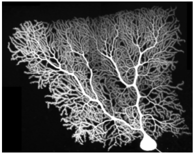
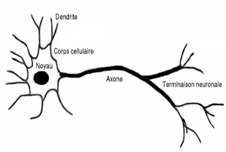
PDEs for neural networks

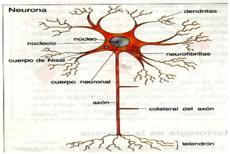
analysis and behaviour

Benoît Perthame

Course III. Integrate and Fire networks







Plan of the course

I. The single neuron,

II. Networks, examples

III. Networks, Integrate & Fire

- **III. 1.** LIF networks
- **III. 2.** Blow-up and spontaneous activity
- **II. 3.** Mean field learning

IV. Networks, time elapsed models

Integrate & Fire

Goals :

- understand physiologically based models of information processing

- **'small homogeneous'** neural networks

- Recover properties as synchronization

Leaky Integrate & Fire (linear)

The Leaky Integrate & Fire model is simpler

$$dV(t) = \big(- V(t) + I(t) \big) dt + \sigma dW(t), \qquad V(t) < V_{\mathrm{Firing}}$$

$$V(t_-) = V_{\mathrm{Firing}} \quad \Longrightarrow \quad V(t_+) = V_{\mathrm{Reset}}$$

$$0 < V_R < V_F$$

- $I(t)$ input current
- Noise or not
- Much simpler than Hodgkin-Huxley/FitzHugh-Nagumo models

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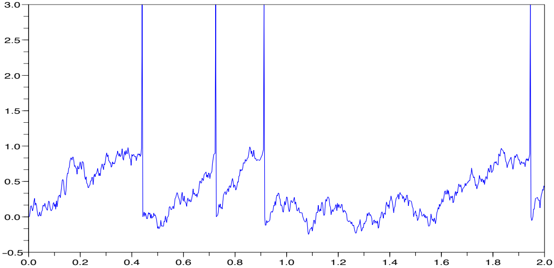

Solution to the LIF model

- N. Brunel and V. Hakim, R. Brette, W. Gerstner and W. Kistler, Omurtag, Knight and Sirovich, Cai and Tao...
- Fit to measurements
- Use more realistic dynamics in place of $-\mathbf{v}$

Leaky Integrate & Fire (linear)

FIGURE 4 | Fitting spiking models to electrophysiological recordings. (A) The response of a cortical pyramidal cell to a fluctuating current (from the INCF competition) is fitted to various models: MAT (Kobayashi et al., 2009), adaptive integrate-and-fire, and Izhikevich (2003). Performance on the training data is indicated on the right as the gamma factor (close to the proportion of predicted spikes), relative to the intrinsic gamma factor of the neuron (i.e., proportion of common spikes between two trials). Note that the voltage units for the models are irrelevant (only spike trains are fitted). **(B)** The response of an anteroventral cochlear nucleus neuron (brain slice made from a P12 mouse, see Methods in Magnusson et al., 2008) to the same fluctuating current is fitted to an adaptive exponential integrate-and-fire [Brette and Gerstner, 2005; note that the responses do not correspond to the same portion of the current as in **(A)**]. The cell was electrophysiologically characterized as a stellate cell (Fujino and Oertel, 2001). The performance was $\Gamma = 0.39$ in this case (trial-to-trial variability was not available for this recording).

From C. Rossant et al, Frontiers in Neuroscience (2011)

Leaky Integrate & Fire (linear)

The probability $n(v,t)$ to find a neuron at the potential v solves the Fokker-Planck Eq. on the half line

$$\begin{cases} \frac{\partial n(v,t)}{\partial t} + \frac{\partial}{\partial v} \overbrace{\left[\left(-v + I(t)\right) n(v,t)\right]}^{\text{leak+external currents}} - a \overbrace{\frac{\partial^2 n(v,t)}{\partial v^2}}^{\text{Noise}} = \overbrace{N(t)\,\delta(v=V_R)}^{\text{neurons reset}}, \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad v \leq V_F, \\ n(V_F,t) = 0, \qquad n(-\infty,t) = 0, \\ N(t) := -a \frac{\partial n(V_F,t)}{\partial v} \geq 0, \qquad\qquad \text{(flux of neurons firing at } V_F\text{)} \end{cases}$$

Leaky Integrate & Fire (linear)

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\end{cases}
$$

$N(t)$ is also a Lagrange multiplier for the constraint

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

Leaky Integrate & Fire (linear)

