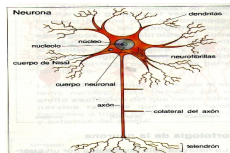
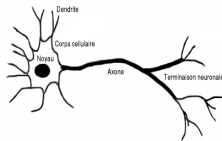


PDEs for neural networks analysis and behaviour

Benoît Perthame



- I. The single neuron,

- II. Networks, examples
 - II 1. Goodwin
 - II 2. Kuramoto
 - II 3. Wilson-Cowan
 - II 4. LNIF (linear)

- III. Networks, Leaky noisy I&F

- IV. Networks, time elapsed models

$$\begin{cases} \frac{d}{dt}y_0(t) + ay_0(t) = \phi(y_l(t)), \\ \frac{d}{dt}y_i(t) = \frac{1}{\tau_i}(y_{i-1}(t) - y_i(t)), \quad i = 1, \dots, l. \end{cases}$$

with $a > 0$, $\tau_i > 0$, $\phi \in C^2(\mathbb{R}^+; \mathbb{R}^+)$

- Input y_0 reacts to output y_l
- An *inhibitory* network is $\phi'(\cdot) < 0$, for instance

$$\phi(y) = \frac{b}{1 + y^k}, \quad k > 0$$

Question : Will an inhibitory network bring the system to rest ?

$$\begin{cases} \frac{d}{dt}y_0(t) + ay_0(t) = \phi(y_l(t)), \\ \frac{d}{dt}y_i(t) = \frac{1}{\tau_i}(y_{i-1}(t) - y_i(t)), \quad i = 1, \dots, l. \end{cases}$$

with $a > 0$, $\tau_i > 0$, $\phi \in C^2(\mathbb{R}^+; \mathbb{R}^+)$

- Input y_0 reacts to output y_l
- An *inhibitory* network is $\phi'(\cdot) < 0$, for instance

$$\phi(y) = \frac{b}{1 + y^k}, \quad k > 0$$

Question : Will an inhibitory network bring the system to rest ?

Small network : With $l = 2$, $y_i(t) \rightarrow \bar{y}_i$ as $t \rightarrow \infty$.

$$\begin{cases} \frac{d}{dt}y_0(t) + ay_0(t) = \phi(y_l(t)), \\ \frac{d}{dt}y_i(t) = \frac{1}{\tau_i}(y_{i-1}(t) - y_i(t)), \quad i = 1, \dots, l. \end{cases}$$

with $a > 0$, $\tau_i > 0$, $\phi \in C^2(\mathbb{R}^+; \mathbb{R}^+)$

- Input y_0 reacts to output y_l
- An *inhibitory* network is $\phi'(\cdot) < 0$, for instance

$$\phi(y) = \frac{b}{1 + y^k}, \quad k > 0$$

Question : Will an inhibitory network bring the system to rest ?

Claim : An inhibitory network can generate activity (patterns) !

Claim : A LARGE inhibitory network can generate activity (patterns) !

$$\begin{cases} \frac{d}{dt}y_0(t) + ay_0(t) = \phi(y_l(t)), \\ \frac{d}{dt}y_i(t) = \frac{1}{\tau_i}(y_{i-1}(t) - y_i(t)), \quad i = 1, \dots, l. \end{cases}$$

Take the limit $l \rightarrow \infty, \tau_i \rightarrow 0$

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} + \frac{\partial u(x,t)}{\partial x} = 0, \quad 0 < x < L, t \geq 0, \\ u(x=0, t) = \phi(u(L, t)). \end{cases}$$

Claim : An inhibitory network can generate activity (patterns)!

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} + \frac{\partial u(x,t)}{\partial x} = 0, & 0 < x < L, t \geq 0, \\ u(x=0, t) = \phi(u(L, t)). \end{cases}$$

Theorem

- There is a constant steady state $\bar{u} = \phi(\bar{u})$
- If $\phi'(\bar{u}) < -1$ then \bar{u} is linearly unstable

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} + \frac{\partial u(x,t)}{\partial x} = 0, & 0 < x < L, t \geq 0, \\ u(x=0, t) = \phi(u(L, t)). \end{cases}$$

- Theorem** ■ There is a constant steady state $\bar{u} = \phi(\bar{u})$
- If $\phi'(\bar{u}) < -1$ then \bar{u} is linearly unstable

