Chapter II   Neural Networks Dynamics

Coupling neurons via a synapse.

Neural network definition

From now on we shall consider that a <u>neural network</u> is :

i) A collection of <u>nodes</u>, called <u>neurons</u>, characterized by a state X_i which can be the membrane potential V, but it can also include additional variables as in the Hodgkin-Huxley model, in which case $X_i = (V, n, m, h)$ or the Fitz Hugh-Nagumo model, in which case $X_i = (V_i, w_i)$. Other types of neuron model can be considered as well.

ii) A set of synaptic weights connecting neurons. We note W_{ij} the synaptic weight from neuron j to i, with the convention that $W_{ij} = 0$ if there is no synaptic connection from j to i. We will note W the matrix of W_{ij}'s.

   The synaptic weight may have their own evolution (synaptic plasticity).

iii) The synaptic weights define an <u>oriented graph</u> $\mathcal{G}$ such that there is an edge from j to i iff $W_{ij} \neq 0$.

Denote by $X(t) = \{X_i(t)\}_{i=1}^{N}$ the state of a neural network composed of N neurons at time t. Call $W(t)$ the synaptic matrix at time t. Neurons and synapses evolve jointly where neurons dynamics depend on synapses and synapses evolution depend on <u>neurons state</u>. We write this coupled evolution in the form :

(<u>Continuous time</u>)

$$
\begin{cases}
\dfrac{dX_i}{dt} = F_i\left[X, W_{ij}; \vec{\gamma}_1, \vec{\xi}_i(t)\right] \\[4mm]
\dfrac{dW_{ij}}{dt} = G_{ij}\left[X_i, X_j, W_{ij}; \vec{\gamma}_2\right]
\end{cases}
\qquad (1.1\text{-}1)
$$

where $\vec{\gamma}_1, \vec{\gamma}_2$ are a set of <u>fixed parameters</u> such as the physical characteristics of the neurons ($C, R, -$) and synapses (decay rate, propagation delay $--$). $\vec{\xi}_i(t)$ is some time dependent external signal received by the neuron i.

We may write this equation in a more compact, vector form:

$$\begin{cases} \dfrac{d\vec{X}}{dt} = \vec{F}(\vec{X}, N; \vec{\gamma}_1, \vec{\xi}(t)) \\[2mm] \dfrac{dN}{dt} = G(X, N; \vec{\gamma}_2). \end{cases} \qquad (1.1\text{-}2)$$

Using a slight abuse of notation where X includes derivatives of membrane potential, we may write eq(1.1-2) in this form:

$$\begin{cases} \dfrac{dV_i}{dt} = V_i^{(1)}; \quad \dfrac{dV_i^{(1)}}{dt} = V_i^{(2)} \cdots \dfrac{dV_i^{(\ell-1)}}{dt} = V_i^{(k)} \\[3mm] \dfrac{dV_i^{(k)}}{dt} = \dfrac{1}{a_i^{(k)}} \sum_{\ell=0}' a_i^{(\ell-1)} V_i^{(\ell-1)} + \cdots \end{cases}$$

We shall also consider <u>discrete time evolutions</u>.

$$\begin{cases} \vec{X}(t+1) = \vec{F}(\vec{X}(t), N(t); \vec{\gamma}_1, \vec{\xi}(t)) \\[2mm] W(t+1) = G(X(t), N(t); \vec{\gamma}_2) \end{cases}$$

- It is not necessary that X and N evolve according to the same time scale. In fact, typically N evolves slower than X and the time scales are rather different. Then N contains the <u>accumulated activity</u> of neurons over a <u>long history</u>. In other words N can <u>memory</u> of the system's <u>past activity</u> and evolves slowly according to this activity.

This type of coupled dynamical systems are actively coupled, and there are rather few <u>results</u> concerning this evolution. In most classical studies N is kept constant, considered as additional parameters on which dynamics depends. The study of neurons dynamics dependence on W is already a formidable task and there are very few analytical or In the following we shall mainly consider the case where N is constant. We shall however consider examples of coupled evolution at the end of this chapter.

1.2) Example

1.2.1) Voltage based firing-rate models

We have already seen the evolution equations of neurons characterized by their firing rate (eq 1.3.1 - 2)

$$(1.2.2\text{-}1) \quad \sum_{\ell=0}^{k} a_{\ell}^{(\ell)} \frac{d^{\ell}}{dt^{\ell}} V_i = \sum_{j=1}^{N} w_{ij} \cdot S_j (V_j(t)) + \xi_i(t) + B_i(t)$$

In this type of modelling, where spikes have disappeared in the firing rate, one can not consider STDP rule of type ( ). Typically Hebb like rules are considered with many variants.

1.2.2) Cohen-Grossberg model:

A simple implementation of (1.2.2-1) is:

$$(1.2.2\text{-}1) \quad \boxed{\frac{dV_i}{dt} = - \frac{V_i(t)}{\tau_i} + \sum_{j=1}^{N} w_{ij} \, S_j (V_j(t)) + \xi_i(t) + B_i(t)}$$

corresponding to first order synaptic response. An extension has been proposed by Cohen M.A, Grossberg S. "Absolute stability of global pattern formation and parallel storage by competitive neural networks", IEEE Transaction on system, man, and cybernetics, vol SMC-13:

$$(1.2.2\text{-}2) \quad \boxed{\frac{dV_i}{dt} = a_i(V) \left[b_i (u_i(t)) + \sum_{j=1}^{N} w_{ij} S_j (V_j(t)) + \xi_i(t) + B_i(t) \right],}$$

where a_i, b_i are mild function (a_i is bounded, positive and locally lipchitz continuous and b_i, b_i^{-1} are locally lipchitz continuous)!

1.2.3) Discrete time Cohen-Grossberg model

The discrete time version of (1.2.2-1), with $dt = 1$, is:

$$(1.2.3\text{-}1) \quad \boxed{V_i(t+1) = \left(1 - \frac{1}{\tau_i}\right) V_i(t) + \sum_{j=1}^{N} w_{ij} S_j (V_j(t)) + \xi_i(t) + B_i(t)}$$

The first term introduces "memory" effect with severe implications on dynamics (we shall see an example). A way to circumvent the difficulty is to consider the case where $\tau_i = 1$. Then (1.2.3.1) becomes:

$$V_i(t+1) = \sum_{j=1}^{N} W_{ij} \cdot S_j(V_j(t)) + \xi_i(t) + B_i(t). \qquad (1.2.3.2)$$

It can be written, in vector form, as:

$$V(t+1) = W S(V(t)) + \xi(t) + B(t).$$

Set $X = S(V)$ and note that S convertible. Then:

$$X(t+1) = S\Big(W X(t) + \xi(t) + B(t) \Big).$$

which gives the evolution of the frequency rate $S(V)$.

Finally, we obtain a paradigmatic example that we shall consider in several occasions, called the SNT (Simple but Non Trivial) m

$$X_i(t+1) = S_j\Big(\sum_{j=1}^{N} W_{ij} X_j(t) + \xi_i(t) + B_i(t) \Big) \qquad (SNT)$$

2) Spiking models.

1.2.1) The leaky integrate and Fire model (LIF).

We have introduced this model in section 1.2.5. At the level of networks it writes:

(1.2.1-1)
$$\begin{cases} \tau_i \dfrac{dV_i}{dt} = -V_i(t) + R\, I_i(t) \; ; & (\text{if } V_i(t) < \Theta \text{ otherwise reset}) \\[2mm] R I_i(t) = \tau_i \sum_{j=1}^{N} W_{ij} \sum_{n=0}^{M_j(t)} \delta(t - t_j^{(n)} - \tau_j) + \xi_i(t) + B_i(t) \end{cases}$$

where, for simplicity we have considered instantaneous synaptic response. We assume that there are finitely many "spikes δ" within a finite time interval.

Here all type of plasticity (see section   ) could be considered as well.

1.2.2) The Berlon Maze & Saila (BMS) model

This is a discrete time version of the LIF proposed by :

A time discretization of (1.2.1-1) gives:

$$V_i(t+1) = \left(1 - \frac{1}{\tau_i}\right) V_i(t) + \frac{R I_i(t)}{\tau_i} \qquad \text{if } V_i(t) < \Theta.$$

It is possible to write integration and reset in a compact form, introducing the function

$$Z(x) = \begin{cases} 0 & \text{if } x < 0 \\ 1 & \text{if } x \geq 0 \end{cases} .$$

Then BMS model evolution equations writes

$$V_i(t+1) = \gamma_v V_i(t)\left[1 - Z(V_i(t))\right] + \sum_{j=1}^{N} W_{ij}\, Z(V_j(t)) + \xi_i(t) + B_i(t)$$

(BMS)

with $\gamma_i = 1 - \frac{1}{\tau_i}$ and where we set $\theta = 1$ for simplicity and $\overline{z_i} = 0$

This equation is easy to interpret. z_i mem is a spike and whenever the neuron's membrane potential exceeds the threshold. Thus if $V_j(t) \geq 0$ neuron i's membrane potential increases (or decreases) of an amount W_{ij} at time $t+1$. Besides, if $V_i(t) \geq 0$ then at time $t+1$ $V_i(t+1)$ is set to 0 if there is no spike coming from other neurons.

Note that time discretization introduces an ambiguity at the storage. Do we have to consider that when i fires, V_i is reset at time t or at time $t+1$, (or in between). In fact the mathematical characterization of this model dynamics applies to both cases. On phenomenological grounds there is not a model which is better than the other. This ambiguity is a spurious effect not only due to the discretization, but to the notion of instantaneous reset, which is ill posed.

1.2.3) The Generalized Integrate and Fire model

We have already met this model in section I.1.3.5]. In some sense eq. (I§ 1.3.5-1) provides directly the network dynamics since evolution of neuron k already depends on presynaptic neuron activity. We saw that (1.3.5-1) can be written in a more compact form

$$C \frac{dV_k}{dt} + g_k V_k = i_k, \qquad (1.2.3\text{-}1)$$

where g_k, i_k are given by (1.3.5-3), (1.3.5-5). The conductance g_k is the sum of conductances g_{kj} corresponding to synaptic response of neuron k to spikes coming from neuron j.

$$g_{kj} = \overline{G}_{kj} \sum_n \alpha(t-t_j^{(n)}), \quad g_k = \frac{1}{\tau_L} + \sum_{j \in I} E_j \, g_{kj} + \sum_{j \in \mathcal{E}} E_j \, g_{kj} \cdot T]$$

synaptic weight W_{ij} reads

$$W_{kj} = \overline{G}_{kj} E_j \qquad (1.2\text{-}3\text{-}2)$$

In the same way i_k reads

$$i_k = \frac{E_L}{\tau_L} + \sum_{j \in I} E_j \, g_{kj} + \sum_{j \in \mathcal{E}} E_j \, g_{kj} + i_{ext}(t)$$

Consequently, eq. (1.3.3-1) can be written:

$$33) \quad C\frac{dV_k}{dt} + g_k(t, \{t_j^n\})V_k = \frac{E_L}{\tau_L} + \sum_j W_{kj} \sum_n \alpha(t-t_j^{(n)}) + i_{ext}(t)$$

It has the generic form of a voltage based model (I. 1.3.2-1) but here the coefficient $a^{(0)}$ in the differential equation (l.h.s) depends on past neurons activity via the conductance $\underline{g_k}$.

Note that g_k depends on synaptic weights:

$$g_k(t, \{t_j^{(n)}\}) = \frac{1}{\tau_L} + \sum_j W_{kj} \sum_n \alpha(t-t_j^{(n)}).$$

Not equivalent to the classical form unless α is of first order.

Here we have assumed that synaptic weights are constant. Plasticity mechanisms of each form can be implemented here. To the best of our knowledge it has not been done yet.
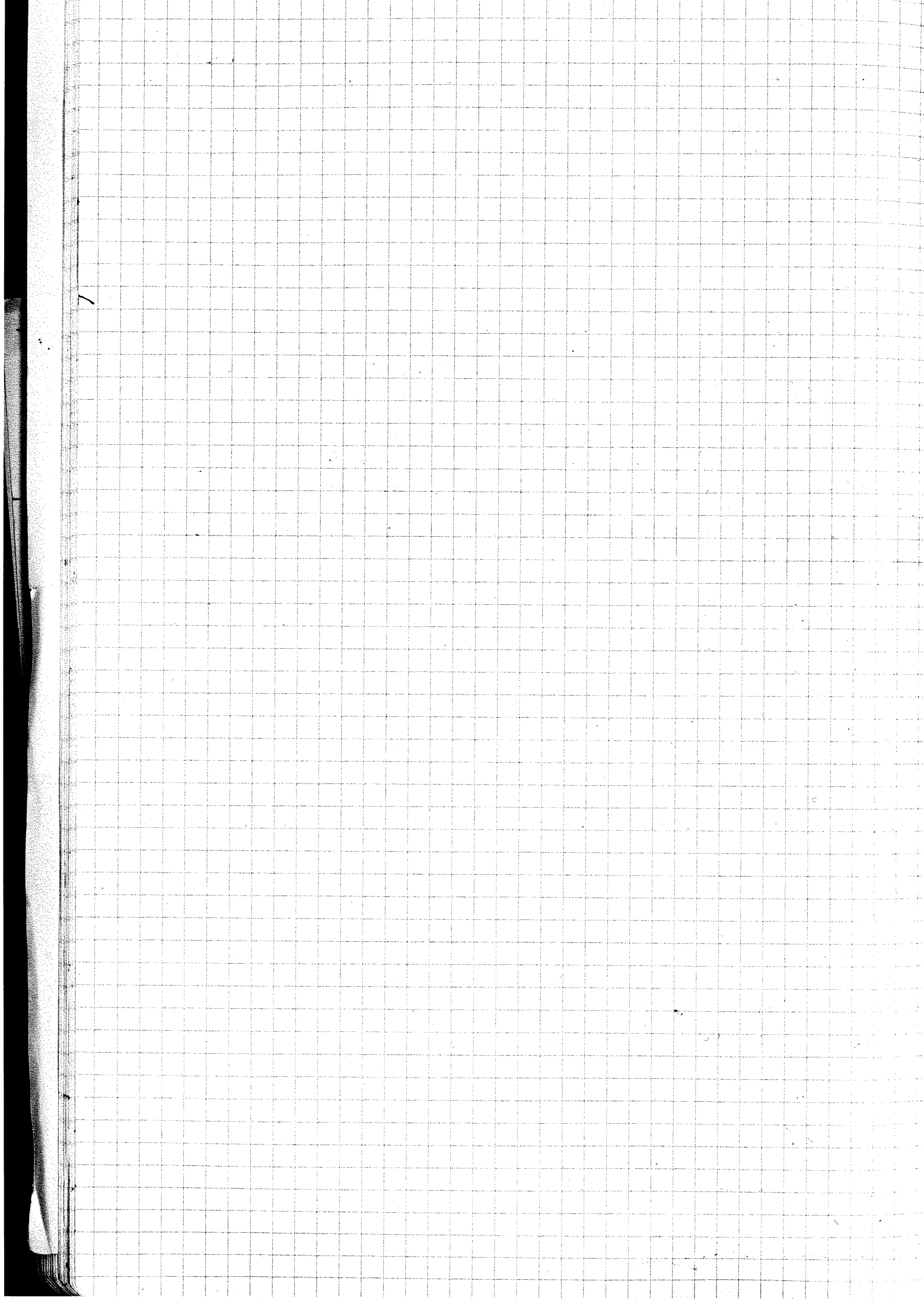
2) Weakly coupled neural networks

Before analyzing some examples of neural networks models and presenting the main tools coming from dynamical systems theory, allowing to characterize to some extension these models-dynamics, let us make here a fundamental argument due to __Izhikevich__ and Hoppensteadt.

Izhikevich E. ...

2.1) The main philosophy

Assume that we have defined a model for the characterization of isolated neurons, like Hodgkin-Huxley's, Fitz Hugh-Nagumo and so on. Eventually, we have seen in chapter 1 how dynamics can be rich, for e.g. Hodgkin-Huxley model, in determined regions of parameters.

An important question now is: "what remains of this dynamics, when coupling neurons together via synapses?". As we shall see, it is not because a neuron can have a complex dynamics when isolated, that it exhibits so much dynamics when coupled to other neurons. On the opposite, the isolated neuron dynamics can be fairly simple, nevertheless, a network of such neurons can exhibit a very rich dynamics.

The main notion that we would like to introduce along these lines is the concept of [emergence]. It characterizes the fact that the behaviour of a set of nonlinear units, coupled together, is not directly predictible from the behaviour of isolated units. It can be more complex, or less, and in most case it is drastically different, as it depends mostly on coupling parameters. This is a philosophy that we shall develop and illustrate all along the lecture. Let us start from the first step.

Assume that isolated neurons are characterized by an equation of the form:

$$\frac{dX_i}{dt} = f_i(X_i; \lambda_i) \iff \frac{dX}{dt} = f(X; \lambda) \qquad (2.1-1)$$

and assume that we couple them with synaptic weights of very small amplitude ε, so that the coupled dynamics reads:

$$\frac{dX}{dt} = f(X; \lambda) + \varepsilon \, g(X; \lambda, \rho, \varepsilon), \qquad (2.1-2)$$

where ρ is a set of additionnal parameters corresponding e.g. to external constraint.

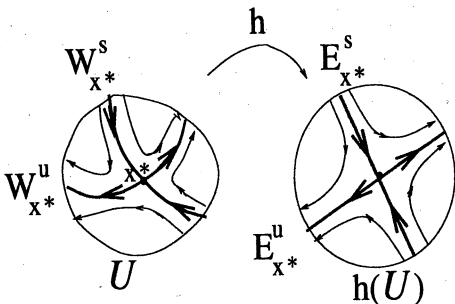This case can be viewed as an expansion of the vector field (2.1

when synaptic couplings have _small values_.

Let us analyze the expected effect of this coupling. Even with these simplifications it is not possible to study this in full generality - some specific situations are rather _instructive_.

Let us then consider the case when dynamics has a _stable fixed point_. The main action of weakly coupling neurons is provided by Hartman - Grobman theorem

2.2) The hyperbolic case.

Let X^{**} be an hyperbolic fixed point for a vector field F. Then there exists an homeomorphism h, preserving the sense of orbits locally mapping the orbits of the flow to the linear flow

$$e^{t \, DF_{X^*}}$$

$W^s_{x^*}$, $W^u_{x^*}$, U (left circle); $E^s_{x^*}$, $E^u_{x^*}$, $h(U)$ (right circle); h

The same theorem holds for maps

Basically, it says that the local behaviour of the nonlinear system near the hyperbolic fixed point is not more _complex_ than a _linear dynamical system_

The consequence of this theorem (for our case) is that the uncoupled system ($\varepsilon = 0$) the coupled system, and the linear system

$$\frac{dX}{dt} = L X \quad , \quad \text{with } L = DF_{X^*} (\lambda \neq 0, \ \varepsilon = 0)$$

are _topologically conjugated_. We are (locally) equivalent up to a _continuous variable change._

In other words _no chaotic change arise_ when coupling neurons and dynamics is not more complex (locally) than a linear system.

On the opposite, it is observed in the brain, or in smaller neural networks that the synaptic coupling can induce sharp changes in dynamics, we shall see. Therefore, the main conclusion of this short argument is that:

" To be interesting, the situation of weakly coupling neural networks where isolated are on a stable fixed, one must consider the case of a non hyperbolic fixed point"

Basically, this occurs if neurons (_isolated_) are close to a _bifurcation point._

So, starting from this point of view, Izhikevich and coll. have considered the effects of weakly coupling neurons when some of those neurons are "critical" when $\varepsilon = 0$ close to a bifurcation point. They focused on bifurcations of fixed points and they have considered that both "critical" neurons are close to the same type of bifurcation of fixed point. They have focused on codimension 1 bifurcations.

Exercise for students : Read Izhikevich book on thesis and show the following results.