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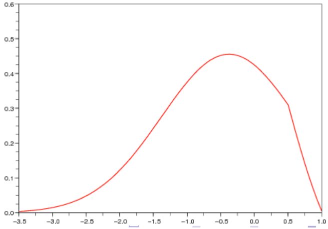
Properties (Cáceres, Carrillo, BP) For $I(t) \equiv 0$ the solutions satisfy

- $n \ge 0, \qquad \int_{-\infty}^{V_F} n(v,t)dv = 1,$
- $n(v,t) \underset{t\to\infty}{\longrightarrow} P(v)$ the unique steady state (probability density)
- The convergence rate is exponential

Conclusion : Total desynchronization



Leaky Integrate & Fire (linear)

The proof uses

- the Relative Entropy. For $H(\cdot)$ convex,

$$\frac{d}{dt}\int_{-\infty}^{V_F} P(v)H\Big(\frac{n(v,t)}{P(v)}\Big)dv = -D_{\text{diff}} - D_{\text{jump}},$$

- Hardy/Poincaré inequality,

$$\int_{-\infty}^{V_F} P(v)|u(v)|^2 dv \le C \overbrace{\int_{-\infty}^{V_F} P(v)|\nabla u(v)|^2 dv}^{D_{\text{diff}}},$$

when

$$\int_{-\infty}^{V_F} P(v)u(v)dv = 0, \qquad P(V_F) = 0$$

See : Ledoux, Barthe and Roberto (2006)

Noisy LIF networks

For networks, the current $I(t) = bN(t)$ is related to the network activity

$$\begin{cases} \frac{\partial n(v,t)}{\partial t} + \frac{\partial}{\partial v}\left[\left(-v + bN(t)\right) n(v,t)\right] - a\left(N(t)\right) \frac{\partial^2 n(v,t)}{\partial v^2} = N(t)\, \delta_{V_R}(v), \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad v \leq V_F, \\ n(V_F, t) = 0, \qquad n(-\infty, t) = 0, \\ N(t) := -a\left(N(t)\right) \frac{\partial}{\partial v} n(V_F, t) \geq 0, \qquad \text{flux of firing neurons at } V_F \end{cases}$$

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Constitutive laws

- $b =$ connectivity
- $b > 0$ excitatory neurones
- $b < 0$ inhibitory neurones
- $a(N) = a_0 + a_1 N$

Noisy LIF networks

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Derived from a system of N interacting neurons, see Delarue, Inglis, Rubenthaler, Tanre, Tallay, Faugeras, Fournier, Locherbach..., for $1 \leq i \leq N \to \infty$

$$\frac{d}{dt}V_i(t) = -V_i(t) + \underbrace{\frac{\beta}{N}\sum_{j=1}^{N}\sum_{k}\delta(t-t_j^k)}_{\text{current generated by spikes}} + \sigma dW_i(t), \qquad V_i(t) < V_F$$

with t_j^k the spiking times : $V_j(t_j^k) = V_F$.

Noisy LIF networks

Theorem (J. Carrillo, D. Salort, BP, D. Smets) [existence]

Assume $a = a_0 > 0$. Being given an initial data $n^0(v)$

- for $b \leq B(n^0)$ there is a solution $(B > 0)$,
- for $b \leq 0$ the solution is globally bounded,
- for $|b|$ small, it converges to the steady state (exponential rate),

Open question : Large time convergence to the unique steady state

See also Carrillo, Gonzalés, Gualdani, Schoenbeck for a reduction to Stefan problem

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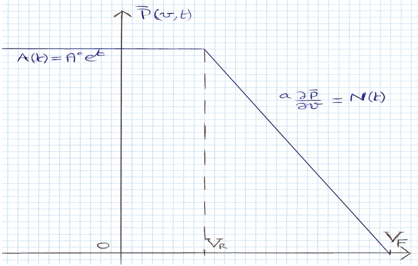
Noisy LIF networks (inhibitory)

Proof ingredients :

1. (Existence)
A universal supersolution
$(b < 0)$

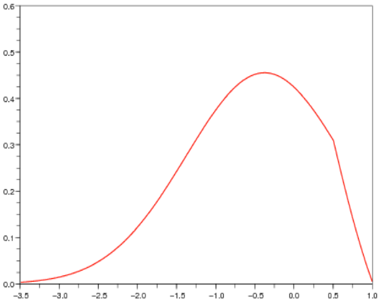


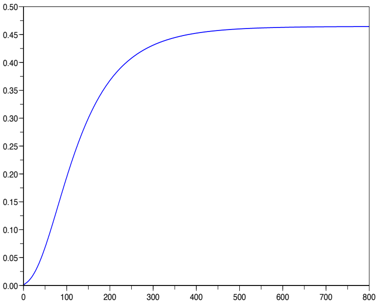
2. (Existence) For the Fokker-Planck equation, regularizing effects $L^1 \to L^\infty$

