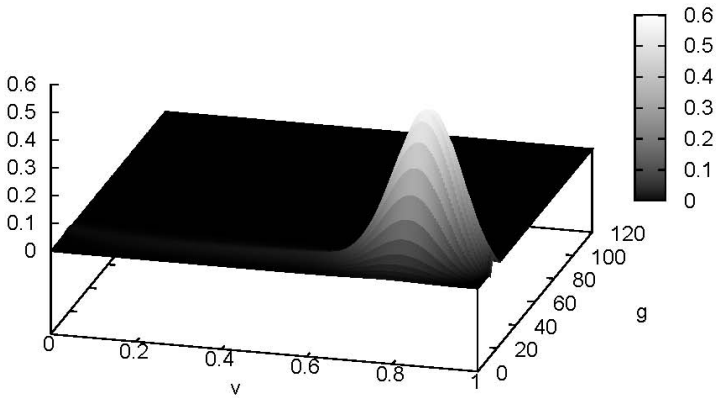
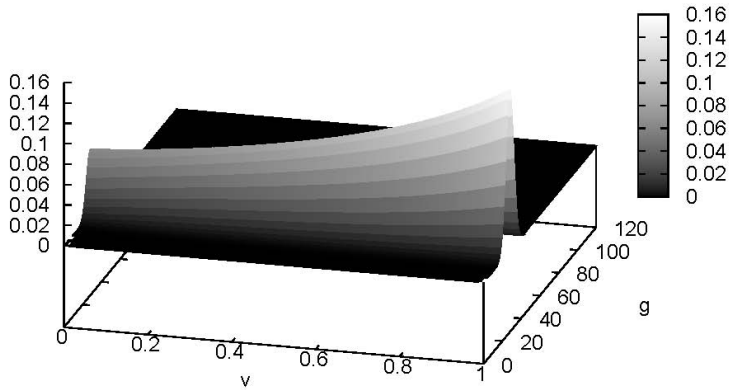
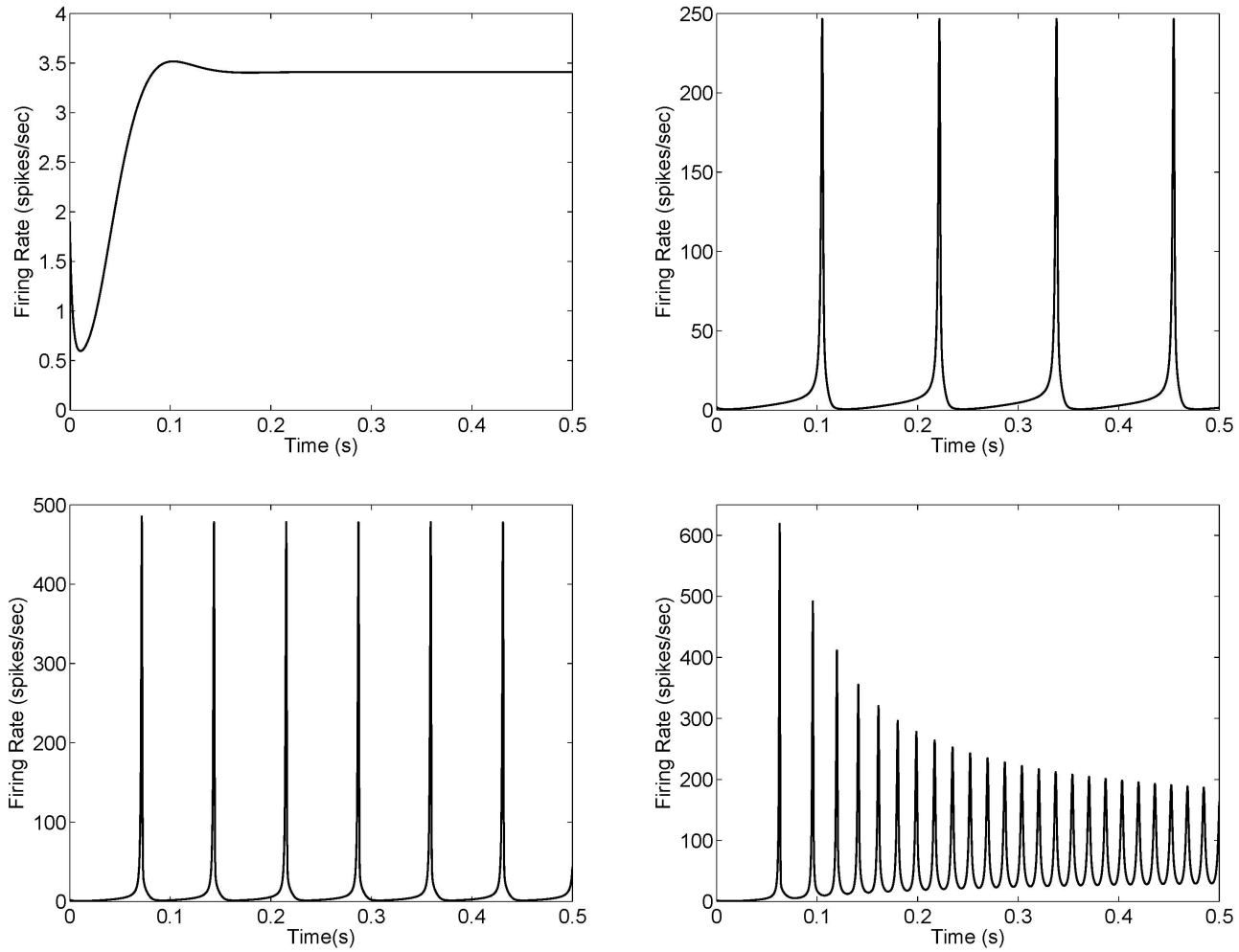
Bistability







Periodicity



Concluding Remarks

- Simple Stochastic Models of Neuron networks lead to nonstandard boundary value problems for Fokker-Planck like equations.
- The stability of stationary states in the nonlinear problem is still an open problem.
- Understanding the blow-up mechanism and its relation to synchronization.
- Conductance-Based: no analytical results are available, strange boundary conditions, no control on the firing rate.
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