Central manifold reduction (Izhikevich, 96)

Suppose that there are k non hyperbolic fixed point in the uncoupled system. Then the coupled system, for small ε is governed by a dynamical system of the form:

$$\frac{dx_i}{dt} = f_i'(x_i; \lambda) + \varepsilon g_i'(x; \lambda, \rho, \varepsilon) \; ; \quad i = 1 \dots k \qquad (2.3\_1)$$

i.e. only critical neurons have a non trivial dynamics

Normal form

about $\lambda = 0$, ρ_0 $\begin{cases} \lambda = \lambda(\varepsilon) = 0 + \varepsilon \lambda_1 + \varepsilon^2 \lambda_2 + O(\varepsilon^3) \\ env \; \rho(\varepsilon) = \rho_0 + \varepsilon \rho_1 + O(\varepsilon^2) \end{cases}$

Using an ε expansion the previous dynamical system can be written as

$$(2.3\_2) \quad \frac{dx_i}{dt} = \frac{\partial f_i'}{\partial x_i}(0;0) \, x_i + h_i x_i^2 + \varepsilon a_i + \varepsilon^2 d_i + \varepsilon \sum_{j=1}^{k} \sigma_{ij} x_j + O\varepsilon^3$$

with

$$a_i = D_\lambda f_i'(0,0) \lambda_1 + g_i'(0;0,\rho_0,0)$$

$$h_i = \frac{1}{2} \frac{\partial^2 f_i'}{\partial x_i^2}(0,0)$$

$$(2.3\_3) \quad d_i = D_\lambda^2 f_i'(0;0)(\lambda_1,\lambda_1) + D_\lambda f_i'(0;0)\cdot\lambda_2 + D_\lambda g_i'(0;0,\rho_0,0)$$
$$\qquad\qquad + D_\rho g_i(0;0,\rho_0,0)\cdot\rho_1 + \frac{\partial g_i}{\partial \varepsilon}$$

$$\sigma_{ij} = \frac{\partial g_i'}{\partial x_j}(0;0,\rho_0,0)$$

Note that σ_{ij} act as formal synapses, but with a crucial differe-
nce can act i via σ_{ij} even if there is no direct connection (synapse) $j \rightarrow i$
This is an important effect of the non linear collective dynamics.

2.4) Examples

2.4.1) Saddle - node bifurcation

If each critical point is close to a saddle-node bifurcation, the normal form of the _____ _____ for the coupled system is:

$$\frac{dx_i}{dt} = a_i + h_i\, x_i^2 + \xi \sum_{j=1}^{k} e_{ij} x_j + \varepsilon d_i$$

$$\left(\begin{array}{l} x \to \varepsilon^{1/2} x_i \\ t \to \varepsilon^{-1/2} t \end{array} \right.$$

$$\left(\begin{array}{l} \frac{\partial f_i}{\partial x_j}(0,0) = 0 \\ \frac{\partial^2 f_i}{\partial x_i^2} \neq 0, \; \partial_\lambda f_i \end{array} \right.$$

where a_i depends only on ρ_0, λ while h_i is independent of these parameters. If $a_i \neq 0$ this system admits, to the zeroth order in ε, the fixed points: $\pm\sqrt{\dfrac{a_i}{h_i}}$, which are both hyperbolic. Since hyperbolicity is structurally stable this property remains to the next order. Moreover in this setting, ρ_1 which acts as an external stimulus has no effect on these fixed points. Hence, for $a_i \neq 0$, adding a external stimulus does not change dynamics.

The situation is drastically different if $a_i = 0$. Indeed, in the case the variable change $x_i = \varepsilon^{h_i^{-1}} y_i$ and $\tau = \varepsilon t$ lead to:

$$\frac{dy_i}{d\tau} = r_i + \varepsilon y_i^2 + \sum_{j=1}^{k} c_{ij}\, y_j + O(\varepsilon)$$

with $r_i = h_i d_i$, $c_{ij} = h_i s_{ij} h_j^{-1}$. Here the dynamical system depends on ρ_1 via d_i. The fixed points are given by:

$$r_i + \varepsilon y_i^2 + \sum_{j=1}^{n} c_{ij}\, y_j = 0.$$

Thus, they depend on the structure of the matrix $\delta = \{c_{ij}\}_{i,j}^{k}$

The condition $a_i = 0$ writes:

$$D_\lambda f_i'(0,0)\lambda_1 + g_i'(0,0,\rho_0,0) = 0, \qquad i = 1..k.$$

This is called the adaptation condition. Indeed, this is a very specific case which cannot arise spontaneously but is required if one wants the coupled dynamical system to exhibit sensitivity to some stimulus. This condition can be fulfilled via a plasticity mechanism.

Hopf bifurcation

If neurons are close to a Hopf bifurcation, then the normal form writes:

$$\frac{dz_i}{dt} = b_i z_i + d_i z_i |z_i|^2 + \sum_{j \neq i}^{k} C_{ij} z_j + O(\sqrt{\varepsilon})$$
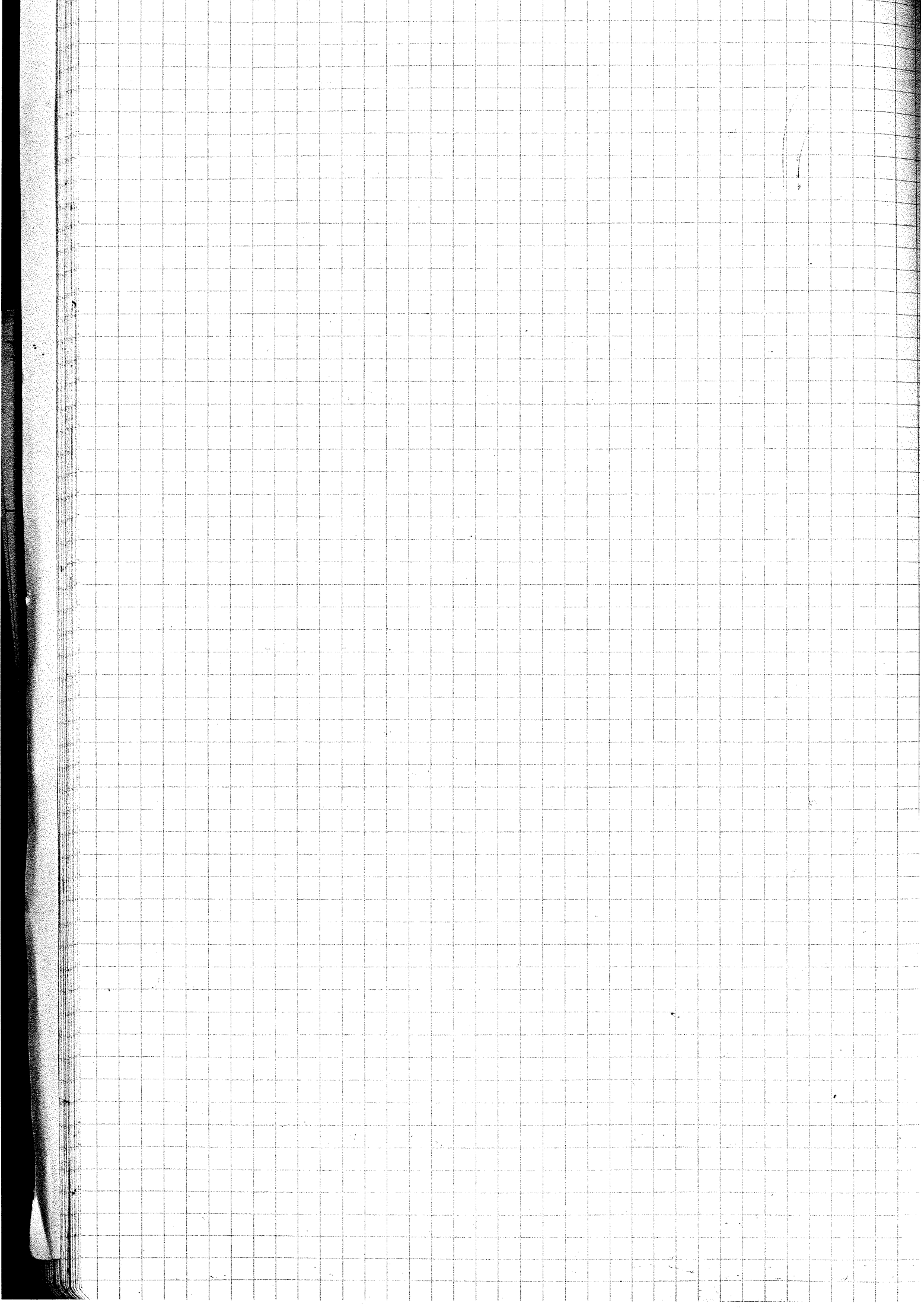
where

$$C_{ij} = \begin{cases} w_i \, D_{zj} \, g'_i \, v_j & \text{if } \omega_i = \omega_j \\ 0 & \text{if } \omega_i \neq \omega_j \end{cases}$$

Here $i\omega_i$ is the ~~imaginary~~ eigenvalue of the Jacobian matrix, of neuron i at the critical point, and v_i, w_i are the corresponding left and right eigenvectors.

This result shows that close to the bifurcation point the oscillating neurons can be divided into pools according to their natural frequency. There is an effective coupling C_{ij} between neurons from the same pool, while the coupling between neurons from different pools is negligible ($O(\sqrt{\varepsilon})$) even if there is a synaptic connection between them in the global system.

This suggests that resonances effects between neurons from the same pool. These resonances can be used e.g. to drive the neural network with a periodic input. One can in this way establish interactions between oscillators transmitting on different frequencies or one can disrupt interactions between oscillators transmitting on the same frequency.

H

3) Dynamical analysis of some neural networks... on of

3.1) Discrete time IF models

3.1.1) Dynamics of BMS model.

Exercise → read the paper and detail the proofs.

This is one of the few examples of neural networks where one can fully characterize dynamics, and especially make a classification of the generic dynamical behaviours encountered. It is then possible to go quite far in understanding collective dynamics of neurons, including spike trains statistics, or of effects of synaptic plasticity. Finally, recent results suggest that a large number of spike trains on finite time horizon, including real biological data, can be exactly reproduced by a BMS model. This suggests that this class of models are somewhat "dense" in the set of neural networks models (though we have yet no rigorous proof of this). This analysis also raises some warnings about interpreting numerical simulation result, and extrapolating single neurons model to biological neurons.

Recall that BMS model dynamics is given by:

$$V(t+1) = F(V(t)) \qquad (3.1.1\_1a)$$

where F is the mapping of components:

$$(3.1.1\_1b) \qquad F_i(V) = \gamma\, V_i\,(1 - Z[V_i]) + \sum_{j=1}^{N} W_{ij}\, Z(V_j) + I_i^{ext}, \quad i = 1 \ldots N,$$

with $\gamma \in [0, 1[$ is called the "leak rate", and I_i^{ext} is an external "current" (setting $C = 1$). The term:

$$I_i^{\,P}(V) = \sum_{j=1}^{N} W_{ij}\, Z(V_j), \qquad (3.1.1\_2)$$

is called "synaptic current".

We define the firing time of neuron i, for the initial condition V, by:

$$t_i^{(k)}(V) = \inf\{\, t \mid t > t_i^{(k-1)}(V),\; V_i(t) \geq \theta \,\}, \qquad (3.1.1\_3)$$

with the convention $t_i^{(0)}(V) = -\infty, \quad \forall V.$

Phase space dl

Define
$$V_{min} = \min\left(0, \frac{1}{1-\gamma}\left[\min_{i=1\ldots N} \sum_{j \mid W_{ij} < 0} W_{ij} + I_i^{ext}\right]\right)$$

$$V_{max} = \max\left(0, \frac{1}{1-\gamma}\left[\max_{i=1\ldots N} \sum_{j \mid W_{ij} > 0} W_{ij} + I_i^{ext}\right]\right)$$

with the convention $\sum_{j \in \emptyset} W_{ij} = 0$. Then, dynamics occurs

the phase space $\mathcal{M} = [V_{min}, V_{max}]^N$. We set $I_0 = [V_{min}, 0[$, $I_1 = [0, V_{max}[$ so that neuron i fires iff $V_i(t) \in I_1$.

Natural partition

Call $\Lambda = \{0, 1\}^N$. A spiking pattern ω is an element of Λ. Then,

$$\boxed{\mathcal{M} = \bigcup_{\omega \in \Lambda} \mathcal{S}_\omega ,} \qquad (3.1.1\text{-}3)$$

where $\mathcal{S}_\omega = \{V \in \mathcal{M} \mid V_i \in I_{\omega_i}\}$. The partition $\mathcal{S} = \{\mathcal{S}_\omega\}_{\omega}$ is called the natural partition. It is easy to show that all partition elements are __connected__, and are __hypercubes__. $\mathcal{S}_\omega = \prod I_{\omega_i}$.

The partition $\mathcal{S}$ allows to classify the membrane potential vector according to their spike state. Indeed

$$V(t) \in \mathcal{S}_\omega \iff \text{Neurons } i \text{ such that } \omega_i(t) = 1 \text{ fires at}$$
$$\qquad\qquad\qquad\qquad\qquad\qquad " \quad j \quad " \quad " \quad \omega_j(t) = 0 \text{ does not}$$

Properties of F

Call $n(\omega) = \sum_{j=1}^{N} \omega_j$, the __number of spiking neurons in the spike__ pattern ω. Denote by F_ω the restriction of F to $\mathcal{S}_\omega$, then $\forall \omega \in \Lambda$.

1) F_ω is __affine__ and __differentiable__ in the interior of its domain $\mathcal{S}$

2) F_ω is a __contraction__ with coef $\gamma(1-\omega_i)$ in direction i

3) DF_ω has $n(\omega)$ 0 eigenvalues and $N-n(\omega)$ eigenvalues $\gamma < 1$.

4)
$$F(\mathcal{S}_\omega) = \prod_{i=1}^{N} F_{\omega,i}(I_{\omega_i}),$$

where $F_{\omega,i}(I_0)$ is the __interval__ $[\gamma V_{min} + \sum_{j=1}^{N} W_{ij} \cdot \omega_j + I_i^{ext},$
$$\gamma \cdot 0 + \sum_j W_{ij}\omega_j + I_i^{ext} [$$

and $F_{\omega,i}(I_1)$ is the __point__ $\sum_{j=1}^{N} W_{ij}\omega_j + I_i^{ext}$. Thus $F(\mathcal{S}_\omega)$ is a $N-n(\omega)$ hypercube, with a value $\gamma^{N-n(\omega)} [0 - V_{min}]^N$

a consequence, of $B_{cu}(\delta) = \{V \in \mathbb{R}^N | d(V, cu) \leq \delta\}$ then

$$F(B_{cu}(\delta)) \subset B_{cu}(\delta) \longrightarrow$$ required to show that there is an open set $\mathcal{U} \supset cu$, such that $F(\mathcal{U}) \subset$ $\Longrightarrow$ existence of a "attractor" as limit set.

Singularity set:

This is the set $\mathcal{S} = \{V \in cu \mid \exists i, V_i = 0\}$, where F is discontinuous. This is a union of $N-1$ dimensional hyperplanes corresponding to faces of ∂cu.

Near $\mathcal{S}$ there is __initial condition sensitivity__

If a small ball $B_\varepsilon(V)$ around V intersects $\mathcal{S}$, then the pieces have strongly separated by dynamics and have a different future.
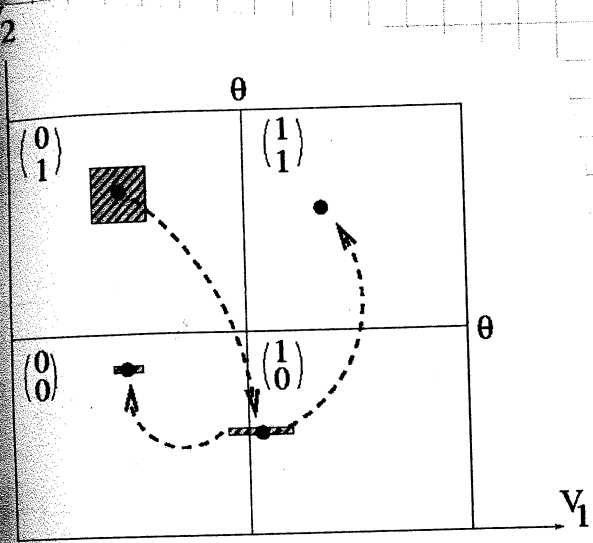
Asymptotic dynamics.

the ω-limit set $\mathcal{A}$ is the set of accumulation points of trajectories in cu.

Here:

$$\mathcal{A} = \bigcap_{t \geq 0} F^t(cu) \qquad (3.1.1-4)$$

This set is identical to the union of attractors, when the set of attractors is __non empty__. It characterizes the asymptotic dynamics.

Let us introduce the distance $d(\mathcal{A}, \mathcal{S})$ between $\mathcal{A}$ and $\mathcal{S}$:

$$d(\mathcal{A}, \mathcal{S}) = \inf_{V \in cu} \inf_{t \geq 0} \min_{i=1-N} \|V_i(t) - 0\| \qquad (3.1.1-5)$$

Theorem: (Lesac, 2008).

If $d(\mathcal{A}, \mathcal{S}) > \varepsilon > 0$ then $\mathcal{A}$ is a finite union of stable periodic orbits with a finite period. Moreover $\mathcal{A}$ is structurally stable.

The maximal period is upper bounded by:

$$T_d = 2^N \frac{\log d(\mathcal{A}, \mathcal{S})}{\log \gamma}$$

Ghost orbits

Def: $\tilde{V}$ has a ghost orbit if $\exists i$ such that

(i) $\forall t > 0 \quad V_i(t) < 0$

(ii) $\overline{\lim_{t \to +\infty}} V_i(t) = 0$
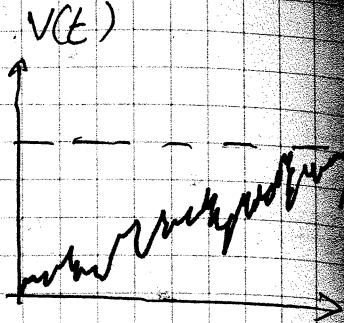
This corresponds to a situation where a neuron can take an arbitrary long time to fire, thus preventing the prediction of dynamics even if it has been observed along a very long time. Indeed if one observes dynamics up to time t_0 and conclude e.g. that it is periodic, then after a long time $t_1 \gg t_0$ it may happen that a neuron that has not fired before suddenly fires, leading to a chain reaction, and a completely different evolution.

Thm: The subset of parameters (W, I^{ext}) such that $d(\mathcal{V}, S) = 0$ is non generic in a topological and measure theoretic sense. As a consequence, ghost orbits are non generic.

General structure of asymptotic dynamics

As a consequence of these results one can distinguish 3 distinct regimes

We assume that the system-dynamics is observed over a finite time horizon

$E[d(\Omega, S)]$

I

III

Numerical limit on periodic orbit characterization

II

σ
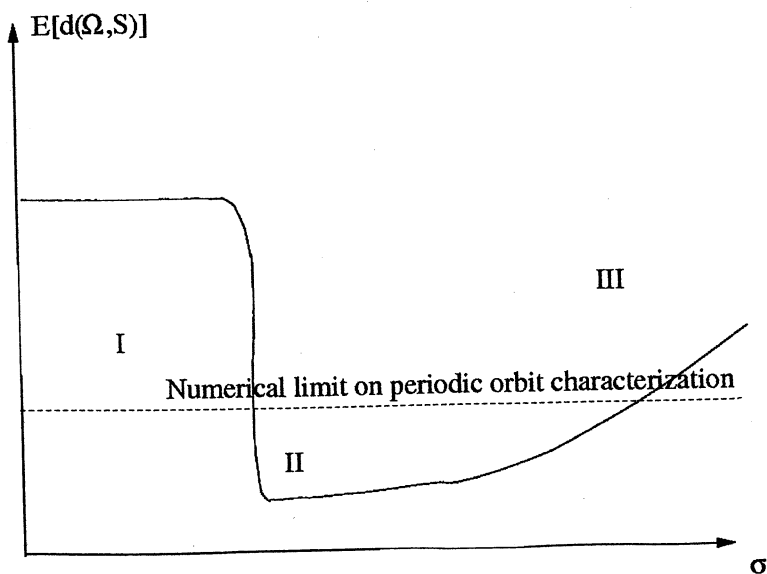
3.1.2) Extension to gIF models.

Recall that, in gIF models, the membrane potential obeys the classical equation

$$\boxed{ C\frac{dV_k}{dt} + g_k\, V_k = i_k, \qquad k = 1 \dots N, }\qquad (3.1.2\text{-}1)$$

but here, the conductance of the punctual neuron depends on past spikes received by the synapses of neuron k, coming from pre-synaptic neurons:

$$\boxed{ g_k \equiv g_k\left(t, \{ t_j^{(n)} \}\right), }\qquad (3.1.2\text{-}2)$$

where $t_j^{(n)}$ is the n-th firing time of neuron j (as usual for IF models, we assume that an instantaneous spike) and $\{t_j^{(n)}\}$ is the list of all spikes times emitted by pre-synaptic neurons.