3. (Long time) Use the gap left by the Poincaré/Hardy inequality

Noisy LIF networks (inhibitory)

$$\begin{cases} \frac{\partial n(v,t)}{\partial t} + \frac{\partial}{\partial v}\left[\left(-v + bN(t)\right) n(v,t)\right] - a\left(N(t)\right) \frac{\partial^2 n(v,t)}{\partial v^2} = N(t)\, \delta_{V_R}(v), \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad v \leq V_F, \\ n(V_F,t) = 0, \qquad N(t) := -a\left(N(t)\right) \frac{\partial}{\partial v} n(V_F,t) \geq 0 \end{cases}$$





Inhibitory case $b < 0$. Left $p(v,t)$, Right : N(t)

Noisy LIF networks (blow-up)

Theorem (M. Cáceres, J. Carrillo, BP) [excitatory, blow-up]
Assume $a \geq a_0 > 0$ and $b > 0$. Then the solution blows-up in finite time in the two cases

- initial data is concentrated enough around $v = V_F$ (depending on b)
- initial data is given, b is large enough

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- initial data is given, b is large enough

Surprisingly

- Noise induced blow-up
- The determinstic LIF does not blow-up
- The kinetic LIF does not blow-up

Noisy LIF networks (blow-up)

Possible interpretation

- $N(t) \to \rho\delta(t - t_{\mathrm{BU}})$ and $t_{\mathrm{BU}} > 0$,
- partial synchronization

Simplified models : Kuramoto, Carillo-Ha-Kang, Dumont-Henry, Giacomin, Pakdaman

Huygens

Noisy LIF networks (blow-up)

- **Noise does not help**

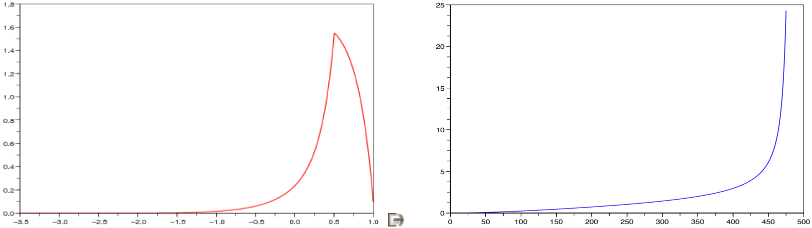
Theorem (J. Carrillo, D. Salort, BP, D. Smets)[inhibitory]
Assume $a = a_0 + a_1 N$ and $b < 0$.

Then the solution blows-up in finite time

- when the initial data is concentrated enough around $v = V_F$

- or for given initial data when a_1 is large enough

Noisy LIF networks (blow-up)



Excitatory integrate and fire model. Blow-up case. Left $p(v,t)$, Right : N(t)

Noisy LIF with refractory state

$$\begin{cases} \frac{\partial n(v,t)}{\partial t} + \frac{\partial}{\partial v}\left[\left(-v+bN(t)\right)n(v,t)\right] - a\left(N(t)\right)\frac{\partial^2 n(v,t)}{\partial v^2} = \frac{R(t)}{\tau}\delta_{V_R}(v), \\ n(V_F,t) = 0, \qquad n(-\infty,t) = 0 \\ N(t) := -a\left(N(t)\right)\frac{\partial}{\partial v} n(V_F,t) \geq 0 \\ \frac{d}{dt}R(t) + \frac{R(t)}{\tau} = N(t). \qquad \text{Refractory state} \end{cases}$$

(See also Brunel for other versions)

Theorem (M.Cáceres, BP) [Refractory]

The solution blows-up in finite time in the 2 cases :

- $b > 0$ is fixed, if the initial data is concentrated enough around V_F.
- The initial data is given, if b large enough