The linearized solution $\bar{u} + \delta e^{\lambda(t-x)}$ and the linearized boundary condition :

$$e^{\lambda t} = e^{\lambda(t-L)} \phi'(\bar{u}), \quad 1 = e^{-\lambda L} \phi'(\bar{u}).$$

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} + \frac{\partial u(x,t)}{\partial x} = 0, & 0 < x < L, t \geq 0, \\ u(x=0, t) = \phi(u(L, t)). \end{cases}$$

Theorem ■ There is a constant steady state $\bar{u} = \phi(\bar{u})$

■ If $\phi'(\bar{u}) < -1$ then \bar{u} is linearly unstable

The linearized solution $\bar{u} + \delta e^{\lambda(t-x)}$ and the linearized boundary condition :

$$e^{\lambda t} = e^{\lambda(t-L)} \phi'(\bar{u}), \quad 1 = e^{-\lambda L} \phi'(\bar{u}).$$

With $\lambda = \lambda_r + i\lambda_i$ this gives

$$e^{\lambda_r L} = -\phi'(\bar{u}) \quad e^{i\lambda_i L} = -1$$

This is possible with $\lambda_r > 0$ under the condition $\phi'(\bar{u}) < -1$

Question : Will an EXCITATORY network generate activity?

Question : Will an EXCITATORY network generate activity?

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} + \frac{\partial u(x,t)}{\partial x} = 0, & 0 < x < L, t \geq 0, \\ u(x=0, t) = \phi(u(L, t)). \end{cases}$$

Theorem If $-a < \phi'(u) < a$ for some $a \in]0, 1[$, there is a steady state $\bar{u} = \phi(\bar{u})$ which is globally attractive.

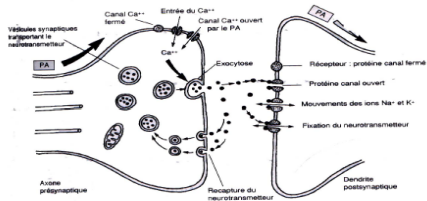
$$\begin{cases} \frac{\partial u(x,t)}{\partial t} + \frac{\partial u(x,t)}{\partial x} = 0, & 0 < x < L, t \geq 0, \\ u(x=0, t) = \phi(u(L, t)). \end{cases}$$

Theorem If $-a < \phi'(u) < a$ for some $a \in]0, 1[$, there is a steady state $\bar{u} = \phi(\bar{u})$ which is globally attractive.

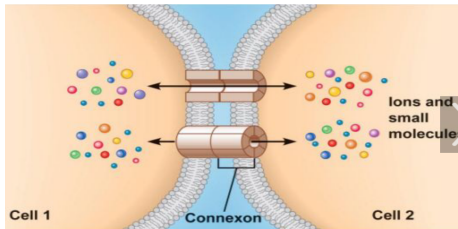
$$\frac{\partial [u(x, t) - \bar{u}]}{\partial t} + \frac{\partial [u(x, t) - \bar{u}]}{\partial x} = 0,$$

$$\frac{\partial |u(x, t) - \bar{u}|^2}{\partial t} + \frac{\partial |u(x, t) - \bar{u}|^2}{\partial x} = 0,$$

$$\begin{aligned} \frac{d}{dt} \int_0^L |u(x, t) - \bar{u}|^2 dx + |u(L, t) - \bar{u}|^2 &= |u(0, t) - \bar{u}|^2 \\ &= |\phi(u(L, t)) - \phi(\bar{u})|^2 \\ &\leq a^2 |u(L, t) - \bar{u}|^2. \end{aligned}$$



Chemical synapse. Neurotransmitters are released when spikes occur



Electrical synapse. Gap junctions directly exchange ions

The Kuramoto/Goodwin model. work on \mathbb{S}^1 . The potential of the neuron is

$$V_i(t) = V_{\text{ref}} + V_{\text{norm}} \cos(\theta_i(t))$$

$$\frac{d\theta_i(t)}{dt} = \omega_i + \underbrace{b_n \sum_j h(V_i(t)) g(V_j(t))}_{\text{chemical synapses}} + \underbrace{b_g(V_i(t)) \sum_j k(V_j(t) - V_i(t))}_{\text{electric synapses}}$$

- g_n stands for the neurotransmitter force (inhibitory)
- b_g stands for gap junctions

For instance, the spike is when $\theta(t) = \pi + 2k\pi$.