This modelling correspond to the fact that the occurence of a post-synaptic potential on synapse j at time $t_j^{(n)}$ results in a change of the (local) conductance of neuron k. But here, since neuron is punctual, this change apply to the "whole" neuron (cf sections I.1.3.5)

Here the conductance g_k has the form:

$$g_k\left(t, \{t_j^{(n)}\}\right) = \frac{1}{\tau_L} + \underbrace{\left(\sum_{j=1}^{N} G_{kj}^{+} \overbrace{\sum_{n=1}^{M_j(t,V)} \alpha^{+}(t - t_j^{(n)})}^{M_j(t,V)} \right)}_{g_{kj}^{+}} + \sum_{j=1}^{N} G_{kj}^{-} \overbrace{\sum_{n=1}^{M_j(t,V)} \alpha^{-}(t - t_j^{(n)})}^{M_j(t,V)},$$

where τ_L is the leak state, $G_{kj}^{+,-}$ is a positive constant, $+,-$ refer to excitatory / inhibitory neurons, and α is the classical PS profile. Note that g_k is always positive.

Introducing a current:

We assume here that E_j c.eq. (1.3.5.4) depends only on the excitatory/inhibitory nature of the neuron.

$$i_k\left(t, \{t_j^n\}\right) = \frac{E_L}{\tau_L} + \boxed{E^{+}} \sum_{j=1}^{N} g_{kj}^{+}\left(t, \{t_j^{(n)}\}\right) + E^{-} \sum_{j=1}^{N} g_{kj}^{-}(t, t_j^{(n)}) + i_k^{ext}(t)$$

eq (3.1.2-1) reads:

$$\frac{dV_k}{dt} = -\frac{1}{\tau_L}(V_k - E_L) - (V_k - E^{+})\sum_{j=1}^{N} g_{kj}^{+}(\;) - (V_k - E^{-})\sum_{j=1}^{N} g_{kj}^{-} + i^{ext}_{(k)}$$

where we set $C = 1$ for simplicity. Here we have introduced

reversal potential $E^+ \sim 0\,mV$ and $E^- \sim -75\,mV$, closely related to ions concentrations.

The sign of the respective contributions $+/-$ depends on the value of V. At rest, $+$ leads to a positive PSP, while $-$ leads to a negative PSP.

We introduce synaptic weights (cf section II.1.2.3)

$$\begin{cases} W_{kj} = E^+ G_{kj} \\ W_{kj} = E^- G_{kj} \end{cases}$$

and the convention that $W_{kj} = 0$ when there is no synapse from j. We can write (   ) in the form (I.1.2.3)

Time discretisation

As emphasized several times in this lecture, a spike is not instantaneous. Here we assume that spike time is known within a precision $\delta > 0$. From now on we make the following assumptions:

(E) $\delta > 0$ such that:

i) a neuron can fire at most once between $[t, t+\delta]$ (i.e, $\delta <$)

ii) the spike time is known within a precision δ.

iii) Conductances are updated at time multiples of δ.

iv) The mesoscopic time scale dt is $\ll \delta$, allowing to keep differential equations for the evolution of the membrane potential.

The more delicate part is iii, since it introduces a time description on a grid. What are the effects of this, we shall see it. These assumptions, as we saw, release a certain number of quite delicate and spurious properties of IF models. In particular, we can properly define the notion of raster plot, introduced in section (   ), and characterize dynamics.

Recall that a raster plot is an infinite list $\omega = \{\omega_i(t)\}$, where time is discrete, so that the set of raster plots is countable and

$$\omega_i(t) = 1 \qquad \text{if neuron } i \text{ fires between } [t, t+\delta]$$
$$\qquad = 0 \qquad \text{otherwise.}$$

Then, we may rewrite the conductance in the form

$$g_k(t, [\omega]_t) = \sum_j G_{kj} \sum_{n=1}^{\eta_j(t,\omega)} \alpha(t - t_j^{(n)}) \qquad (3.1.2.3)$$

where $[\omega]_t$ is the raster plot truncated at time t, while V_k evolves according to:

$$(3.1.2-4)$$

$$\frac{dV_k}{dt} + g_k(t, [\omega]_t) V_k = i_k(t, [\omega]_t), \quad \text{whenever } V_k < \theta.$$

If the neuron does not fire between $[t, t+\delta[$ we can **integrate** this equation on this time interval. This gives

$$(3.1.2.5)$$

$$V_k(t+\delta) = \gamma_k(t, [\omega]_t) V_k(t) + J_k(t, [\omega]_t),$$

where

$$\gamma_k(t, [\omega]_t) = e^{-\int_t^{t+\delta} g_k(\sigma, [\omega]_t) d\sigma} < 1$$

and

$$J_k(t, [\omega]_t) = \int_t^{t+\delta} i_k(\sigma, [\omega]_t) \nu_k(\sigma, t+\delta, [\omega]_t) d\sigma$$

$$\nu_k(\sigma, t+\delta, [\omega]_t) = e^{-\int_\sigma^{t+\delta} g_k(\sigma', [\omega]_t) d\sigma'}.$$

Finally, we can include the reset condition or dynamics, in the same way as we did for BMS model. We finally obtain:

$$(3.1.2-6) \quad V_k(t+1) = \gamma_k(t, [\omega]_t) [1 - Z(V_k(t))] V_k(t) + J_k(t, [\omega]_t)$$

This equation has the same structure as BMS model. But the main difference is that here, γ_k, the leak rate and J_k the integrated current depend on the whole past of the network, via the raster plot $[\omega]_t$.

Let us now briefly describe the main mathematical results for this model

~~Exercise for student:~~ Do the proofs.

The same conclusions hold as for the BMS model. The genericity condition requires however the additional assumption that g depends on $[\omega]$ over a finite time horizon.
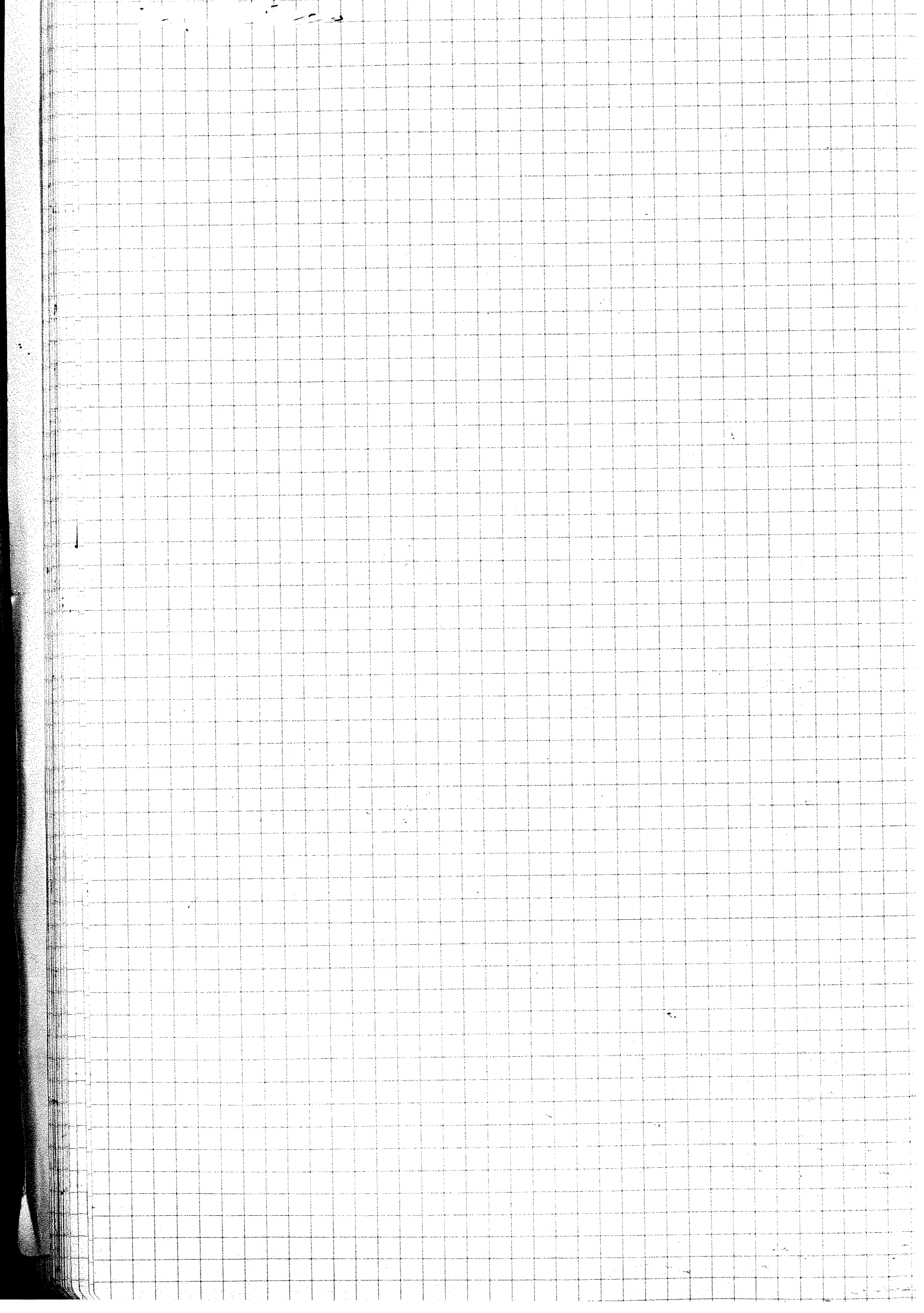
3.2) Continuous time IF models.

3.2.1) The Brunel-Hakim analysis.

In their paper:

Brunel N., Hakim V.,
"Fast Global Oscillations in Networks of Integrate and Fire Neurons with Low firing rates", Neural Computation, 11, 1621-1671 (1999)

Nicolas Brunel and Vincent Hakim consider a network of LIF neurons, continuous time and analyze the bifurcations in the model under some specific conditions on connectivity and synaptic weights.

More precisely they consider a network of LIF neurons:

$$\tau \dot{V_i} = -V_i + RI_i, \qquad (3.2.1-1)$$

with synaptic current:

$$RI_i(t) = \tau \sum_j w_{ij} \sum_k \delta(t - t_j^k - \delta), \qquad (3.2.1-2)$$

where δ is the transmission delay, uniform for all neurons, and where the synaptic weights have a specific form. Synapses are of 2 types:

<u>Excitatory:</u>

$$\left\| w_{ij} = J_{ext} = cste > 0, \right.$$

corresponding to neurons external to the network, and whose activity is Poissonian. Each neuron receives C_{ext} oscillatory connection. Frequency rate ν_{ext}.

to be discussed in the section "spike statistics"

<u>Inhibitory:</u>

$$\left\| w_{ij} = -J, < 0 \right.$$
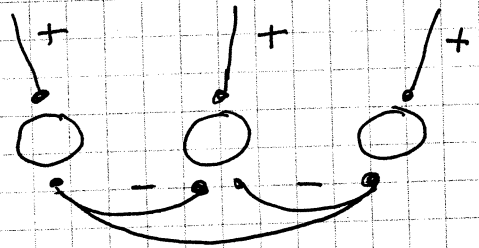
corresponding to intra network connections. Moreover, it is assumed that these connections are <u>sparse</u>, i.e, each neuron receives C inhibitory connections, where $\frac{C}{N} \ll 1$ (strong dilution)

As usual, there is a <u>threshold</u> θ and a neuron emits an incoherent neuron spike whenever $V_i > \theta$, in which case it is reset to V_r after a refractory period $\boxed{\tau_p = 0.}$

Finally the authors make the prior assumption that the frequency rate of internal neurons have a <u>low firing rate</u> ν, compared to the inverse integration time τ, each input making a <u>small contribution</u> compared to the firing threshold.

$$J \ll \theta$$

(typically $C = 5000$, $\tau = 20ms$, $\nu = 5 H_3$, $J = 0.1 mV$, $\theta = 20 mV$ $\Rightarrow$ $C\nu\tau \sim$ several hundreds, while $\theta / J \sim 100$).

Also it is assumed that *pair correlations* between neurons become ~~ay~~
as $N \to +\infty$ ($\frac{c}{N} \to 0$) $\to$ This is a classical *mean-field* appr.

Under these hypotheses, using the *central limit theorem*, one appro
the synaptic current by a Gaussian process:

$$\boxed{R I_i(t) = \mu(t) + \sqrt{\tau}\sigma \,\widehat{\lambda_i(t)}} \longrightarrow \text{standard white noi}$$
$$(3.1.2-3)$$

which:

$$\langle R I_i(t) \rangle = \mu(t) = \tau \left\langle \sum_j w_{ij} \sum_k \delta(t - t_j^k - \delta) \right\rangle =$$
$$= \tau \, C J \nu(t-\delta) + \tau J_{ext} \, C_{ext} \, \nu_{ext}.$$

$$\Rightarrow \left\| \mu(t) = \mu_I(t) + \mu_{ext} \right. ; \qquad \mu_I(t) = -C J \nu(t-\delta)\tau$$
$$\mu_{ext} = C_{ext} J_{ext} \nu_{ext} \tau.$$

The variance of $R I_i(t)$ is controlled by the *fluctuating part*,
and is given by:

$$\mathrm{Var}(R I_i(t)) = \langle (R I_i(t) - \mu(t))^2 \rangle = \langle (\tau \sum_j w_{ij} \sum_k \delta(t-t_j^k) $$
$$- \mu(t))$$

$$= \tau^2 \left[\mathrm{Var}\left(\substack{\text{internal}\\ \text{current}}\right) + \mathrm{Var}\left(\substack{\text{external}\\ \text{contrib}}\right) \right] = \tau^2 \left[C \nu(t-\delta) J^2 + C_{ext} \nu_{ext}^2 \right.$$

$$\underbrace{\qquad\qquad\qquad}_{\text{indep by assumption}}$$

$$\left\| = \tau \sigma^2 = \tau (\sigma_I^2 + \sigma_{ext}^2), \right.$$

with $\quad \sigma_I^R = J \sqrt{C \nu(t-\delta)\tau} \; ; \quad \sigma_{ext}^{\bullet} = J_{ext} \sqrt{C_{ext} \nu_{ext}} \tau.$

Fokker-Planck equation

As a consequence, we have, under these assumptions, a family
stochastic differential equations:

$(3.1.2-4)$

$$\boxed{\tau \, dV_i = f(V_i, t)\, dt + \underbrace{\boxed{\sigma \sqrt{\tau}\, dB_i}}}, \qquad \text{(independent)}$$

Effective in
between neuro

with $\boxed{f(V_i, t) = (\boxed{\mu(t)} - V_i)}$ (drift term), (mean fiel

dB_i (Wiener process (=diffusion term

As a consequence, the probability distribution function P obeys

$$\tau \frac{\partial P}{\partial t} = -\frac{\partial}{\partial V}[fP] + \frac{\sigma^2}{2}\frac{\partial^2 P}{\partial V^2} \qquad (3.1.2-5)$$

or, equivalently, $\quad \dfrac{\partial P}{\partial t} + \operatorname{div} j = 0 \quad$, with

$$j(V,t) = \frac{1}{\tau}\left[fP - \frac{\sigma^2}{2}\frac{\partial P}{\partial V}\right]. \qquad (3.1.2-6)$$

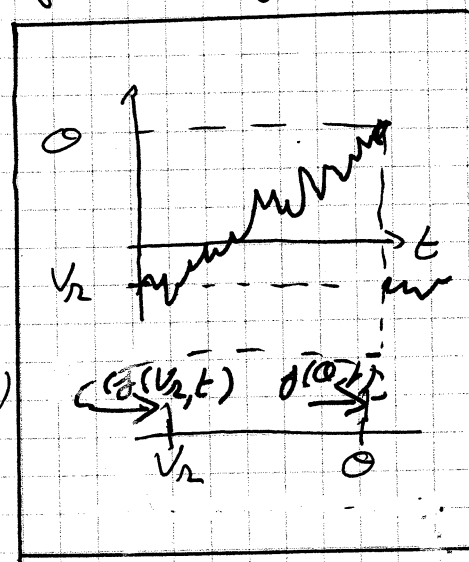This equation corresponds to the evolution of the membrane potential in the integrate regime. But there are here specific boundary conditions.

i) When the membrane potential reaches 0 it is reset to V_r, thus

$$P(0,t) = 0, \quad \forall t \quad (\text{ with } P(0,t^-) > 0 \Rightarrow \text{discontinuity on } P)$$

ii) Due to integration there is a probability current j which goes out of $V = 0$ and is reinjected at $V = V_r$.

iii) The current $j(0,t)$ is therefore the probability that a neuron reaches the threshold at t, which is exactly the frequency rate

$$j(0,t) = \frac{1}{\tau}\left[f(0)\underbrace{\boxed{P(0,t)}}_{0} - \frac{\sigma^2}{2}\frac{\partial P}{\partial V}(0,t)\right] = \nu(t)$$

$$\Rightarrow \quad \left\Vert \frac{\partial P}{\partial V}(0,t) = -\frac{2\nu(t)\tau}{\sigma^2(t)}\right.$$

iv) The reinjection at $V = V_r$ introduces a source term at $V = V_r$ inducing a discontinuity at this point.

$$j(V_r^+,t) = j(V_r^-,t) + j_{\text{reinj}}(t) \quad\Rightarrow$$

$$\frac{1}{\tau}\left[f(V_r^+,t)P(V_r^+,t) - \frac{\sigma^2(V)}{2}\frac{\partial P}{\partial V}(V_r^+,t)\right] = \frac{1}{\tau}\left[f(V_r^-,t)P(V_r^-,t) - \frac{\sigma^2}{2}\frac{\partial P}{\partial V}(V_r^-,t)\right] + \nu($$

On the other hand; f is continuous and P too (but not (differentiable))

$$\Rightarrow \quad \left\Vert \frac{\partial P}{\partial V}(V_r^+,t) = \frac{\partial P}{\partial V}(V_r^-,t) + \frac{2\tau\nu(t)}{\sigma^2(t)}\right.$$

(IV) Finally it is reasonable to assume that $\|P(\pm 8, t), \frac{\partial P}{\partial V}(-8,$

One has additionally $\quad \|\int_{-8}^{0} P(V,t) = 1, \forall t.$

Including all these conditions the final equation for P writes

$$\frac{\partial P}{\partial t} = \frac{1}{\tau}\left[-\frac{\partial}{\partial V}(fP) + \frac{\sigma^2}{2}\frac{\partial^2 P}{\partial V^2}\right] + \nu(t)\,\delta(V-V_2) \qquad (3.1.2.$$

$$\Rightarrow \quad \frac{\partial P}{\partial t} + \operatorname{div} g = J_{neq}(t, V_2) = \nu(t)\,\delta(V-V_2)$$

Stationary solutions

set $\langle \psi, \varphi \rangle = \int_{-8}^{0} \psi(x)\varphi(x)\,dx \quad \Rightarrow \quad \langle 1, P \rangle = \langle P, 1 \rangle =$

we use $\langle \frac{\partial \psi}{\partial V}, \varphi \rangle = [\psi\varphi]_{-8}^{0} - \langle \psi, \frac{\partial \varphi}{\partial V} \rangle$

Stationary corresponds to $\frac{\partial P}{\partial t} = 0, \quad V \equiv V_0, \mu \equiv \mu_0, \sigma \equiv \sigma_0$

$-\langle \frac{\partial}{\partial V}(fP), \varphi \rangle + \frac{\sigma_0^2}{2}\langle \frac{\partial^2 P}{\partial V^2}, \varphi \rangle + \nu_0 \langle \delta(V-V_2), \varphi \rangle = 0, \quad \forall \varphi \text{ test fcn}$

$\stackrel{\Rightarrow}{0=} -\underbrace{[fP\varphi]_{-8}^{0}}_{0} + \langle fP, \frac{\partial \varphi}{\partial V} \rangle + \frac{\sigma_0^2}{2}\underbrace{[\frac{\partial P}{\partial V}\varphi]_{-8}^{0}}_{} - \frac{\sigma_0^2}{2}\langle \frac{\partial P}{\partial V}, \frac{\partial \varphi}{\partial V} \rangle \quad \Big| \; + \nu_0\,\varphi(V_2)$

$\underbrace{\frac{\sigma_0^2}{2}\frac{\partial P}{\partial \sigma}\varphi(\cdot)}_{} = -\nu_0\tau\varphi(0)$

$0 = \langle fP - \frac{\sigma_0^2}{2}\frac{\partial P}{\partial V}, \frac{\partial \varphi}{\partial V} \rangle - \tau\nu_0\underbrace{(\varphi(0) - \varphi(V_2))}_{\langle H(V-V_2), \frac{\partial \varphi}{\partial V}\rangle = [H(V-V_2)\varphi]_{-8}^{0} - \langle \delta($}$

This equation holds for any φ thus:

$$fP - \frac{\sigma_0^2}{2}\frac{\partial P}{\partial V} = -\tau\nu_0\,H(V-V_2). \qquad (3.1.2-8)$$

Solutions (exercise) are given by:
Hint multiply left and right by $e^{\frac{(V-\mu_0)^2}{\sigma_0^2}}$

$$P(V) = -\frac{2\nu_0\tau}{\sigma_0^2} e^{-\frac{(V-\mu_0)^2}{\sigma_0^2}} \int^{\frac{V-\mu_0}{\sigma_0}} H\left(u - \frac{V_R-\mu_0}{\sigma_0}\right) e^{u^2} du. \quad (3.1.2.9)$$

Explicit form for the probability density of V.