Noisy LIF with refractory state

Proof. For $\mu = 2\max(\frac{1}{b}, \frac{V_F}{a_0})$, define

$$\phi(v) = e^{\mu v}, \qquad M_\mu(t) := \int_{-\infty}^{V_F} \phi(v) n(v,t).$$

For smooth solutions, we prove that $M_\mu(t)$ becomes larger than $e^{\mu V_F}$

$$\frac{dM_\mu}{dt} = \mu \int_{-\infty}^{V_F} (bN(t) - v + \mu a)\phi(v)p(v,t) - N(t)\phi(V_F) + \frac{R(t)}{\tau}\phi(V_R)$$

$$\geq N(t)\underbrace{\left[b\mu M_\mu(t) - \phi(V_F)\right]} + \mu \underbrace{\left[\mu a_0 - V_F\right]}_{\geq \mu V_F > 0} M_\mu(t)$$

$\searrow$

> 0 is needed only initially

OK for b large enough or $M_\mu(0)$ large enough

To go further : the difficulty : no relation between M_μ and N

Spontaneous activity (regularized)

Assume refractory state and that the firing potential V_F is random.

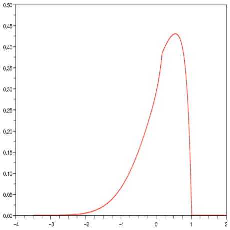
$$\frac{\partial n(v,t)}{\partial t} + \frac{\partial}{\partial v}\left[\left(-v+bN(t)\right)n(v,t)\right] - a\left(N(t)\right)\frac{\partial^2 n(v,t)}{\partial v^2} + \frac{n(v,t)}{\varepsilon}\mathbb{I}_{\{v>V_F\}}$$

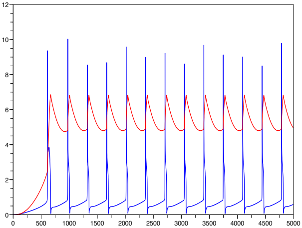
$$= \frac{R(t)}{\tau}\delta_{V_R}(v),$$

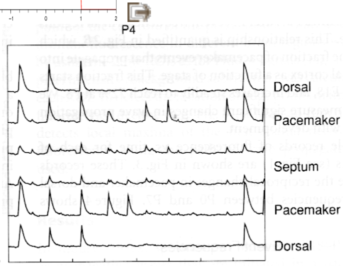
$$\begin{cases} N(t) := -\int \dfrac{n(v,t)}{\varepsilon}\mathbb{I}_{\{v>V_F\}}dv \\ \frac{d}{dt}R(t) + \frac{R(t)}{\tau} = N(t). \qquad \text{Refractory state} \end{cases}$$

Solutions are globally bounded.

Spontaneous activity (regularized)







Left : Excitatory integrate and fire model with refractory state and random firing threshold

Right : Conhaim et al (2011) J. of physiology 589(10) 2529-2541.

Similarity with a Keller-Segel type model

by V. Calvez and R. Voituriez

for microtubules arrangments on the membrane

$$\begin{cases} \frac{\partial n(z,t)}{\partial t} - \frac{\partial}{\partial z}\left[\mu(t) n(z,t)\right] - \frac{\partial^2 n(z,t)}{\partial z^2} = 0, \qquad z \geq 0, \\ \frac{\partial}{\partial z} n(0,t) + \mu(t) n(0,t) = 0, \\ \frac{d\mu(t)}{dt} = n(0,t) - \frac{\mu(t)}{L}. \end{cases}$$

- Blow-up for large mass
- Smooth solutions for small mass (and stable steady state)

Mean field learning in LIF networks

For Wilson-Cowan model,

$$\frac{d}{dt}N_i(t) = -N_i(t) + \sigma\left(\sum_j w_{i,j}(t)N_j(t) + s_j(t)\right)$$

One completes the with a rule

$$\frac{d}{dt}w_{i,j}(t) = f(N_i(t))\, f(N_j(t))$$

If both N's are active together, increase the weight. Otherwise decrease it
Hebbian learning

$$\frac{d}{dt}w_{i,j}(t) = k_{ij}N_i(t)\, N_j(t) - w_{i,j}(t)$$

Mean field learning in LIF networks

Learning reinforces synaptic weights w which are activated

$$\begin{cases} \frac{\partial p}{\partial t} + \frac{\partial}{\partial v}\left[\left(-v + I(w) + w\sigma(\bar{N}(t))\right) p\right] \\ \qquad\qquad + \varepsilon \frac{\partial}{\partial w}\left[(\Phi - w)p\right] - a\frac{\partial^2 p}{\partial v^2} = N(w,t)\delta(v - V_R), \\ N(w,t) := -a\frac{\partial p}{\partial v}(V_F, w, t) \geq 0, \qquad \bar{N}(t) = \int_{-\infty}^{\infty} N(w,t)dw, \end{cases}$$

- $I(w)$ input current
- $\Phi(w) = K(w)N(w,t)\bar{N}(t)$ Learning rule (Hebbian type)
- $N(w,t)$ output activity (sub-network activity)

Mean field learning in LIF networks

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- $I(w)$ input current
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- $N(w,t)$ output activity (sub-network activity)
- $C(w,t) = \int p(v,w,t)dv =$ connectivity - number of elements with synaptic weight w

Mean field learning in LIF networks

Questions

- Given a weight distribution $C(w)$,

  What are the possible outputs ?