Simplest example

$$\frac{d\theta_i(t)}{dt} = \omega_i + \frac{K}{N} \sum_{j=1}^N \sin(\theta_i(t) - \theta_j(t))$$

For $\omega_j \equiv \omega$,

$$\bar{\theta}_j = \frac{2\pi j}{N}.$$

desynchronised or *incoherent* state

Simplest example

$$\frac{d\theta_i(t)}{dt} = \omega_i + \frac{K}{N} \sum_{j=1}^N \sin(\theta_j(t) - \theta_i(t))$$

There are also stable *synchronised* or *coherent* states

$$\nu_i + \frac{K}{N} \sum_{j=1}^N \sin(\bar{\theta}_j - \bar{\theta}_i) = 0, \quad i = 1, \dots, N.$$

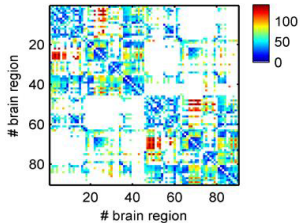
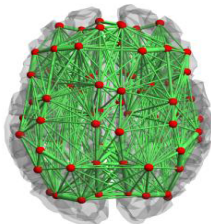
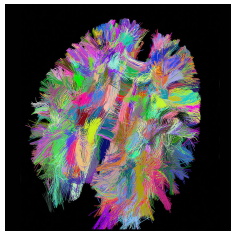
Strogatz, Carillo-Ha-Kang, Giacomin, Pakdaman...



Huygens

Aim : Describe the activity of

- an organ of the brain
- a full brain

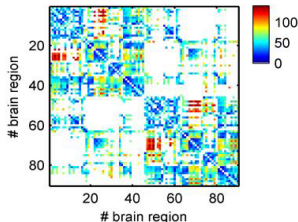
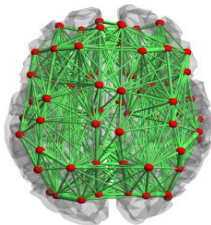
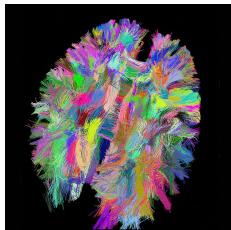


- Physiological connectivity
- Functional connectivity

The **Wilson-Cowan** model (1972) describes the firing rates $N(x, t)$ of neuron assemblies located at position x through an integral equation

$$\frac{d}{dt}N(x, t) = -N(x, t) + \sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)$$

- $\sigma(\cdot)$ = sigmoid
- $w(x, y)$ = connectivity matrix
- s = source



The **Wilson-Cowan** model (1972) describes the firing rates $N(x, t)$ of neuron assemblies located at position x through an integral equation

$$\frac{d}{dt}N(x, t) = -N(x, t) + \underbrace{\sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)}_{\text{Model of information processing}}$$

Can be seen as a generic model of network
Not physiologically based

The **Wilson-Cowan** model (1972) describes the firing rates $N(x, t)$ of neuron assemblies located at position x through an integral equation

$$\frac{d}{dt}N(x, t) = -N(x, t) + \underbrace{\sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)}_{\text{Model of information processing}}$$

Can be seen as a generic model of network.
Not physiologically based

Feature : multiple steady states and bifurcation theory (S. Amari, Bressloff-Golubitsky, Chossat-Faugeras-Faye)

The **Wilson-Cowan** model (1972) describes the firing rates $N(x, t)$ of neuron assemblies located at position x through an integral equation

$$\frac{d}{dt}N(x, t) = -N(x, t) + \underbrace{\sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)}_{\text{Model of information processing}}$$

Feature : multiple steady states and bifurcation theory (S. Amari, Bressloff-Golubitsky, Chossat-Faugeras-Faye)

Non-uniqueness is a desirable property : Interpretation of visual illusions

Feature : multiple steady states and bifurcation theory (S. Amari, Bressloff-Golubitsky, Chossat-Faugeras-Faye)

Non-uniqueness is a desirable property : Interpretation of visual illusions



The **Wilson-Cowan** model (1972) describes the firing rates $N(t, x)$ of neuron assemblies located at position x through an integral equation

$$\frac{d}{dt}N(x, t) = -N(x, t) + \sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)$$

Aim : large scale brain activity, visual hallucinations (Klüver, Oster, Siegel...)