Additionally:

$$\begin{cases} \mu_0 = -CJ\nu_0\tau + \mu_{ext} \\ \sigma_0^2 = CJ^2\nu_0\tau + \sigma_{ext}^2 \end{cases}$$

Finally using the normalisation condition $\langle P, 1 \rangle = 1$, one obtains (exercise)

$$\frac{1}{\nu_0\tau} = \int_{\Theta}^{+\infty} e^{-u^2} \left[\frac{e^{2y_\Theta u} - e^{2y_R u}}{u} \right] du \quad (3.1.2\_10)$$

with $\boxed{y_R = \frac{V_R - \mu_0}{\sigma_0} , \quad y_\Theta = \frac{\Theta - \mu_0}{\sigma_0}} \quad (3.1.2\_11)$

This equation is called "self-consistent" since μ_0 appears both in the l.h.s and the r.h.s. In statistical physics μ_0 is called an order parameter. It allows the descrimination of distinct dynamical regimes. Note that $P(V)$ depends on μ_0.

Weak fluctuations limit:

Assume that $\sigma_0 + \mu_0 \ll \Theta \iff y_\Theta \gg 1$.

We may always write the EDS $(3.1.2.4)$ in the form:

$$\tau dV_i = -\frac{\partial U}{\partial V} + \sigma\sqrt{\tau} dB_i , \quad \text{with} \quad \frac{\partial U}{\partial V} = -f \Rightarrow$$

$$U(V) = \frac{1}{2}(V-\mu)^2$$

This is the motion of a particle in a potential well, at temperature $\sigma\sqrt{\tau}$. If fluctuations are small around the minima (i.e. $\Theta - \mu_0 \gg \sigma_0$) then the stationary distribution is essentially

a Gibbs distribution with potential ψ => $P(V) \sim e^{} \quad \frac{}{\sqrt{2\pi}\sigma_0}$

$$P(V) \sim K e^{-\frac{1}{2}\left(\frac{V-\mu_0}{\sigma_0^2}\right)^2}$$

In this case the characteristic time to reach $V = \theta$ (inverse of firing ra

is given by Arrhenius law.

$$\nu_0 \tau \sim \frac{(\theta - \mu_0)}{\sigma_0 \sqrt{\pi}} \exp - \frac{(\theta - \mu_0)^2}{\sigma_0^2}$$

<u>Linear stability of stationary states</u>   (see appendix for details)

This analysis is technical but finally provides a norma
form of a <u>Hopf bifurcation</u>

$$\boxed{\tau \frac{dn_1}{dt} = A n_1 - B |n_1|^2 n_1}$$

where A, B depend on system parameters and boundary condi
(see notes). As a consequence, there is an (global) oscillatory regi
in this model.

This analysis extends to the follo
cases

i) <u>inhomogeneous synaptic time</u> (
  → this modifies the <u>instabili
  line</u>

ii) <u>inhomogeneous connectivity</u>
  random number of connections.
  → no net change on the instabi
  line and the frequency of global

iii) <u>more realistic synaptic response</u>
  → temporal correlations
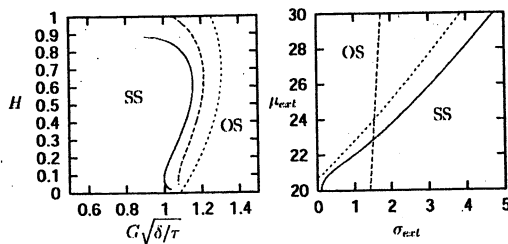
Figure 5: (Left) Instability line in the plane $(H, G\sqrt{\delta/\tau})$. Solid line: Instability line for parameters of Figure 3 and $\delta = 0.1\tau$. Long-dashed line: $\delta = 0.05\tau$. Short-dashed line: asymptotic limit $\delta/\tau \to 0$. The stationary state (SS) is unstable to the right of the instability line, where an oscillatory instability (OS) develops. (Right) Instability line in the plane $(\mu_{ext}, \sigma_{ext})$. Solid line: Parameters of Figure 2, and $\delta = 0.1\tau$. The short-dashed line is constructed taking the asymptotic instability line in the plane $(H, G\sqrt{\delta/\tau})$ and calculating the corresponding instability line in $(\mu_{ext}, \sigma_{ext})$ with $\delta = 0.1\tau$. The SS becomes unstable above the instability line. The long-dashed line shows the average (μ_{ext}) and the fluctuations (σ_{ext}) of the external inputs when the frequency of a Poissonian external input through synapses of strength $J_{ext} = 0.1$ mV is varied. For low external frequencies, the network is in its stationary state. When the external frequency increases, the network goes to OS.

iv) <u>Finite size effects</u>. This ana
  holds for $N \to \infty$. In the fin
  case, corrections such as no
  transition, additional noise in th
  form, <u>phase diffusion</u>.

Journal of Nature

Le travail proposé montre l'existence d'une transition entre un état stationnaire et un régime oscillant par bifurcation de Hopf

spike postsynaptic

modèle réalité PSP

τ_L : transmission delay

réalité avec cinétique

$\hat{L}$ modèle

τ_S : type caractéristique de la synapse

Modèle

Neurones IF

$$\tau \dot{V}_i = -V_i + R I_i$$

Courant synaptique

$$R I_i(t) = \tau \sum_j J_{ij} \sum_k \delta(t - t_j^k - \delta)$$

$$\delta = \tau_L + \tau_S$$

* t_j^k : tps d'émission du $k$ième spike du neurone j

* δ : délai de transmission

Synapses : 2 types

* Excitatrices , $J_{ij} = J_{ext} = \text{cste} > 0$

  neurones externes au réseau . C_{ext} par neurone i. Activés par un Poisson

* Inhibitrices : $J_{ij} = -J < 0$.

  C par neurone . $C << N$ (forte dilution)
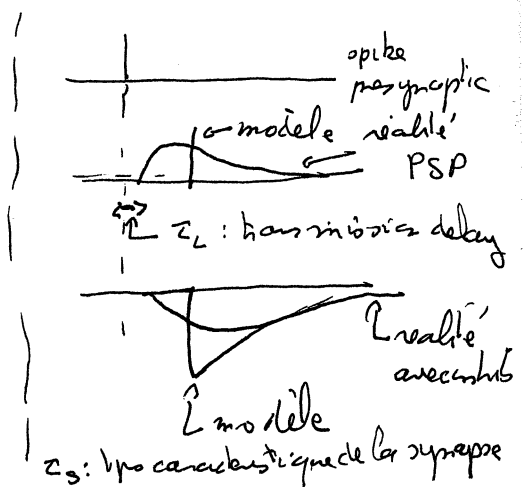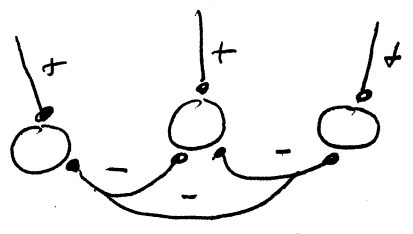
Seuil de décharge

$$V_i(t) > \Theta \Rightarrow \text{décharge} + \text{reset à } V_r < \Theta$$

Période réfractaire $\tau_p = 0$

$*$ $\frac{C}{N} \to 0$ (faible dilution) $\Rightarrow$ corrélation de paires négligeable (t borné)

$*$ On suppose que la fréquence de décharge est petite devant la fréq caractéristique $1/\tau$ $\Rightarrow$ gd nombre d'impacts par unité de tps τ

$\Rightarrow$ On approxime le courant synaptique par un processus Gaussien (TCL)

$$R I_i(t) = \mu(t) + \sigma \sqrt{\tau} \, \eta_i(t)$$

+ Emission de spikes décrite par un processus de Poisson de fréquence $\nu(t)$: l'émissions de spikes des deux neurones distincts sont indépendantes

On a dans ces hypothèses:

$$R I_i(t) = \tau \sum_j J_{ij} \sum_k \delta(t - t_j^k - \delta)$$

$$\Rightarrow \langle R I_i(t) \rangle = \mu(t) = \tau C \langle J_{ij} \rangle \langle \delta(t - t_j^k - \delta) \rangle$$
$$\underset{=\tau J C}{} \qquad + \tau C_{ext} J_{ext} \, \nu_{ext}$$

$$= -\tau C J \nu(t - \delta) + \tau C_{ext} J_{ext} \nu_{ext}$$

Sat

$$\mu(t) = \mu_I(t) + \mu_{ext} \; ; \; \mu_I(t) = -C J \nu(t-\delta) \tau$$
$$\mu_{ext} = C_{ext} J_{ext} \nu_{ext} \tau$$

La partie η est la partie fluctuante (centrée) de $R I_i(t)$.

Sa variance est donc donnée par

$$\tau^2 J^2 C \langle \left(\sum_k \delta(t - t_k^j - \delta) \right)^2 \rangle + \tau^2 J_{ext}^2 C_{ext} \nu_{ext}$$

$$\sigma^2 = \sigma_I^2 + \sigma_{ext}^2$$

avec
$$\sigma_{ext}^2 = J_{ext}\sqrt{C_{ext}\,\nu_{ext}\,\tau}$$

et
$$\left\langle \left(\sum_k \delta(t - t_k^j - \delta)\right)^2 \right\rangle = \sum_k \left\langle \delta^2(t - t_k^j - \delta) \right\rangle = C\nu(t-\delta)$$

$$\Rightarrow \quad \sigma_I = J\sqrt{C\nu(t-\delta)\tau}$$

Equation de Fokker-Planck

On a donc une famille d'équations différentielles stochastiques, <u>décoraplée</u> par l'ansatz de champ moyen :

$$\tau\frac{dV_i}{dt} = f(V_i, t) + \sigma\, \eta_i(t)$$

où le terme de dérive
$$f(V_i, t) = (\mu(t) - V_i)$$

et le terme de diffusion est un brownien) pondéré par σ.

L'équation de Fokker-Planck associée a donc pour opérateur d'évolution (σ ne dépend pas de V)

$$\tau\,\mathcal{L}_{FP}\,P = -\frac{\partial}{\partial V}[f\,P] + \frac{\sigma^2}{2}\frac{\partial^2}{\partial V^2}P$$

On y associe le courant

$$j(V,t) = \frac{1}{\tau}\left[f\,P - \frac{\sigma^2}{2}\frac{\partial P}{\partial V}\right] \qquad \Rightarrow \quad \mathcal{L}_{FP}\,P = -\operatorname{div} j$$

Dans le problème considéré on a des conditions aux bords particulières.

* $P(0,t) = 0 \quad \forall t$

* Par ailleurs cela se traduit dans l'équation de Fokker Planck par le fait que le courant sortant en 0 est réinjecté en V_n. (autrement dont le potentiel vaut 0 à t aura son potentiel à V_n à $t+dt$). Le courant sortant est simplement la fréquence moyenne de décharge (e.g. $\frac{\partial P}{\partial t} = -\frac{\partial \dot{y}}{\partial V}$ $\Rightarrow$ qd V varie de dV, P perd $\frac{\partial \dot{y}}{\partial V} dt$)

On a donc $\mathcal{I} \dot{y}(0,t) = + f(0,t) P(0,t) - \frac{\sigma^2(t)}{2} \frac{\partial P}{\partial \theta} = V\tau$

$$\Rightarrow \boxed{\frac{\partial P}{\partial \theta} = -\frac{2 V\tau}{\sigma^2(t)}}$$

* La réinjection de ce flux en V_n introduit une discontinuité en ce point.

$$\dot{y}(V_n^+, t) = \dot{y}(V_n^-, t) + \dot{y}_{reinj}(t)$$

$$\Rightarrow \frac{1}{\tau} \left[f(V_n^+, t) P(V_n^+, t) - \frac{\sigma^2(t)}{2} \frac{\partial P}{\partial V}(V_n^+, t) \right]$$

$$= \frac{1}{\tau} \left[f(V_n^-, t) P(V_n^-, t) - \frac{\sigma^2}{2} \frac{\partial P}{\partial V}(V_n^-, t) \right]$$

$$+ V(t)$$

f, P sont continues en V et le terme de source se manifeste par un saut dans la dérivée (source de courant) $\Rightarrow$

$$-\frac{\sigma^2}{2\tau} \frac{\partial P}{\partial V}(V_n^+, t) = -\frac{\sigma^2}{2\tau} \frac{\partial P}{\partial V}(V_n^-, t) + V(t)$$

$$\Rightarrow \frac{\partial P}{\partial V}(V_n^+, t) = \frac{\partial P}{\partial V}(V_n^-, t) - \frac{2\tau V(t)}{\sigma^2(t)}$$

$$\boxed{\frac{\partial P}{\partial V}(V_1^+, t) - \frac{\partial P}{\partial V}(V_2^-, t) = -\frac{2\tau \nu(t)}{\delta^2(t)}}$$

* Enfin à $-\infty$ $P, \frac{\partial P}{\partial V}$ s'annulent

  et $\displaystyle\int_{-\infty}^{0} P(V, t) = 1$ (normalisation).

Au final l'équation complète s'écrit :

$$\frac{\partial P}{\partial t} + \text{div } j = f_{\text{ranj}}(t, V_2) = \nu(t)\, \delta(V - V_2)$$

Ext :

$$\boxed{\frac{\partial P}{\partial t} = \frac{1}{\tau}\left[-\frac{\partial}{\partial V}(f P) + \frac{\delta^2}{2}\frac{\partial^2 P}{\partial V^2}\right] + \nu(t)\, \delta(V - V_2)} \qquad (A)$$

Solution stationnaire

On pose $\displaystyle \langle \varphi, \psi \rangle = \int_{-\infty}^{0} \varphi(x)\,\psi(x)\,dx \implies \langle P, \mathbb{1} \rangle = 1$

En stationnaire $\dfrac{\partial P}{\partial t} = 0 \implies$ $\nu \equiv \nu_0,\ f \equiv f_0,\ \delta \equiv \delta_0$

$$-\left\langle \frac{\partial}{\partial V}(f P), \psi \right\rangle + \frac{\delta^2}{2}\left\langle \frac{\partial^2 P}{\partial V^2}, \psi \right\rangle + \tau \nu_0 \, \psi(V_2) = 0$$

$$\implies -\left[f P \psi \right]_{-\infty}^{0} + \left\langle f P, \frac{\partial \psi}{\partial V} \right\rangle + \frac{\delta_0^2}{2}\left[\frac{\partial P}{\partial V}\psi \right]$$

$$-\frac{\delta_0^2}{2}\left\langle \frac{\partial P}{\partial V}, \frac{\partial \psi}{\partial V} \right\rangle + \tau \nu_0 \, \psi(V_2) = 0$$

$$+ < \beta P - \frac{\sigma^2}{2} \frac{\partial P}{\partial V}, \frac{\partial \varphi}{\partial V} > + \underbrace{\tau \nu_0 \; \varphi(V_2) + \frac{\sigma_0^2}{2} \frac{\partial P}{\partial c} \varphi(0)}_{-\nu_0 \tau \varphi(0)} = 0$$

$$< \beta P - \frac{\sigma^2}{2} \frac{\partial P}{\partial V}, \frac{\partial \varphi}{\partial V} > \bullet \tau \nu_0 \underbrace{\int_{-\infty}^{0} H(V-V_2) \frac{\partial \varphi}{\partial V} dV}_{< H(V-V_2), \frac{\partial \varphi}{\partial V} >} = 0$$

$$\Rightarrow \quad \boxed{\beta P - \frac{\sigma^2}{2} \frac{\partial P}{\partial V} = + \tau \nu_0 \, H(V-V_2)}$$

Résolution

$$\frac{\partial P}{\partial V} + \frac{2}{\sigma_0^2}(V-\mu_0) P = - \frac{2\tau \nu_0}{\sigma_0^2} H(V-V_2)$$

$$e^{\frac{(V-\mu_0)^2}{\sigma_0^2}} \left[\frac{\partial P}{\partial V} + \frac{2}{\sigma_0^2}(V-\mu_0)P \right] = - \frac{2\tau \nu_0}{\sigma_0^2} H(V-V_2) e^{\frac{(V-\mu_0)^2}{\sigma_0^2}}$$

$$\frac{\partial}{\partial V} \left(e^{\frac{(V-\mu_0)^2}{\sigma_0^2}} P \right) = - \frac{2\tau \nu_0}{\sigma_0^2} H(V-V_2) e^{\frac{(V-\mu_0)^2}{\sigma_0^2}}$$

$$e^{\frac{(V-\mu_0)^2}{\sigma_0^2}} P(V) - e^{\frac{(\Theta-\mu_0)^2}{\sigma_0^2}} \underbrace{P(\Theta)}_{0} = - \frac{2\tau \nu_0}{\sigma_0^2} \int^{\Theta} H(V-V_2) e^{\frac{(V-\mu_0)^2}{\sigma_0^2}} dV$$

On pose $u = \frac{V-\mu_0}{\sigma_0}$; $V > V_2 \Leftrightarrow u > \frac{V_2-\mu_0}{\sigma_0}$

$$P(V) e^{\frac{(V-\mu_0)^2}{\sigma_0^2}} = - \frac{2\nu_0 \tau}{\sigma_0} \int_{\frac{V-\mu_0}{\_}}^{\frac{\Theta-\mu_0}{\sigma_0}} H\left(u - \frac{V_2-\mu_0}{\sigma_0}\right) e^{u^2} du$$
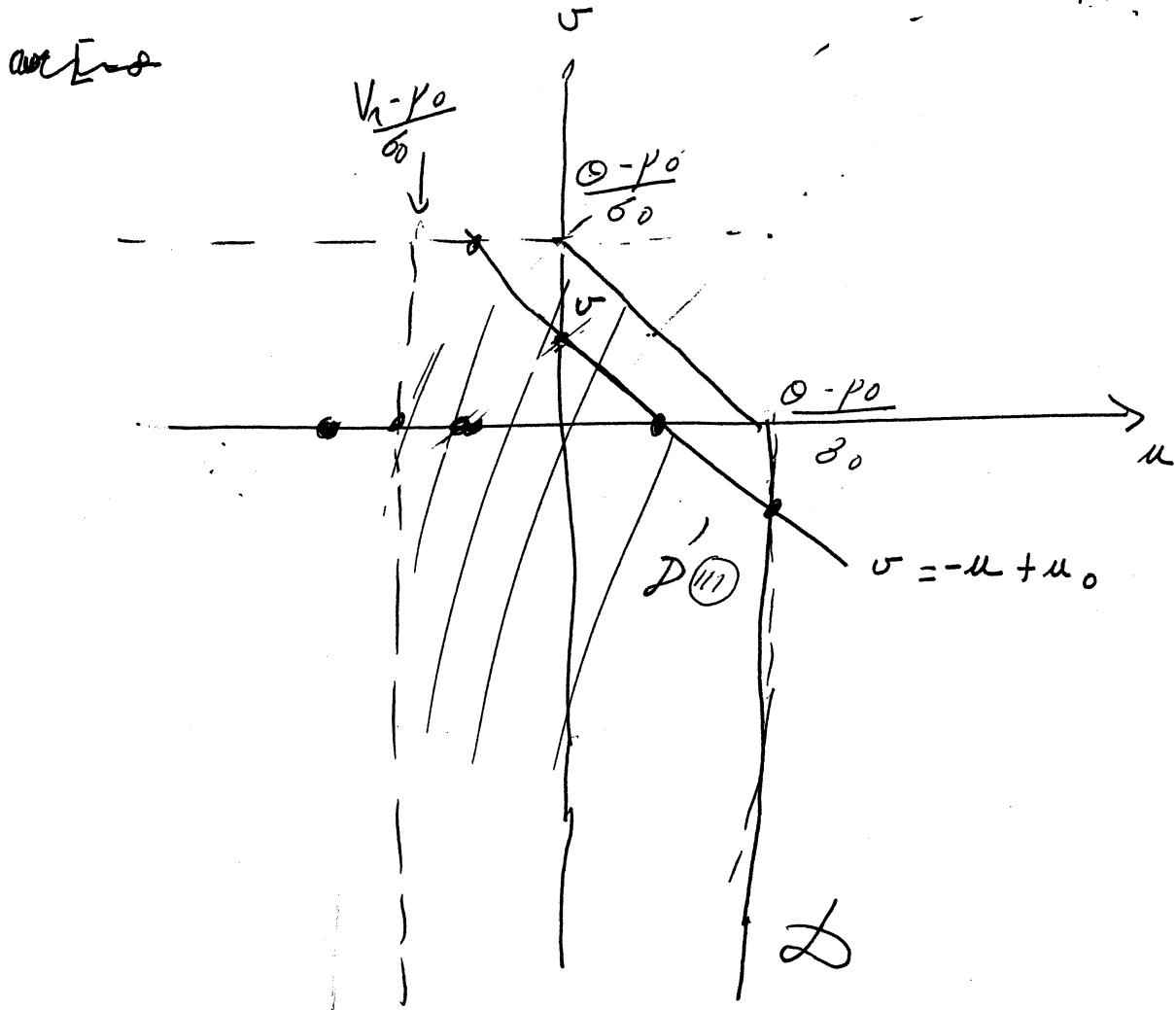
$$P(V) = -2\frac{V_0 \tau}{\sigma_0} e^{-\frac{(V-\mu_0)^2}{\sigma_0^2}} \int_{\frac{V-\mu_0}{\sigma_0}}^{\frac{\Theta-\mu_0}{\sigma_0}} H\left(\mu - \frac{V_h - \mu_0}{\sigma_0}\right) e^{\mu^2} d\mu$$