  Is the mapping one-to-one : $I(w) \mapsto N(w)$

- Which connectivities $C(w)$ can be learned from an input $I(w)$?

- Discrimination property : For which learning rules can a network distinguish the signal used for learning ?

Mean field learning in LIF networks

Theorem (Representation)
Being given the input signal $I(w)$ and the output $N(w)$, then there is always a compatible synaptic weight distribution $C(w)$.

Mean field learning in LIF networks

Theorem (Representation)
Being given the input signal $I(w)$ and the output $N(w)$, then there is always a compatible synaptic weight distribution $H(w)$.

Theorem (Discrimination property)
Being given two currents $I(w)$, $J(w)$ and a synaptic weight distribution $C(w)$, then

$$\int |N_I(w) - N_J(w)| dw \geq C \int L(w) C(w) |I(w) - J(w)| dw$$

with $L(w)$ a weight to avoid too large $w \gg 1$.

Mean field learning in LIF networks

Learning reinforces synaptic weights w which are activated

$$
\begin{cases}
\frac{\partial p}{\partial t} + \frac{\partial}{\partial v}\left[\left(-v + I(w) + w\sigma(\bar{N}(t))\right) p\right] \\
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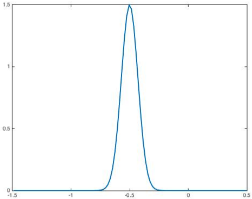
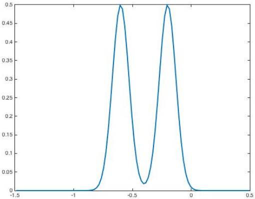
Theorem (Connectivity arising from a learning rule)
For inhibitory networks, being given the input signal, the learning rule K, there is a (unique) connectivity $C(w)$ generated by the Hebbian learning.

Mean field learning in LIF networks

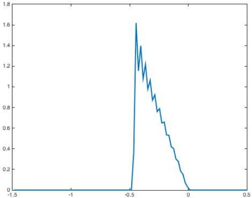
Learned

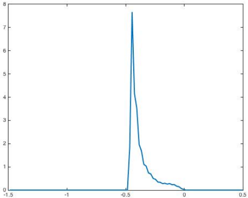




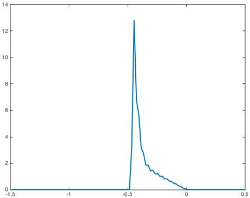
Other input

Output



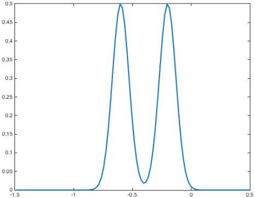


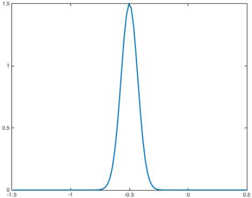
Connect.



Mean field learning in LIF networks

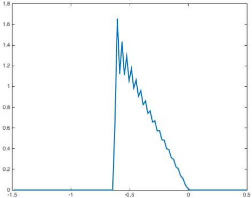
Learned

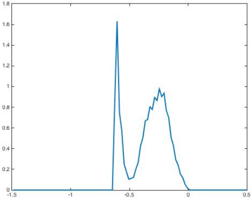




Other input

Output





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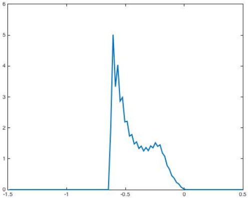

CONCLUSION

- Several highly nonlinear PDEs are used in the neuroscience
- One of the questions is emergence of synchronization
- Networks of nertworks
- Open problems
    - coupled inhibitory/excitatory
    - convergence to a steady state (inhibitory)
    - Derivation of LIF models

CONCLUSION

THANKS TO MY COLLABORATORS

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CONCLUSION

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THANK YOU