The firing rate $N(x, t)$ model

$$\frac{d}{dt}N(x, t) = -N(x, t) + \sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)$$

The potential $V(x, t)$ model

$$\frac{d}{dt}V(x, t) = -V(x, t) + \int w(x, y)\sigma(V(y, t))dy + I(x, t)$$

The firing rate $N(x, t)$ model

$$\frac{d}{dt}N(x, t) = -N(x, t) + \sigma \left(\int w(x, y)N(y, t)dy + s(x, t) \right)$$

The potential $V(x, t)$ model

$$\frac{d}{dt}V(x, t) = -V(x, t) + \int w(x, y)\sigma(V(y, t))dy + I(x, t)$$

If $w(x, y)$ is invertible as an operator, they are equivalent

$$V(x, t) = \int w(x, y)N(y, t)dy + s(x, t)$$

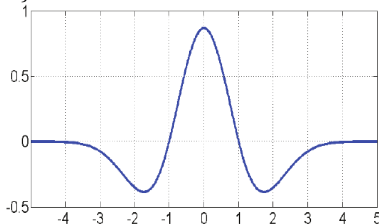
Shun-Ichi Amari

- *Homogeneous nets of neuron-like elements*, Biol. Cybernetics (1975)
- *Existence and stability of local excitations in homog.neural fields*, J. Math. Biol. (1979)

Theorem There are infinitely many solutions steady states, i.e.,

$$u(x) = \int_{-\infty}^{\infty} w(x-y)\sigma(u(x)-h)dy,$$

when $\sigma(u) = \mathbb{I}_{\{u>0\}}$ and w is mexican-hat shaped



Theorem There are infinitely many solutions steady states, i.e.,

$$u(x) = \int_{-\infty}^{\infty} w(x-y)\sigma(u(x)-h)dy,$$

when $\sigma(u) = \mathbb{1}_{\{u>0\}}$ and w is mexican-hat shaped.

Proof. Find a 'one-bump' solution

$$\{x, u(x) > h\} = (-a, a)$$

Then we derive immediately the formula

$$u_a(x) = \int_{-a}^a w(x-y)dy$$

Can one get both constraints ?

$$\{x, u(x) > h\} = (-a, a), \quad u_a(x) = \int_{-a}^a w(x-y) dy.$$

Lemma Assume that w satisfies

$$w(x) = w(-x), \quad h = \int_0^{2\bar{a}} w(z) dz \text{ for some } \bar{a} > 0,$$

$$w(x + \bar{a}) \leq w(x - \bar{a}), \quad \forall x \geq 0.$$

Then,

u_a is even, $u_{\bar{a}}(\bar{a}) = h$

$u_{\bar{a}}$ is increasing for $x < 0$ and decreasing for $x > 0$

Consequently, $u_{\bar{a}}$ is an even, 'one-bump' solution

Goals :

- understand physiologically based models of information processing
- **'small homogeneous'** neural networks
- Recover properties as synchronization

The Leaky Integrate & Fire model is simpler

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

$$V(t_-) = V_{\text{Firing}} \implies V(t_+) = V_{\text{Reset}}$$

$$0 < V_R < V_F$$

The idea was introduced by **L. Lapicque (1907)**

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

Brother of Charles Lapicque



The Leaky Integrate & Fire model is simpler

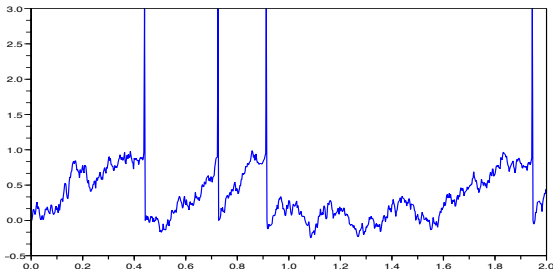
$$dV(t) = (-V(t) + I(t))dt + \sigma dW(t), \quad V(t) < V_{\text{Firing}}$$

$$V(t_-) = V_{\text{Firing}} \implies V(t_+) = V_{\text{Reset}}$$

$$0 < V_R < V_F$$

The idea was introduced by [L. Lapicque \(1907\)](#)

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



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 $-v$

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., 2008), adaptive integrate-and-fire, and Izhikovich (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 Nageswaran et al., 2008) to the same fluctuating current is fitted to an adaptive exponential integrate-and-fire (Erretti 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 Certei, 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)



Observation :

The Integrate and Fire model is an approximation of the FHN system.

The proof uses

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

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

- Hardy/Poincaré inequality,

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

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

See : Ledoux, Barthe and Roberto (2006)