Par ailleurs, en régime stationnaire :

$$\boxed{\begin{aligned} \mu_0 &= -CJ V_0 \tau + \mu_{ext} \\ \sigma_0^2 &= CJ^2 V_0 \tau + \sigma_{ext}^2 \end{aligned}}$$

(NB: Ces termes ressemblent beaucoup aux ECM de notre modèle)

La condition de normalisation permet d'obtenir une équation auto cohérente :

$$<P,\mathbb{1}> = 1 \implies \frac{2V_0 \tau}{\sigma_0} \int_{-\infty}^{\Theta} e^{-\frac{(V-\mu)^2}{\sigma_0^2}} \left(\int_{\frac{V-\mu_0}{\sigma_0}}^{\frac{\Theta-\mu_0}{\sigma_0}} H\left(\mu - \frac{V_h - \mu}{\sigma_0}\right) e^{\mu^2} d\mu \right) dV = 1$$

On pose $\sigma = \frac{V-\mu_0}{\sigma_0} \implies$

$$\frac{2V_0 \tau}{\sigma_0} \times \sigma_0 \int_{-\infty}^{\frac{\Theta-\mu_0}{\sigma_0}} e^{-\sigma^2} \left(\int_{\sigma}^{\frac{\Theta-\mu_0}{\sigma_0}} H\left(\mu - \frac{V_h - \mu}{\sigma_0}\right) e^{\mu^2} d\mu \right) d\sigma = 1$$

$$\implies \iint_{\mathcal{D}} e^{-\sigma^2} e^{\mu^2} H\left(\mu - \frac{V_h - \mu}{\sigma_0}\right) d\mu \, d\sigma = \frac{1}{2V_0 \tau}$$

où $\mathcal{D}$ est le domaine $\mathcal{D} = \left\{ \sigma \in \left] -\infty, \frac{\Theta-\mu_0}{\sigma_0} \right], \mu \in \left[\sigma, \frac{\Theta-\mu_0}{\sigma_0} \right] \right\}$

$$\sigma \leq \mu \leq \mu_0 = \frac{\Theta-\mu_0}{\sigma_0}$$

$$\implies$$

Mais par ailleurs $\quad u \geqslant \dfrac{V_2 - \mu_0}{\sigma_0} \quad \Rightarrow \quad$ Domaine $\mathcal{D}' = \mathcal{D} \cap \left\{ u \geqslant \dfrac{V_1 - \mu_0}{\sigma_0} \right\}$

avec $\{\ldots$

$$\Rightarrow \quad u \in \left[\dfrac{V_1 - \mu_0}{\sigma_0} , \dfrac{\theta - \mu_0}{\sigma_0} \right] , \quad v \in \; \left] -\infty , u \right]$$

$$\Rightarrow \quad \dfrac{1}{2 v_0 \tau} = \int_{\frac{V_1 - \mu_0}{\sigma_0}}^{\frac{\theta - \mu_0}{\sigma_0}} e^{u^2} du \int_{-\infty}^{u} e^{-v^2} dv = \int_{y_1}^{y_\theta} e^{u^2} \left[\int_{-\infty}^{u} e^{-v^2} dv \right] du$$

On pose $\boxed{ \; y_1 = \dfrac{V_1 - \mu_0}{\sigma_0} \; ; \; y_\theta = \dfrac{\theta - \mu_0}{\sigma_0} \; }$

$$\frac{1}{v_0 \tau} = \int_0^{+\infty} du\, e^{-u^2} \left[\frac{e^{2y_0 u} - e^{2y_n u}}{u} \right] \qquad (F)$$

__NB__ Régime de petites fluctuations

si $\quad \sigma_0^2 \ll \Theta - \mu_0 \iff \mu_0 + \delta_0 \ll \Theta$
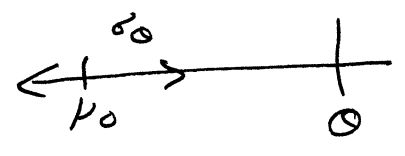
$\longrightarrow$ faible fréquence de déchange

y_0 grand $\implies \dfrac{1}{v_0 \tau} \sim \displaystyle\int_0^{+\infty} e^{-u^2 + 2y_0 u}\, \dfrac{du}{u} = \int_0^{+\infty} \dfrac{e^{-(u-y_0)^2}\, y_0^2}{u}\, e\, du = \dfrac{\sqrt{\pi}}{2} e^{y_0^2}$

$$\boxed{ v_0 \tau \sim \frac{(\Theta - \mu_0)}{\sigma_0 \sqrt{\pi}} \exp - \left(\frac{\Theta - \mu_0}{\sigma_0^2} \right)^2 } = \frac{y_0\, e^{-y_0^2/2}}{\sqrt{\pi}}$$

On peut retrouver ce résultat par Freidlin - Wentzel.

On a une dynamique stochastique du type :

$$\tau \frac{dV_i}{dt} = -\frac{\partial \vartheta}{\partial V} + \eta \qquad \text{où} \quad \frac{\partial \vartheta}{\partial V} = -\beta \implies \vartheta = \frac{1}{2}(V-\mu)^2$$

$$\boxed{ \begin{array}{l} \text{pour } V < \Theta \\ \implies \mu + \Theta \ll \sigma \end{array} }$$

Dans ce cas la distribution stationnaire autour
de l'équilibre st une distribution de Gibbs

$$e^{-\frac{\vartheta(V)}{\sigma_0}}$$

et le tps d'atteinte du bord de potentiel $\;(V = \Theta)\;$ est

$$v_0 \tau^{-1} \propto \frac{1}{\tau} \exp \frac{\vartheta(\Theta)}{\sigma_0} \implies \boxed{ v_0 \tau \sim \exp - \frac{1}{2} \frac{(\Theta - \mu_0)^2}{\sigma_0^2} }$$

Analyse de stabilité des équations brationelles

On pose :

$$P = \frac{2\tau v_0}{\sigma_0} Q \quad ; \quad y = \frac{V - \mu_0}{\sigma_0} \quad ; \quad \nu = \nu_0 (1 + n(t))$$

où $n(t)$ correspond à une perturbation autour de la fréquence moyenne de décharge. L'équation (A) devient :

$$\frac{\partial P}{\partial t} = \frac{2\tau v_0}{\sigma_0} \frac{\partial Q}{\partial t} = +\frac{1}{\tau}\left[+\frac{\partial}{\partial V}\left[(V - \mu(t)\frac{2\tau v_0}{\sigma_0} Q)\right] + \frac{\sigma^2(t)}{2}\frac{2\tau v_0}{\sigma_0}\frac{\partial^2 Q}{\partial V^2}\right]$$

$$+ \nu_0(1 + n(t))\, \delta(V - V_r)$$

avec
$$\mu(t) = \mu_{ext} - cJv(t - \delta)\tau \quad = \mu_{ext} - cJv_0\tau - cJv_0\, n(t-\delta)\tau$$
$$\sigma^2(t) = J^2 c\, v(t - \delta)\tau + \sigma_{ext}^2 = \sigma_{0c}^2 + J^2 c\tau v_0 + J^2 c\tau v_0 n(t-\delta)$$

$$\Rightarrow \boxed{\begin{array}{l} \mu(t) = \mu_0 - cJ\tau v_0\, n(t-\delta) \\[2mm] \sigma^2(t) = \sigma_0^2 + J^2 c\tau v_0 n(t-\delta) \end{array}}$$

$$\Rightarrow \frac{2\tau v_0}{\sigma_0}\frac{\partial Q}{\partial t} = \frac{1}{\tau}\left[\frac{\partial}{\partial y}\left[\frac{(V - \mu_0 + cJ\tau v_0 n(t-\delta)) \times 2\tau v_0 Q}{\sigma_0}\right] \times \frac{1}{\sigma_0}\right.$$

$$+ \left(\frac{\sigma_0^2 + J^2 c\tau v_0 n(t-\delta)}{2}\right) \times \frac{2\tau v_0}{\sigma_0}\frac{\partial^2 Q}{\partial y^2} \times \frac{1}{\sigma_0^2}$$

$$\left. + \nu_0(1 + n(t))\, \delta(y - y_r)\right]$$

$$\left(\times \frac{\sigma_0}{2\tau v_0}\right) \times \frac{\partial y}{\partial V}$$

$$\tau\frac{\partial Q}{\partial t} = \frac{\partial}{\partial y}\left[\frac{(y + cJ\tau v_0\, n(t-\delta))Q}{\sigma_0}\right] + \frac{1}{2}\left(1 + \frac{J^2 c\tau v_0 n(t-\delta)}{\sigma_0^2}\right)\frac{\partial^2 Q}{\partial y^2}$$

$$+ \frac{\sigma_0 \tau}{2\tau}(1 + n(t))\, \delta(y - y_r)$$

On pose :

$$\text{?} = \frac{CJ\tau V_0}{\sigma_0} = -\frac{\rho_{0,I}}{\sigma_0}$$

$$H = \frac{CJ^2\tau V_0}{\sigma_0^2} = \frac{\sigma_{0,I}^2}{\sigma_0^2}$$

(rapport entre la variance du courant inhibiteur et la variance totale du courant total)

(rapport entre la variance du courant inhibiteur et la variance du courant total)

$$G = \frac{\sigma_{0,I}^2}{\sigma_{0,I}^2 + \sigma_{sc}^2} = \frac{1}{1 + \dfrac{\sigma_{sc}^2}{\sigma_{0,I}^2}}$$

$\Rightarrow$

$$\tau \frac{\partial Q}{\partial t} = \frac{1}{2}\frac{\partial^2 Q}{\partial y^2} + \frac{\partial}{\partial y}(yQ) + n(t-\delta)\left(H\frac{\partial Q}{\partial y} + \frac{G}{2}\frac{\partial^2 Q}{\partial y^2}\right) + \frac{\text{?}}{2\text{?}}(1+n(t-\delta))$$
$$\times \delta(y-y_1)$$

$$\boxed{\tau \frac{\partial Q}{\partial t} = \frac{1}{2}\frac{\partial^2 Q}{\partial y^2} + \frac{\partial}{\partial y}(yQ) + \frac{\sigma_0}{2\tau}\delta(y-y_1)} \longrightarrow \text{partie stationnaire}$$

$$+ n(t-\delta)\left[\text{?}\frac{\partial Q}{\partial y} + \frac{H}{2}\frac{\partial^2 Q}{\partial y^2} + \frac{\text{?}}{2\text{?}}\delta(y-y_1)\right] \longrightarrow \text{perturbation}$$

(B)

En particulier la condition de réinjection de flux s'écrit maintenant

$$\frac{\partial P(V_1^+,t)}{\partial V} - \frac{\partial P(V_1^-,t)}{\partial t} = -2\frac{\tau V(t)}{\sigma^2(t)} \Rightarrow$$

$$\frac{2\tau V_0}{\sigma_0}\left[\frac{\partial Q}{\partial y}(y_1^+,t)\times\frac{1}{\sigma_0} - \frac{\partial Q}{\partial y}(y_1^-,t)\times\frac{1}{\sigma_0}\right] = -\frac{2\tau V_0(1+n(t))}{\sigma_0^2 + J^2 C\tau V_0 n(t-\delta)}$$

$$\boxed{\frac{\partial Q}{\partial y}(y_1^+,t) - \frac{\partial Q}{\partial y}(y_1^-,t) = -\frac{1+n(t)}{1+H n(t-\delta)}}$$

On réécrit (B) sous la forme

$$I \frac{\partial Q}{\partial t} = \mathcal{L}_{FP}[Q] + n(t-\delta)\left(\sigma \frac{\partial Q}{\partial y} + H \frac{\partial^2 Q}{\partial y^2}\right) + \frac{n(t-\delta)}{2\pi} \delta(y - y_r)$$

où $\mathcal{L}_{FP}$ est l'opérateur $\boxed{\dfrac{\partial}{\partial y}(y Q) + \dfrac{1}{2}\dfrac{\partial^2 Q}{\partial y^2}}$ (linéaire).

On peut également enlever le terme source et écrire les conditions aux bords

$$Q(y_0, t) = 0 ; \quad \frac{\partial Q}{\partial y}(y_0, t) = -\frac{1 + n(t)}{1 + H n(t-\delta)} = \left[\frac{\partial Q}{\partial y}\right]_{y_r^-}^{y_r^+}$$

La solution stationnaire s'écrit:

$$\mathcal{L}[Q_0] = 0 ; \quad \frac{\partial Q_0}{\partial y}(y_0) = -1 = \left[\frac{\partial Q_0}{\partial y}\right]_{y_r^-}^{y_r^+} = -1$$

(resp: $\mathcal{L}[Q_0] = -\delta(y - y_r)$)

La solution est donnée par (cf F_0)

$$\frac{\partial}{\partial y}(y Q) + \frac{1}{2}\frac{\partial^2 Q}{\partial y^2} = -\delta(y - y_r)$$

$$\Rightarrow \quad y Q + \frac{1}{2}\frac{\partial Q_0}{\partial y} = -H(y - y_r) \qquad \text{(en intégrant entre } -\infty \text{ et } y\text{)}$$

$$\Rightarrow \quad Q(y) = e^{-y^2}\int_0^{y_0} H(y - y_r) e^{y^2} dy$$

$$\boxed{Q_0(y) = \begin{cases} e^{-y^2}\displaystyle\int_y^{y_0} e^{u^2} du & ; \quad y > y_r \\[3mm] e^{-y^2}\displaystyle\int_{y_r}^{y_0} e^{u^2} du & ; \quad y < y_r \end{cases}}$$

Par ailleurs

$$\frac{\partial^2 Q_0}{\partial y^2} = -2\delta(y - y_r) - \frac{2\partial}{\partial y}(y Q_0)$$

$$= -2\delta(y - y_r) - 2Q_0(y) - 2y\frac{\partial Q_0}{\partial y}$$

$$\Rightarrow \frac{\partial^3 Q_0}{\partial y^3} = -2\delta'(y - y_r) - 2\frac{\partial Q_0}{\partial y} - 2\frac{\partial Q_0}{\partial y} - 2y\frac{\partial Q_0^2}{\partial y^2}$$

$$\boxed{\frac{\partial^n Q_0}{\partial y^n}(y) = -2y \frac{\partial^{n-1}}{\partial y^{n-1}} Q_0(y) - 2(n-1)\frac{\partial^{n-2}}{\partial y^{n-2}} Q^0(y) - 2\delta^{(n-1)}(y-y_n)}$$

Stabilité linéaire

$$Q(y) = Q_0(y) + Q_1(y,t) + Q_2(q,t) + \cdots$$

$$n(t) = n_1(t) + n_2(t) + \cdots$$

$$\tau\left(\frac{\partial Q_0}{\partial t} + \frac{\partial Q_1}{\partial t} + \frac{\partial Q_2}{\partial t}\right) = \mathcal{L}[Q_0] + \mathcal{L}[Q_1] + \mathcal{L}[Q_2] + O(3)$$

$$+ \left(n_1(t)^{-\delta} + n_2(t)^{-\delta} + \alpha_3\right)^{-\delta} +$$

$$\times \left[G\left(\frac{\partial Q_0}{\partial y} + \frac{\partial Q_1}{\partial y} + \frac{\partial Q_2}{\partial y} + O(3)\right) + \frac{H}{2}\left(\frac{\partial^2 Q_0}{\partial y^2} + \frac{\partial^2 Q_1}{\partial y^2} + \cdots\right) \right]$$

$$+ \left(n_1(t-\delta) + n_2(t-\delta)\cdots\right), \quad \delta(y-y_n)$$

Ordre 1

$$\tau\frac{\partial Q_1}{\partial t} = \mathcal{L}[Q_1] + n_1(t-\delta)\left(G\frac{\partial Q_0}{\partial y} + \frac{H}{2}\frac{\partial^2 Q_0}{\partial y^2} + \delta(y-y_n)\right)$$

Ordre 2

$$\tau\frac{\partial Q_2}{\partial t} = \mathcal{L}[Q_2] + n_2(t-\delta)\left(G\frac{\partial Q_0}{\partial y} + \frac{H}{2}\frac{\partial^2 Q_0}{\partial y^2} + \quad \cdot \right)$$

$$+ n_1(t-\delta)\left(G\frac{\partial Q_1}{\partial y} + \frac{H}{2}\frac{\partial^2 Q_1}{\partial y^2}\right)$$

Ordre 3

$$\tau\frac{\partial Q_3}{\partial t} = \mathcal{L}[Q_3] + n_3(t-\delta)\left(G\frac{\partial Q_0}{\partial y} + \frac{H}{2}\frac{\partial^2 Q_0}{\partial y^2} + \quad \right)$$

$$+ n_2(t-\delta)\left(G\frac{\partial Q_1}{\partial y} + \frac{H}{2}\frac{\partial^2 Q_1}{\partial y^2}\right)$$

$$+ n_1(t-\delta)\left(G\frac{\partial^2 Q_2}{\partial y_2^2} + \frac{H}{2}\frac{\partial^2 Q_2}{\partial y_2^2}\right)$$

dalle jusqu'à l'ordre 3.

Par la suite on posera

$$\mathcal{M}\, Q = G\, \frac{\partial Q}{\partial y} + \frac{H}{2}\, \frac{\partial^2 Q}{\partial y^2}$$

Instabilité

L'instabilité est donnée par le terme d'ordre 1

$$\tau\, \frac{\partial Q_1}{\partial t} = \mathcal{L}[Q_1] + n_1(t-\delta)\Big(\mathcal{M}[Q_0] + \delta(y-y_n)\Big)$$

On cherche alors des modes du type

$$Q_1(y,t) = e^{\lambda t/\tau}\, \hat{n}_1(\lambda)\, \hat{Q}_1(y,\lambda)$$
$$n_1(t) = e^{\lambda t/\tau}\, \hat{n}_1(\lambda)$$

$$\Rightarrow \quad \lambda\, \hat{Q}_1(y,\lambda) = \mathcal{L}[\hat{Q}_1](y,y) + e^{-\delta\lambda/\tau}\Big(\mathcal{M}[Q_0] + \delta(y-y_n)\Big)$$

Les solutions de cette équation peuvent être trouvées analytiquement. Ce sont la somme de 2 solutions indépendantes φ_1, φ_2 de l'équation homogène

$$\frac{1}{2}\varphi'' + y\varphi'' + (1-y)\varphi = 0 \quad \text{plus une solution particulière de l'équation}$$

complète notée $\hat{Q}_1^p$.

L'analyse détaillée révèle une instabilité associée à une valeur propre imaginaire $\boxed{\lambda = i\omega_c}$ avec

$$\boxed{\begin{aligned} G_c &= \sqrt{\omega_c}\, \sin(\omega_c \delta/\tau) = -\frac{\mu_0 I_e}{\sigma_0} \\ H_c &= \sin(\omega_c \delta/\tau) + \cos(\omega_c \delta/\tau) = \frac{\sigma_{0,I_e}^2}{\sigma_0^2} \end{aligned}}$$

H varie entre $[0,1]$ $\Rightarrow$ $\left(\dfrac{\omega_c}{\tau} = \dfrac{3\pi}{4\delta} \text{ pour } H=0 ; \quad \dfrac{\omega_c}{\tau} = \dfrac{\pi}{2\delta} \text{ pour } H=1 \right)$

étorne (y_{ext}, σ_{ext}).

Pour déterminer la forme normale il faut pousser le développement des termes non linéaires jusqu'aux premiers termes qui saturent l'instabilité. Par ailleurs la forme des termes non linéaires (cf Q_2 et Q_3 eq ( )( )) ajoute un terme de forçage qui peut être résonant. Plus précisément l'équation de Q_2 fait apparaître un terme à la fréquence 0 et un terme à la fréquence $2\omega_c$. En effet.

$$\begin{cases} Q_1(y,t) = e^{i\omega_c t/\tau} \, \hat{n}_1 \, \hat{Q}_1(y, i\omega_c) + c.c. \\ n_1(t) = e^{i\omega_c t/\tau} \, \hat{n}_1(i\omega_c) + c.c. \end{cases}$$

qui injecté dans ( ) donne

$$\mathcal{U} = \mathcal{G}\frac{\partial}{\partial y} + \frac{H}{2}\frac{\partial^2}{\partial y^2}$$

$$\tau\frac{\partial Q_2}{\partial t} = \mathcal{L}[Q_2] + n_2(t-\delta)\,\mathcal{U}[Q_0]$$
$$+ \; n_1(t-\delta)\,\mathcal{U}(Q_1)$$

$$= \mathcal{L}[Q_2] + n_2(t-\delta)\mathcal{U}[Q_0] + e^{-\frac{i\omega_c \delta}{\tau}}\left[e^{\frac{2i\omega_c t}{\tau}}\,\hat{\mathcal{U}}\hat{Q}_1\hat{n}_1 + e^{0}\,\hat{\mathcal{U}}\hat{Q}_1\bar{n}_1 \right.$$
$$\left. + \; c.c \right]$$

On cherche alors à éliminer ces termes par changement de variable. On peut les éliminer car ils sont non résonants.

Pour le terme d'ordre 3 on fait apparaître des termes en $e^{i\omega_c}$ et $e^{i3\omega_c}$. Le premier est résonant

L'analyse complète est technique mais la démarche est classique

Au final on retrouve la forme normale de la bifurcation de Hopf

$$\tau \frac{d\hat{n}_1}{dt} = A\hat{n}_1 - B |\hat{n}_1|^2 \hat{n}_1$$

où A, B sont donnés par des relations complexes faisant intervenir les conditions aux bords. Ici $Re(B) > 0$ ce qui signifie que la bifurcation est super critique. La forme de A se simplifie lorsque $H = 0$.

Finalement le calcul explicite de la fonction d'auto corrélation oscille périodiquement alors que les simulations montre qu'elle décroit exponentiellement en oscillant. Cet amortissement est en fait dû aux corrections de taille finie.

Corrections de taille finie

Pour un système de taille finie la transition n'est pas brutale mais adoucie par les effets de taille finie. Dans ce cas les fluctuations sur l'input d'un neurone proviennent de 2 processus différents. Le processus d'émission de spikes par l'ensemble du réseau, et le fait que pour un spike émis par le réseau il peut y avoir ou ne pas avoir de synapse entre le neurone émetteur et le récepteur. Soit $P_i(t)$ la variable t.q. si un spike est émis par le réseau $P_i(t) = 1$ avec proba $\frac{c}{N}$ (i reçoit le spike) et 0 avec proba $1 - \frac{c}{N}$. Alors le courant reçu par i à t est

$$RI_i(t) = -Jz\, P_i(t)\, S(t-\delta)$$

On a donc bien 2 processus : $S(t)$ et $P_i(t)$

On a :

$$\begin{cases} \rho_i(t) = \dfrac{c}{N} + \delta\rho_i(t) \\ S(t) = N\nu(t) + \delta S(t) \end{cases}$$

et

$$RI_i(t) = \mu(t) - J\tau\, N\nu(t)\,\delta\rho_i(t) - J\tau\,\frac{c}{N}\,\delta S(t)$$

où $\mu(t)$ est donnée par ( ).

Le premier processus peut être décrit comme la somme de N processus gaussiens non corrélés $\sigma\sqrt{\tau}\,\eta_i(t)$. Le second terme ne dépend pas de i. Il provient des fluctuations intrinsèques de le tirade de spikes de l'ensemble du réseau et elles entrent partout les neurones.

Lorsque $N \to +\infty$, seul le premier terme intervient, mais pour N fini le second joue un rôle. On peut voir $S(t)$ comme un processus de Poisson de fréquence $N\nu(t)$ ↗ pris en compte de $\mu(t)$ et de variance $N\nu(t)\,\delta(t-t')$. On approxime la partie fluctuante par un bruit gaussien $\sqrt{N\nu_0}\,\delta S(t)$. On suppose la variance indép. de t.

On obtient alors une correction au courant donné par ( ). (reçu par les neurones)

Le courant moyen devient :

$$cJ\tau\nu(t) + \mu_{ext} + J\sqrt{\varepsilon c\nu_0\tau}\,\sqrt{\tau}\,S(t)\ ,\quad \varepsilon = \frac{c}{N}$$

Cela rajoute un terme stochastique à l'équation de F.P.

$$\tau\,\frac{\partial Q}{\partial t} = \frac{\partial}{\partial y}\left\{\left[y + G\,n(t-\delta) + \eta\sqrt{\tau}\,S(t)\right]Q\right\} + \frac{1}{2}\frac{\partial^2\Phi}{\partial y^2}$$

$$\eta = \sqrt{\varepsilon} \frac{\delta_0^{\mathrm{I\!I}}}{\delta_0}$$

L'ajout de ce terme se manifeste par un terme de bruit supplémentaire dans la forme normale:

$$\tau \frac{d\hat{n}_\perp}{dt} = A\hat{n}_\perp - B|\hat{n}_\perp|^2 \hat{n}_\perp + D\sqrt{\tau}\, S(t)$$

où l'expression analytique de D peut être déterminée exactement.
$S(t)$ est un bruit blanc complexe t.q. $\langle S(t) S^*(t') \rangle = \delta(t-t')$.

On a:
$$C(0) = \langle |n_\perp^2(t)| \rangle - \langle n_\perp(t) \rangle^2 \overset{?}{=} 1 + 2\langle |\hat{n}_\perp(t)|^2 \rangle$$

L'évolution de $\rho = |\hat{n}_\perp|^2$ est donnée par une équation de Fokker-Planck.
En effet.

$$\tau \frac{d\rho}{dt} = \tau \bar{n}_\perp \frac{dn_\perp}{dt} + \tau n_\perp \frac{d\bar{n}_\perp}{dt}$$

$$= \tau\left(A|n_\perp|^2 - B|n_\perp|^4 + D\sqrt{\tau}\,\bar{n}_\perp S(t)\right)$$
$$+ \tau\left(\bar{A}|n_\perp|^2 - \bar{B}|n_\perp|^4 + \bar{D}\sqrt{\tau}\, n_\perp \bar{S}(t)\right)$$

$$= \tau\left(2A_r\rho - 2B_r\rho^2\right) + \tau\sqrt{\tau}\left(D\bar{n}_\perp S(t) + \bar{D}n_\perp \bar{S}(t)\right)$$

où $A_r = \mathrm{Re}(A)$; $B_r = \mathrm{Re}(B)$.

On a $\langle (D\bar{n}_\perp S(t) + \bar{D}n_\perp \bar{S}(t))^2 \rangle = \langle D\bar{n}_\perp^2 \rangle \langle S(t)^2 \rangle + \langle (\bar{D}n_\perp)^2 \rangle \langle \bar{S}(t)^2 \rangle$
$$+ \langle |D|^2 \rho \rangle \langle S(t)\bar{S}(t) \rangle$$

$$= \langle (D\bar{n}_\perp)^2 \rangle \times \underset{0?}{?} + \langle (\bar{D}n_\perp)^2 \rangle \times \underset{0?}{?} + \langle |D|^2 \rho \rangle$$

ce qui donne l'équation de Fokker Planck :

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial \rho}\left([2A_n \rho - 2B_n \rho^2]P\right) + \frac{\partial}{\partial \rho}\left[|D|^2 \rho \frac{\partial P}{\partial \rho}\right]$$

qui donne en régime stationnaire :

$$\boxed{\frac{\partial}{\partial \rho}\left[|D|^2 \rho \frac{\partial P}{\partial \rho}\right] = \frac{\partial}{\partial \rho}\left([2A_n \rho - 2B_n \rho^2]P\right)}$$

La solution est

$$|D|^2 \rho \frac{\partial P}{\partial \rho} = [2A_n \rho - 2B_n \rho^2]P + \text{cste}$$

$$\rho \frac{\partial P}{\partial \rho} = \left[\frac{2A_n \rho}{|D|^2} - \frac{2B_n \rho^2}{|D|^2}\right]P + \frac{\text{cste}}{|D|}$$

$$= \rho \frac{\partial}{\partial \rho}\left[2\frac{A_n}{|D|^2}\rho - \frac{B_n}{|D|^2}\rho^2\right] + \text{cste}$$

$$\frac{\partial P}{\partial \rho} - \frac{\partial}{\partial \rho}\left[\frac{2A_n}{|D|^2}\rho - \frac{B_n}{|D|^2}\rho^2\right] = \frac{\text{cste}}{\rho}$$

$$\frac{\partial}{\partial \rho}\left[P e^{-\left(\frac{2A_n}{|D|^2}\rho + \frac{B_n}{|D|^2}\rho^2\right)}\right] = \frac{\text{cste}}{\rho}e^{-\left[\frac{2A_n}{|D|^2}\rho + \frac{B_n}{|D|^2}\rho^2\right]}$$

$$P(\rho)e^{-\left(\frac{2A_n}{|D|^2}\rho - \frac{B_n}{|D|^2}\rho^2\right)} = \int_0^{+\infty}\frac{\text{cste}}{\rho}e^{-\left[\frac{2A_n}{|D|^2}\rho - \frac{B_n}{|D|^2}\rho^2\right]}d\rho$$

3.3) Firing rate models

3.3.1) Cohen Grossberg model.

Recall that this model - dynamics reads:

autonomous

$$(3.3.1-1) \quad \frac{dV_i}{dt} = a_i(V) \left[b_i(V_i(t)) + \sum_{j=1}^{N} W_{ij} S_j(V_j(t)) + I_i(V) \right]$$

where a_i is bounded, positive and locally Lipschitz continuous as well as b_i, b_i^{-1}.

A particular case is:

$$\frac{dV_i}{dt} = -\frac{V_i}{\tau_i} + \sum_{j=1}^{N} W_{ij} S_j(V_j(t)) + I_i(t) . \qquad (3.3.1-2)$$

As we shall see, this model can exhibit an overwhelming variety of dynamics, that have not been <u>fully analyzed</u> yet. Let us consider some prominent cases

3.3.2) Gradient systems.

Here we shall consider dynamics of $(3.3.1-1)$ in a rather abstract setting, forgetting for a while about biology. The following theorem, proved by M. Benaïm is quite useful.

Th: Consider the differential system

$$\frac{dV_i}{dt} = h_i(V) G_i(V) = F_i(V), \quad (3.3.1-3)$$

where $h_i : \mathbb{R}^N \to \mathbb{R}^{*+}$ is <u>strictly positive</u> C^1 and assume that there is a family of strictly <u>positive functions</u> $\psi_i : \mathbb{R} \to \mathbb{R}^{*+}$ such that:

$$\frac{\partial G_j}{\partial V_i} \psi_i(V_i) = \frac{\partial G_i}{\partial V_j} \psi_j(V_j) \qquad (D.B)$$

(called a "<u>detailed balance</u>" condition by analogy with Physics)

Then $(3.3.1-3)$:

1) admits a <u>strict Lyapunov function</u>;

2) Its <u>isolated</u> equilibria are <u>generically</u> hyperbolic.

Proof

* Consider the differential form $\omega = \sum_{i=1}^{N} \psi_i(V_i) G_i(V) dV_i$.

Then

$$dw = \sum_{i=1}^{N} \underbrace{G_i \frac{\partial \psi_i}{\partial V_i} dV_i \wedge dV_i}_{0} + \psi_i \frac{\partial G_i}{\partial V_j} dV_j \wedge dV_i$$

$$= \sum_{i<j} \left[\psi_i \frac{\partial G_i}{\partial V_j} - \psi_j \frac{\partial G_j}{\partial V_i} \right] dV_i \wedge dV_j = 0$$

under condition (D.B.)

Thus ω is exact ($d\omega = 0$). Then it follows from Poincaré the that there exists a function ϑ such that

$$\boxed{\omega = -d\vartheta.}$$

Let us introduce the Riemannian metric:

$$\boxed{<x,y>_V = \sum_{i=1}^{N} \frac{\psi_i(V_i)}{h_i(V)} x_i y_i.}$$

Then

$$d\vartheta = -\sum_{i=1}^{N} \psi_i(V_i) G_i(V) dV_i = -\sum_{i=1}^{N} \frac{\psi_i(V_i)}{h_i(V)} F_i(V) dV_i$$

$$= -<F, dV>.$$

As a consequence, $\dfrac{d\vartheta}{dt} = -<F, \dfrac{dV}{dt}> = -<F,F> \leq 0$
equal 0 at equi

Therefore ϑ is a Lyapunov function. It follows from Lasalle principle that equilibria are isolated.

The Jacobian matrix is $\dfrac{\partial F_i}{\partial V_j} = \dfrac{\partial h_i}{\partial V_j} G_i \delta_{ij} + h_i \dfrac{\partial G_i}{\partial V_j}$

Then:

$$<x, DFy> = \sum_i \frac{\psi_i}{h_i} x_i \sum_j \left(\frac{\partial h_i}{\partial V_j} G_i \delta_{ij} + h_i \frac{\partial G_i}{\partial V_j} \right) y_j = \sum_i \frac{\psi_i}{h_i} x_i \frac{\partial h_i}{\partial V_i} G_i y_i + \sum_i \sum_j \psi_i \psi_i \cdot \partial$$

$$<DF_x, y> = \sum_i \frac{\psi_i}{h_i} \left(\sum_j \left(\frac{\partial h_i}{\partial V_j} G_i \delta_{ij} + h_i \frac{\partial G_i}{\partial V_j} \right) x_j \right) y_i = \sum_i \frac{\psi_i}{h_i} x_i \frac{\partial h_i}{\partial V_i} G_i y_i + \sum_j x_j \psi_i \cdot$$

Since detailed balance condition holds these 2 quantities are equal, then DF

As a consequence all eigenvalues of DF are real, hence isolated poi are hyperbolic

and generically non zero.

vanishes only at infinity one can add conditions on a_i ensuring that dynamics stay in a compact set $\mathcal{M}$ (e.g. a_i vanishes on $\partial \mathcal{M}$). Then we may write:

$$\frac{dV_i}{dt} = \frac{a_i(V)}{S'(V_i)}\left(b_i(V_i) S'(V_i) + \sum_k w_{ik} S(V_k) S'(V_i) + I_i S'(V_i)\right)$$

$$\equiv \frac{G_i(V)}{S'(V_i)} = h_i(V_i) G_i(V).$$

Thus
$$\frac{\partial G_i}{\partial V_j} = \frac{\partial a_i}{\partial V_j}\left[b_i(V_i) S'(V_i) + \sum_k w_{ij} S(V_k) S'(V_i) + I_i S'(V_i)\right]$$

$$+ a_i(V)\left[\delta_{ij}\left(b_i' S' + S''(b_i + I_i)\right) + W_{ik} S'(V_i) S'(V_k)\right].$$

In the classical case where $a_i = 1$, $b_i = -\frac{V_i}{\tau_i}$, the __detailed balance__ condition holds whenever $\boxed{W_{ik} = W_{ki}}$ (with $\psi = 1$). Thus a sufficient condition for (3.3.1-2) to converge is the matrix W __being symmetric__. This is a classical result anticipated by __Hopfield - Tank__.

In this case the lyapunov function is:

$$d\mathcal{V}(V) = -\sum_{i=1}^{N} G_i(V) dV_i = -\sum_{i=1}^{N}\left(-\frac{V_i}{\tau_i} S'(V_i) + \sum_k w_{ik} S(V_k) S'(V_i) + I_i S'(V_i)\right) dV_i$$

giving, up to an irrelevant additive constant:

$$\mathcal{V}(V) = -\sum_{i,k=1}^{N} W_{ik} S(V_i) S(V_k) - I_i S(V_i))$$

$$+ \sum_{i=1}^{N} \int_0^{V_i} \frac{V_i}{\tau_i} S'(V_i) dV_i.$$

The term on the first line looks very much like a __magnetic__ energy and has deserved a long and fruitful analogy between neural networks and __spin-glasses__ with interesting applications. Here is one.

Assume that we are given a set of p N-dimensional vectors $\xi^{(1)} \dots \xi^{(p)}$ corresponding to __data__ that we want to store (e.g. images). Assume moreover that $\xi^{(\mu)}, \xi^{(\mu')}$ are __orthogonal__. Define the synaptic weights with the relation:

$$W_{ij} = \frac{1}{N} \sum_{\mu=1}^{P} \xi_i^{(\mu)} \xi_j^{(\mu)}$$

(Hebb , like rule)

Then, the Lyapunov function reads:

$$\vartheta(\mathbf{V}) = -\frac{1}{N} \sum_{\substack{i=1 \\ \ell=1}}^{N} \sum_{\mu=1}^{P} \xi_i^{(\mu)} \xi_\ell^{(\mu)} S(V_i) S(V_\ell) + \sum_{i=1}^{N} \left(I_i' S(V_i) + \int_0^{V_i} \frac{V_i}{I_i} S'(V_i) \right)$$

For the first term we can write $\sum_{\mu=1}^{P} \left(\sum_{i=1}^{N} \xi_i^{(\mu)} S(V_i) \right) \left(\sum_{\ell=1}^{N} \xi_\ell^{(\mu)} S(V_\ell) \right)$

$$= \sum_{\mu=1}^{P} \left(\xi^{(\mu)}, S \right)^2 ,$$

where $(,)$ is the usual scalar production $\mathbb{R}^N$ and S the vector $S($

In a very rough simplification (from biological point of view) we may assume that the gain of sigmoid tends to infinity. Thus S becomes a step function $S \to H(x - \Theta)$ where Θ is the affine part of the sigmoid and plays now the role of a threshold.
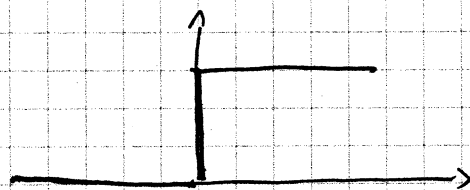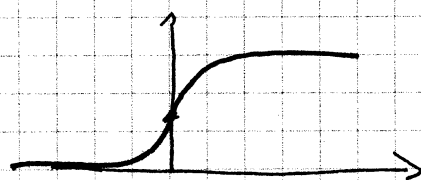
One can easily move the threshold to a value different from zero, inserting e.g. the "current" I_i.

Discussion on timescales and the binding s + δ (see sheet)

Then, dynamics holds on a discrete space (the "limit" of the differential becomes a discrete time synchronous dynamics).

In this case ϑ reads $-\frac{1}{N} \sum (\xi^\mu, S)^2$. If ξ is discrete then the minimum of ϑ is reached iff $S = \xi^\mu$ for μ.

Consider a firing rate model (voltage based)

$$\boxed{\frac{dV_i}{dt} = -\frac{V_i}{\tau_i} + \sum_{j=1}^{N} W_{ij} \, S(V_j) + I_i.} \qquad (1)$$

where S is a sigmoid with slope g.

The Jacobian matrix is given by:

$$\boxed{DF_{ij} = -\frac{\delta_{ij}}{\tau_i} + W_{ij} \, S'(V_j).} \qquad (2)$$

If V^* is a fixed point the eigenvalues of $DF(x)$ define a hierarchy of characteristic time for the convergence (or escape) from this fixed point. For more complex attractors this hierarchy of times is provided by Lyapunov exponents.

Assume for simplicity that S is a ramp function

$$S(x) = \begin{cases} g\,x + \frac{1}{2}, & \text{if } x \in \left[-\frac{1}{2g}\,;\,\frac{1}{2g}\right] \\ 0 & \text{otherwise.} \end{cases}$$
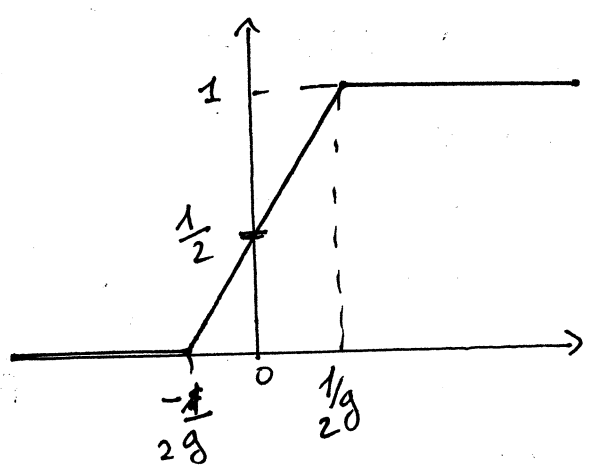
In the limit $g \to +\infty$, S becomes the Heaviside distribution.

In this case $DF = -\tau^{-1} I + g N \pi_g$ where $\tau^{-1} = \text{diag}(1/\tau_i)$, I is the identity matrix, N the synaptic weights matrix and π_g the indicatrice function of the interval $\left[-\frac{1}{2g}\,,\,\frac{1}{2g}\right]$.

than eq. (1) ... the current ... g ... value. g has the dimension of an inverse voltage $1/v$.

In the simplest case where V^* is a fixed point, the eigenvalues of DF_{V^*} are given by $\lambda_i = -\frac{1}{\tau_i} + g\,\sigma_i$, where σ_i are the eigenvalues of W. These last eigenvalues (σ_i) are constant (indep. of g). Since $Re(\lambda_i) = \frac{1}{T_i}$ T_i characteristic.

Thus we see that $T_i = \left[-\frac{1}{\tau_i} + g\,Re(\sigma_i)\right]^{-1}$

$$\Rightarrow \quad \boxed{T_i(g) = \frac{\tau_i}{g\,Re(\sigma_i)\,\tau_i + 1}} \quad (3)$$

Hence T_i depends on g.

As $g \to +\infty$, all T_i's tend to zero.

Note that, in this limit, (1) becomes formally:

$$\boxed{\frac{dV_i}{dt} = -\frac{V_i}{\tau_i} + \sum_j W_{ij}\,\delta_\Theta(V_i) + I_i}$$

where $\delta_\Theta = \begin{cases} 1 & V_i = 0 \\ 0 & \text{otherwise}. \end{cases}$

Dynamics is trivial, outside the singularity set $S = \{\exists i, V_i = 0\}$. On this set V is not continuous anymore (The network structure disappear).

Finally equation (1) comes from an explicit integration on space and time to define the membrane potential. In the limit $g \to +\infty$ time and space ($V = 0$ otherwise dynamics is trivial) tends to zero, and equations loose their physical meaning.

This terminology refers to 3 seminal paper from M. Hirsch in 1989. For a synthesis see:

M. Hirsch, "Convergent activation dynamics in continuous time networks", Neural Networks, 2, 331-349 (1989).

These papers do not focus on neural networks but on a more general class of systems including genetic networks (with current applications).

A dynamical system:

$$\frac{dV_i}{dt} = F_i(V) \qquad (3.3.2-1)$$

is called "cooperative" if:

$$\boxed{\frac{\partial F_i}{\partial V_j}(V) \geq 0, \qquad \forall i \neq j,} \qquad (3.3.2-2)$$

and "competitive" if:

$$\boxed{\frac{\partial F_i}{\partial V_j}(V) \leq 0, \qquad \forall i \neq j.} \qquad (3.3.2-3)$$

Let us first explain this terminology with a handwaving argument.

Consider the dynamical system (3.3.2-1) and assume that we slightly perturb the state (membrane potential or any other variable characterizing neuron state) of neuron j, a time t, with a slight perturbation $\delta_j(t)$, that is $V_j'(t) = V_j(t) + \delta_j(t)$, giving rise to a new evolution:

$$\frac{dV_i'}{dt} = F_i(V_1 \cdots V_j + \delta_j(t), \cdots V_N) = \frac{dV_i}{dt} + \frac{d\delta_i}{dt}$$

Performing a Taylor expansion of F_i about the initial state gives

$$\frac{dV_i}{dt} + \frac{d\delta_i}{dt} = F_i(V) + \frac{\partial F_i}{\partial V_j}\delta_j(t) + \frac{1}{2}\frac{\partial^2 F_i}{\partial V_j^2}\delta_j \quad etc \cdots$$

Thus, at the linear order, the evolution of a perturbation δ is ruled by the linear system:

$$\frac{d\delta}{dt} = DF_V \cdot \delta + O(\delta^2). \qquad (3.3.2.4)$$

This is a well known result, used in the definition of fixed point stability analysis, characterization of chaotic ab?? (lyapunov exponents) and bifurcation analysis. Obviously, this form c? not allow to control the orbit for large time (unless dynamics is contracting) and nonlinear term have to be considered as well.

Nevertheless, a key object in the characterization of th? (fairly general) dynamical system (3.3.2-1), as well as f? its discrete time version, is the Jacobian matrix DF_V.

In this setting, the interpretation of the matrix coeff? $\frac{\partial F_i}{\partial V_j}\big]_V$ is that it quantifies the linear influence of neuron on neuron i, when the system is in the state V: a slight perturb? δ_j on the state of neuron j at time t, induces, to the linear order, a perturbation $\frac{\partial F_i}{\partial V_j}\big]_V \delta_j$ on the state of neuron i, at $t + dt$.

Likewise, the perturbation at some time t, starting from an initial perturbation $\delta(0)$ is given by (to the linear order)

$$\delta(t) = \exp\left(\int_0^t DF_{V(s)} \, ds\right) \delta(0),$$

for a continuous time system; and for a discrete time one:

$$\delta(t) = DF_V^t \, \delta(0) = DF_{V(t-1)} DF_{V(t-2)} \cdots DF_{V(0)} \, \delta$$

where V corresponds to the unperturbed trajectory.

In a cooperative system, the linear influence of neu? on any other is always positive. Hence, if the level of activity (firing rate) of neuron j increases, then the level of activity of i increases, an? an increase in the level of activity of post synaptic neurons etc.

On mathematical grounds cooperativity induces the following property of flow monotony:

Assume that the phase space is convex and define the partial order

$$\vec{u} \leq \vec{\sigma} \iff u_i \leq \sigma_i.$$

A cooperative flow preserves the order $\vec{u}(0) \leq \vec{\sigma}(0) \Rightarrow \vec{u}(t) \leq \vec{\sigma}(t), \forall t$.

Assume moreover that DF_V is irreducible $\forall V$. Then Hirsh has proved that

1. The ω-limit set of almost every bounded trajectory is made of fixed points.

Hence, dynamics is generically convergent in cooperative flows.

Causal circuit.

To each Jacobian matrix DF_V, depending on V, one can associate an oriented graph, $G(V)$ depending on V such that there is an oriented edge

$$j \to i \quad \text{iff} \quad \frac{\partial F_i}{\partial V_j} \neq 0.$$

The edge is positive if $\frac{\partial F_i}{\partial V_j} > 0$ and negative if $\frac{\partial F_i}{\partial V_j} < 0$.

This graph has "circuits" or "feedback loops". If e is an edge then call $o(e)$ the origin (node) of e and $t(e)$ its end.
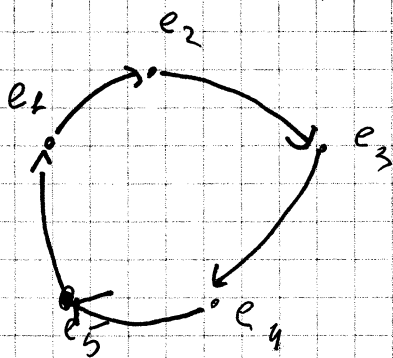
A circuit is a sequence of edges $e_1 \dots e_k$, such that

$$o(e_{i+1}) = t(e_i) \; ; \quad i = 1 \dots k-1$$
$$t(e_k) = o(e_1).$$

A circuit is oriented.

It is positive if the product of its edges is positive, and negative otherwise. Note that circuits depend on V, the current state of the network. In particular the set of circuits, or the sign of edges changes (continuously or more regularly depend on F smoothness) when V varies continuously.

This evolution can be quite complex, but let us consider a few examples.

In Cohen-Grossberg model, where

$$F_i(V) = -\frac{V_i}{z_i} + \sum_{j=1}^{\cdot} W_{ij}\, S(V_j) \neq S_i(V_j)$$

we have $\quad \dfrac{\partial F_i}{\partial V_j} = -\dfrac{\delta_{ij}}{z_i} + W_{ij}\, S'(V_j);$

where $\quad S' > 0$, S being a sigmoid.

Thus, in this case, the structure of the oriented graph is <u>fixed determined</u> by the matrix W, as well as the sign of the edges. Only the intensity of the edge depends on V.
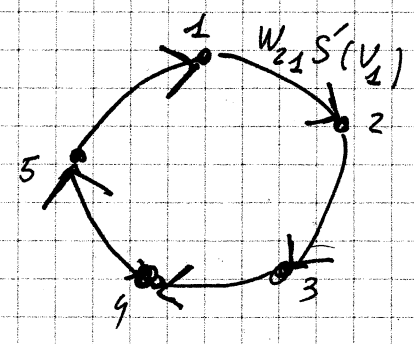
Note that if $|V| \to +\infty$, $S'(V) \to 0$, i.e. the more the neuron is saturated or quiescent, the less its influence on other neurons

The notion of causal graph is easier to understand in a <u>discrete</u> time system. In this case, from ( ) the (linear) action of j on i after t time steps is given by DF_V^t, which writes, component wise

$$DF_{V, ij}^t = \sum_{\gamma \in \mathcal{C}(i,j,t)} \prod_{\ell=1}^{t} \frac{\partial F_{k_\ell}}{\partial V_{k_{\ell-1}}}(V(\ell-1))$$

with $\quad k_0 = j$, $\quad k_t = i$, and $k_0 \longrightarrow k_t$ is a path γ connecting j to i in t time steps. $\mathcal{C}(i,j,t)$ is the set of all such paths.

Hence the action of j on i depends on the paths (and then we connecting j to i, but also on the state of the network at each time $0, 1 \ldots, t$. In the case of a (discrete time version) of Cohen Grossberg the situation is illustrated on the following figure.

In the continuous time case the quantity $\frac{1}{t} \int_0^t DF_{V(\sigma)} \, d\sigma$ is the (time?) average of $DF_{V(\sigma)}$ in the time window $[0, t]$. Then

$$S(t) = \exp t \langle DF_V \rangle \, S(0),$$

and thus this is the average matrix $\underline{\langle DF_V \rangle}$ which plays a role

Feedback loops effects on dynamics.

These loops may have critical effect on dynamics. These 2 conjectures, stated by R. Thomas

have been proved by J.L. Gouzé

under the assumption that the sign of the Jacobian matrix elements does not depend on the state.

1) A positive feedback loop in the graph of interactions of a differential system is a necessary condition for the existence of several equilibria

2) A negative loop is a necessary condition for a stable periodic behaviour.

Exercise: Illustrate these conjectures in the Cohen-Grossberg model and expose the proofs by Gouzé and Thomas.

Example neural oscillator

$$\begin{cases} \dot{V}_1 = -V_1 + W_{11} \, h(g V_1) + W_{12} \, h(g V_2) \\ \dot{V}_2 = -V_2 + W_{21} \, h(g V_1) + W_{22} \, h(g V_2) \end{cases}$$

$V = 0$ always a fixed point.

$$DF_0 = -I + g \, W$$

There is a Hopf bifurcation if:

$$g \cdot \frac{W_{11} + W_{22}}{2} \geq 1$$

$$(W_{11} - W_{22})^2 + 4 W_{12} W_{21} \leq 0$$

3.3.3) Generic case

Questions: Can we fully characterize neural network models when the N^2 synaptic weights, + the N input amplitude + etc... vary

Answer. Definitely NO.

But: Some characterization of generic dynamics h been exposed in sections 3.1.1, 3.1.2. Here are a few m

What means "generic"?

Call λ a vector including all the parameters in the system (neurons characteristics, constant inputs, etc...)

Assume that $\lambda \in \mathcal{H}$, compact set in $\mathbb{R}^p$.

Metric genericity

Choose λ at random in $\mathcal{H}$, with an absolutely continuous probability μ.

λ is generic if it belongs to a set of μ-measure 1.

A dynamical behaviour is metrically generic if it arises for metrically generic values of parameters λ

Example. Rationals in [are not generic

Idea: Sample the parameter space at random with some probability $\longrightarrow$ miss non ge pant

$\longrightarrow$ select properties arising in positive measure sets (open se

Ex. W.j chosen with pr

$$\mathcal{N}\left(\frac{\overline{W}}{N}, \frac{\sigma^2}{N}\right)$$

NB With this strategy it is not possible to vary the parameters continuously

$\Rightarrow$ Assume some "statistical" regularity

non "generic" se

Gaussian with cent

$\frac{\overline{W}}{N}$

vari

$\frac{3\sigma^2}{N}$

Changing $\overline{W}$ moves the b in the phase space.
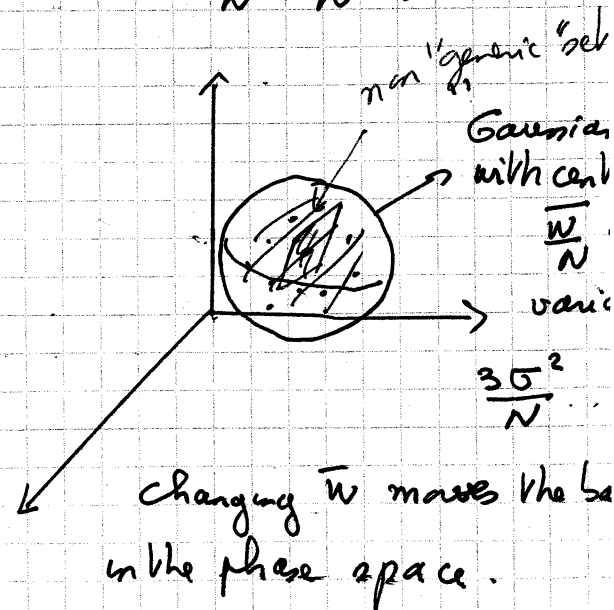
choose λ in a dense set (an countable intersection of dense sets, is dense under Baire theorem).

<u>NB</u> "Difficult" to do simulta-neously on all parameters

Look what happens when continuously varying parameters

B/f manifold

Remarque :

These 2 notions are not equivalent.

No general strategy nor method $\rightarrow$ TRY

3.3.3.1) Once more the Cohen-Grossberg model

Take first $S(x) = \tanh(gx)$, $S_i(k) = 0$

$\Rightarrow \quad \dfrac{dV_i}{dt} = -\dfrac{V_i}{\tau_i} + \sum_{j=1}^{N} W_{ij} \tanh(g V_j)$.

Properties (evident)

i) $V = 0$ is always a fixed point.

ii) It's Jacobian matrix is $-\dfrac{\mathbb{I}}{\tau_i} + g W$.

iii) It is stable if $-\dfrac{1}{\tau_i} + g \, \mathfrak{Re}(\lambda_1) < 0$, where λ_1 is the eigenvalue of W with largest real part $\Rightarrow$

0 is stable if $g < \dfrac{1}{\tau_i \, \mathfrak{Re}(\lambda_1)}$.

For larger values of g bifurcation can occur. Then detail depend on W.

Example :   Take $W_{ij} = \mathcal{N}\left(\dfrac{\overline{W}}{N}, \dfrac{\sigma^2}{N}\right)$ $\overline{W} = 0$

Theorem (Edelman)

Let A be a random $n \times n$ matrix, with Gaussian normali entries. Then

i) The probability that A has k eigenvalues has the form:
$$r + o \sqrt{2}$$
where r, o are rational

ii) The density of a random complex eigenvalue is:
$$P_n(x,y) = \sqrt{\frac{2}{\pi}} \, y \, e^{y^2 - x^2} \operatorname{erfc}(y \sqrt{2}) \, e_{n-2}(x^2 + y^2),$$
$$e_n(z) = \sum_{\ell = 0}^{n} z^{\ell}/\ell!$$

iv)

Th (Ginko)

Let A be a random matrix with Gaussian $d(0, 1/n)$ entries. As $n \to \infty$, eigenvalues are uniformly distributed in the disk $|z| < 1$. Furthermore, each eigenvalue is almost su non real.

NB : For finite n eigenvalues are almost surely non degenerate

Consequences

i) As g increases above the critical value, there is either a pitchfork or a Hopf bifurcation (H). The probability of H increases as N growths

i) A the bifurcation occurs
for

$$g_c = \pm \frac{1}{\tau} \cdot \frac{1}{Re(\lambda_1)}$$
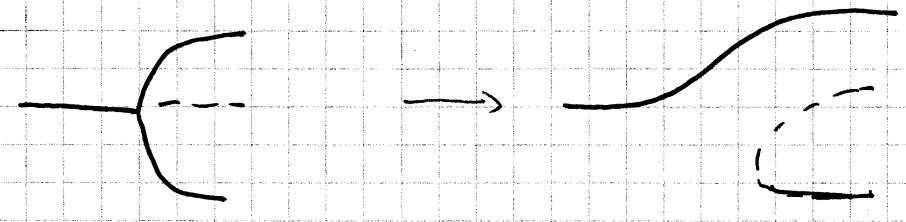
which is a random variable

ii) As $N \to +\infty$:

* Bifurcation becomes infinite
  dimensional

* $g_c \longrightarrow \frac{1}{\tau \sigma}$

Spectrum of W

Spectrum of $-\frac{I}{\tau_i} + gW$

Beyond the first bifurcation?

Sompolinsky, Crisanti, Sommers reported chaotic dynamics.

This can be analyzed in the limit $N \to +\infty$ using mean field
methods (see chapter $\underline{III}$)

What happens if breaking the symmetry $x \to -x$?

i) Pitchfork becomes saddle-node

ii) Multistability

iii) <u>Pb</u>   One can show (Matsuoka) that if g is small
enough there is only one stable fixed point. But
NOW it depends on N and g !

ii) the bifurcation occurs
for
$$g_c = \pm \frac{1}{\tau} \cdot \frac{1}{\ell_e(\lambda_1)}$$

which is a random variable

Spectrum of W

iii) As $N \to +\infty$:

* Bifurcation becomes infinite dimensional

* $g_c \longrightarrow \dfrac{1}{\tau \sigma}$
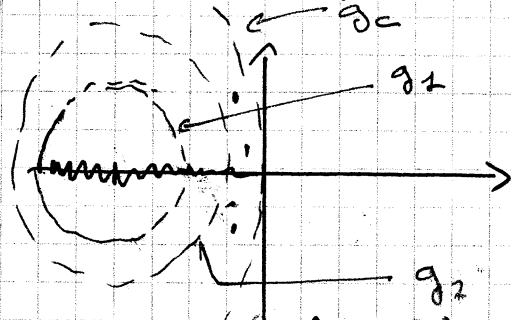
Spectrum of $-\dfrac{I}{\tau_i} + g N$

Beyond the first bifurcation?

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What happens if breaking the symmetry $x \to -x$?

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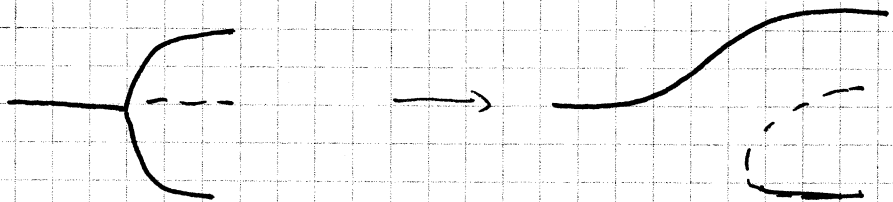
vi) Multistability

iii) Pb One can show (Matsuoka) that if g is small enough there is only one stable fixed point. But Now it depends on N and g !

3.3.3.2) The SNT model

Consider now the SNT model (section

$$X_i(t+1) = S\left(\sum_{j=1}^{N} W_{ij} X_j(t) + \xi_i\right), \qquad (3.3.3.2\text{-}1)$$

where $X_i \in [0,1]$ is the firing rate of neuron i at time t, and ξ_i a constant input. The following can be proved

Th (Cessac, 1994)

For any N there exists a g value, g_{ao}, depending on N and given by:

$$g_{ao} = \frac{1}{\alpha \|W\|},$$

where α is a prefactor depending on the choice of sigmoid, and that is absolutely stable

(Cessac et al, 94)

As g increases above g_{ao},

→ Multistability occurs

→ Fixed point destabilize by Hopf bifurcation

→ There is a transition to chaos by quasiperiodicity

A bifurcation map can be drawn in the thermodynamic limit (see chapter III for the derivation.
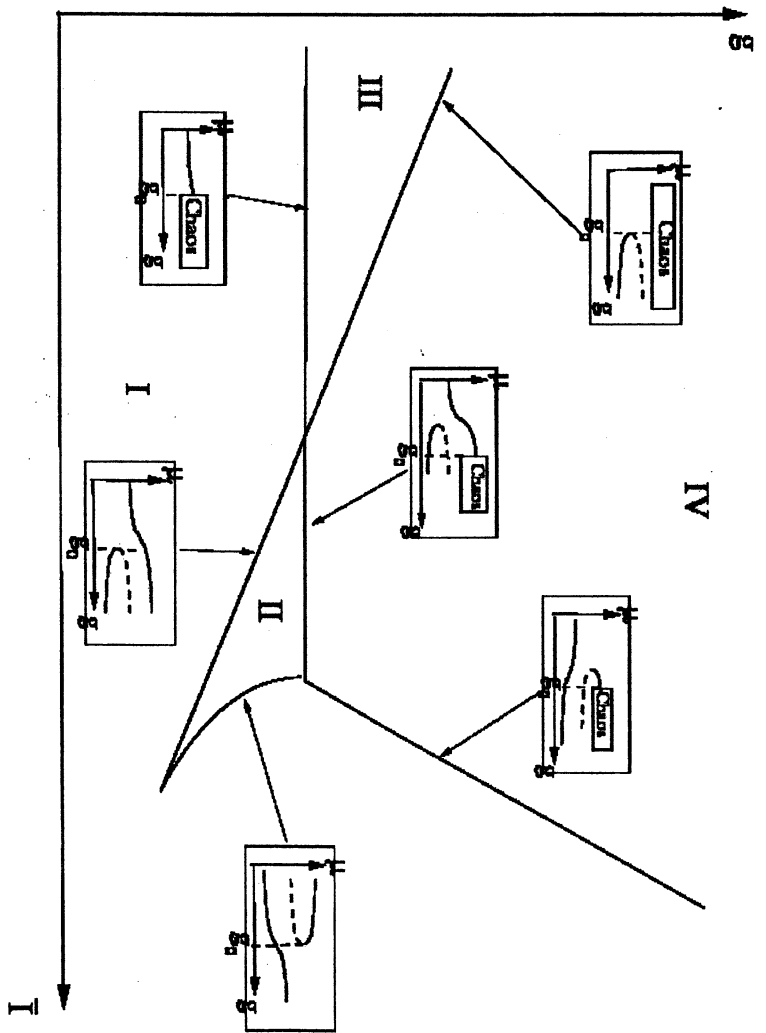
Transition to chaos by quasi-periodicity
(Ruelle Takens)

$$m(t) = \frac{1}{N} \sum_{i=1}^{N} x_i(t)$$

Increasing g

g=1.55, limit cycle.
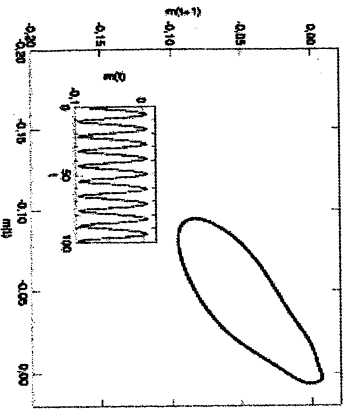
g=1.82, quasi-periodicity

g=3.5, λ_1=0.159
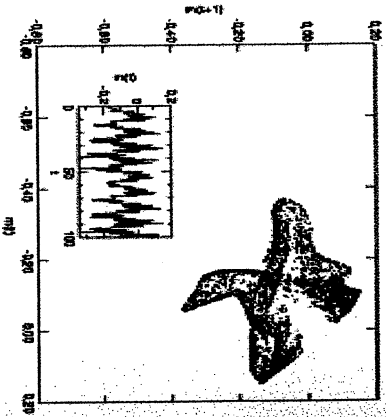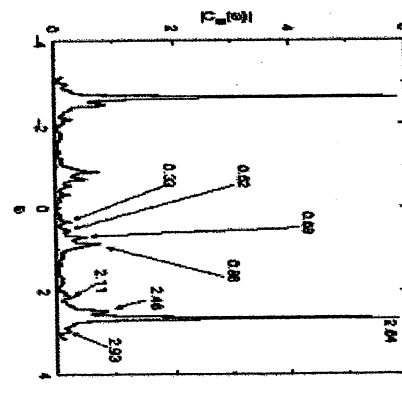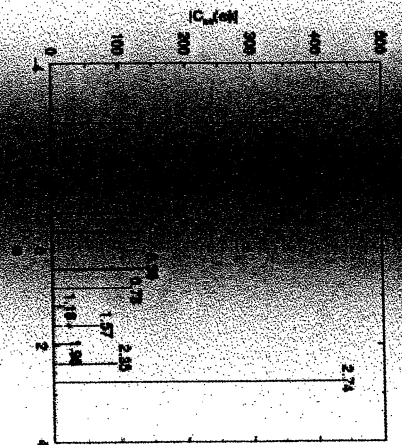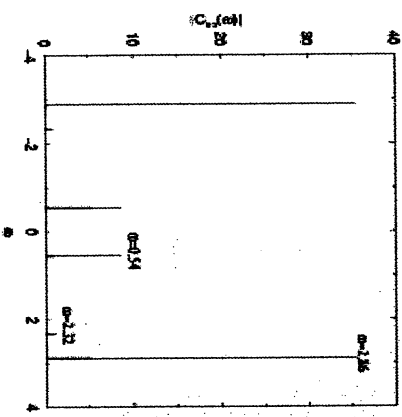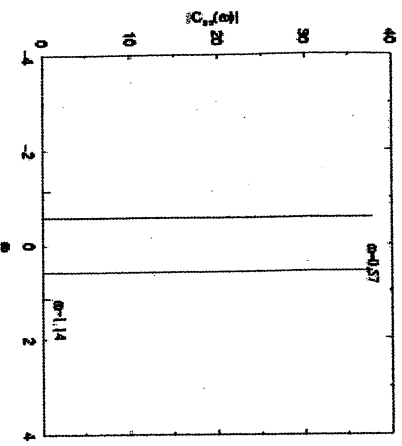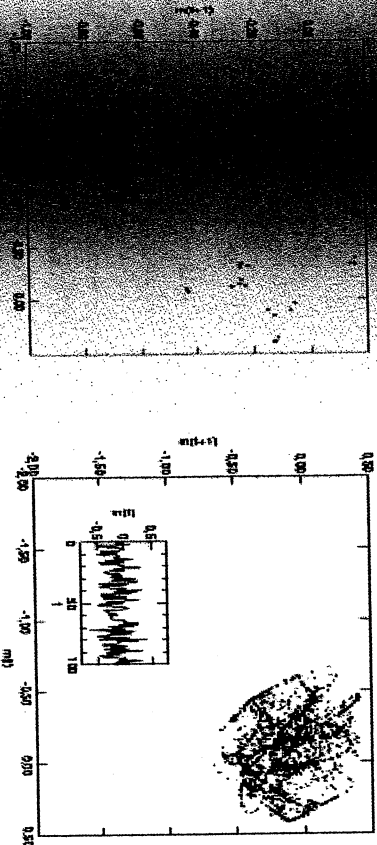
4) Spike train statistics

4.1) Neural "code"?

Neurons interact together sending spikes. Pre-synaptic neurons emit spike trains, which trigger post-synaptic potentials, excitatory or inhibitory, generating or not a response of the post-synaptic neuron as a spike train. This spike train is sent to other neurons and so on.

Therefore the neural network activity is represented by a raster plot, where a vertical bar is plotted, each time a neuron emits a spike. It reflects how neurons behave in spontaneous activity, but also when submitted to "entries".
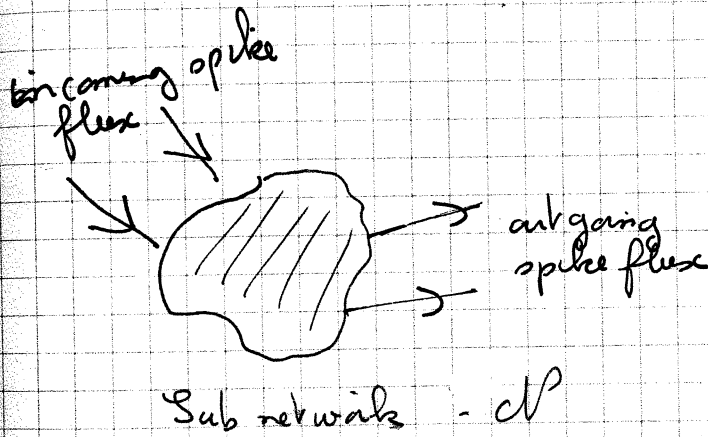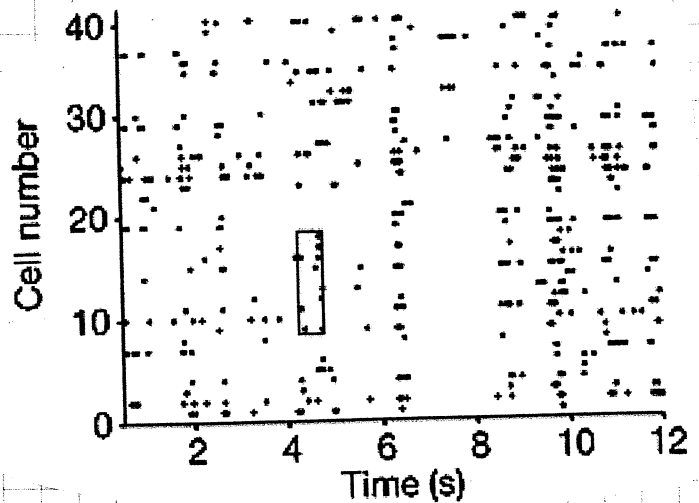
Sub network - $\mathcal{N}$

Typically, delimiting a sub neural network $\mathcal{N}$ in a wider neural system (such as the cortex), this sub neural network receives "entries" and emit "output" in the form of spike trains.

Note that the flux are not necessarily directed as in the left figure. But, thinking of sub networks in a chain of "treatment" units (such as the retina in the visual system), flux are oriented. The entries are not necessarily spike trains. They can be stimuli like light, sound etc...

When $\mathcal{N}$ receives an entry it responds emitting a spike train, which can be visualised in a raster plot, and this response is typically sent to other sub networks, with possible feedbacks.

As we saw the neural network is not a static entity: It has its own, spontaneous, dynamics, which can be quite complex. When this network receives an entry its response is the conjunction of its own internal state and of the entry action. In some sense, the network adapts its response to the entry taking into account its own dynamics.

Consequently, the response to an entry (e.g. a fixed image) is not reproducible exactly. Submitting the same image several times to a person, does not produce the same raster plot from the retina. Consequently the whole chain of responses from perception to action (e.g. the person identifies the image) should be affected by this non reproducibility of the responses. But nevertheless the person is usually able to recognize that this is the same image. This raises therefore several questions.

→ What is the nature /origin of this indeterminacy in spike train response (which is actually observed, see figure on the right)?

→ How can the nervous system conciliate this indeterminacy to the reproducibility, reliability robustness of responses?

→ At which level of precision do we have to go in order, for an artificial neural network, to reproduce (some of) tremendous abilities of the brain?
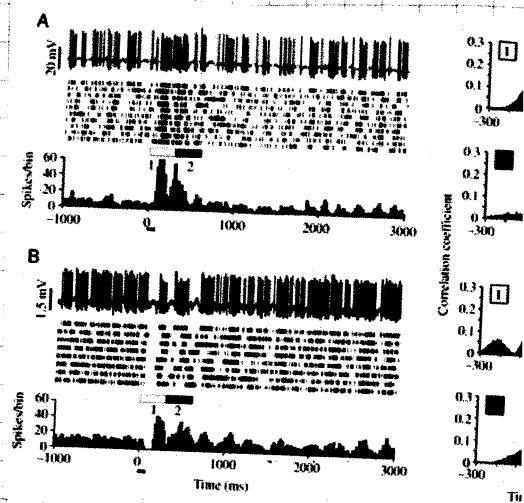
Concerning the first point, indeterminacy and unpredictability is basically at all levels/scales of neural networks. From the ionic channels dynamics, submitted to thermal/quantum fluctuations, to neuron variability in responses according to their state (see f. in section 1.2.3), to collective dynamics etc...
This is often modelled by adding noise to dynamic equation. This noise mimics physical effects such as ...., of neurotransmitters, thermal fluctuations, but also hidden degree of freedom, not taken into account by model. Note however that what people usually call noise is an uncorrelated (whi) noise. Though some effects such as thermal fluctuation can be modelled in this way, it is not evident that this holds e.g. for modelling hidden degrees of freedom.

+ How precise is a spike train? i.e. how dynamics is affected by a slight

The second point is, to my opinion, central in neuroscience community and there is no definite answer yet (and for a long time). At the current state of the art it is widely believed that regularity, robustness in response, can be conciled with spike train variability if neural response is sensitive to statistical characteristics of the spike train instead of the precise time of arrival of spikes emitted by each neuron. In other words, the spike train is not a binary code, encoding the stimulus as it would be in a computer. This statistical robustness compatible with the stochastic/chaotic aspects of dynamics, the same way that heat diffusion is ruled by a deterministic equation for the probability density, whereas molecules dynamics is strongly chaotic.

The third part is closely related to the 2 first ones and it will be addressed in section 6.

Let us now focus on the second part.

4.2) How to characterize spike train statistics?

In section 1.2.7 we have seen several statistical indicators such as the firing rate, the pairwise correlation, the probability of coincidence, the inter spike interval distribution.

More generally a spike train is characterized by a probability of occurrence. Focusing on the symbolic representation of spike train/raster plot introduced in section 1.2.7.1 we denote by $\omega_i(t)$ a raster variable which is one if neuron i fires at time t and 0 otherwise. A spiking pattern is the vector $\omega(t)$, a spike train is an infinite sequence ω, and a spike bloc or "word" is a subsequence

$$[\omega]_{\delta, t}$$ where spiking patterns from time s to time $t - \delta t$ are prescribed.

Note that the notion of raster plot requires the introduction of a time scale resolution δt such that at most one spike can be emitted by each neuron within the time interval $[t, t+\delta t]$ and spike emitted by 2 neurons within this time interval cannot be (experimentally) distinguished. The role of δt is central and is discussed below.

The probability P characterizing spike trains is (mathematically) defined if the probability of any bloc $[\omega]_{s,t}$ is known (there are infinitely many). Experimentally one focuses on small words.

Fix such a word R. The probability of occurrence of this word depend on the stimulus/entity viewed by the network and is given by the conditional probability $P(R|S)$.

Given a set of stimuli $\{S_1 \dots S_k\}$ and the corresponding conditional probabilities $P(R|S_\ell)$, one can determine the probabilities

$$P(S_\ell \mid R) = \frac{P(R|S_\ell) P(S_\ell)}{\sum_{\ell=1}^{k} P(R|S_\ell) P(S_\ell)} \qquad (4.2-1)$$

by Bayes Formula. This provides a way to "read the mind" of the network. Knowing the response, what is the probability that this or this stimulus has been presented? Unfortunately, it is in practice extremely difficult (impossible?) to have a "clean cut" determination of stimuli via conditional probabilities.

There are many reasons for this but one reason is that we have little ideas of what could be the form of P.

On practical grounds one can estimate $P(R|S_e)$ or $P(S|R_e)$ repeating many experiments (and assuming that the system has not evolved meanwhile). Then one will be able to extract useful informations of the responses given the stimulus (or the probabilities of stimuli given the response). A measure of separation is given by

$$\sum_{S_e} P(S) \sum_{R_e} P(R|S) \log_2 \frac{P(R|S_e)}{P(R)} = I(R;S)$$

statistical samples

(4.2-2)

Called the mutual information

$$\left(I(R;S) = \sum_{R_e, S_e} P(R,S) \log_2 \frac{P(R_e, S_e)}{P(R) P(S)} \right)$$

(4.2-3)

It measures how much knowing S reduces the uncertainty on R

Note that $I(R,S) = 0$ iff R, S are independent. Moreover, $I(R,S) \geq 0$ and is symmetric. Thus the larger I the more easy it is to discriminate R from S (or S from R).

Note that

$$I(R,S) = \underbrace{\sum_{S_e} P(S) \sum_{R_e} P(R|S) \log_2 P(R|S)}_{-H(R|S) \text{ conditional entropy}} - \sum_{R_e} P(R) \log P(R) \underbrace{\sum_{S_e} P(S|R)}_{1}$$

Hence:

$$I(R,S) = H(R) - H(R|S)$$ (average reduction in response entropy given stimulus)

$$I(R,S) = H(S) - H(S|R)$$ (average reduction in stimulus entropy given response).

Introducing the Kullback-Leibler divergence between 2 probabilities

$$D(P;Q) = \sum_{r} P(r) \log \frac{P(r)}{Q(r)}$$ (non symmetric measure of difference between P, Q, on the same support)

(4.2-2-4)

we obtain:

$$I(r,s) = \sum_{S} P(s) D(P(\cdot|s); P) = E_s \left[D(P(\cdot|s); P) \right]$$

$$\text{Stimulus} \qquad S \equiv \{S(t)\}_0^T \qquad , \text{ response} \qquad R \equiv \{t_i^n\}_0^T .$$

Measure : $P[R|S]$

- isolated neuron $\rightarrow$ input/output
- neural net. feed forward $\rightarrow$ input/output
- neural net recurrent : $P(R|S)$ depends on S and collective dynamics

Known : $P[S]$

$\Rightarrow$ Compute $P[R,S] = P[R|S] P[S]$

$\Rightarrow$ infer $P[R] = \int P[R,S] \, dS$

$\Rightarrow$ $P[S|R] = \dfrac{P[S] \, P[R|S]}{P[R]}$

Spike triggered average.

Assume that the stimulus S is some stochastic process (typically white noise, which contains all frequencies).

This is a stationary process.

We want to caracterize the average form of the stimulus on a time interval of length τ, before a spike occurs. Fix a neuron j, and let $t_j^{(1)}$ the time of occurence of the first spike (counted from some time origin) then call :

$$\boxed{A_j(\tau) = E\left[S(t_j^{(1)} - \tau)\right]} = E\left[S(t-\tau) \mid t_j^{(1)} = t\right]$$

where the average is taken over the probability distribution of $t_j^{(1)}$, i.e by $P\left[\{t_j^{(n)}\} \mid S\right]$.

In the simplest case where the spike time distribution is stationary $(P(t_j^{(1)}) = P(t_j^{(q)}))$ and where the stimulus is random and stationary we have :

$$A_j(\tau) = E\left[\frac{1}{M_j(T)} \sum_{n=1}^{M_j(T)} S(t_j^{(n)} - \tau)\right],$$

where $M_j(T)$ is the number of spikes occuring between $[0, T]$ where T is some observation time

$s(\tau)$

We have

$$E\left[\frac{1}{M_\delta(T)}\sum_{n=1}^{M_\delta(T)} S(\tau - t_\delta^{(n)})\right] = E_{M_\delta}\left[E\left[\frac{1}{m_\delta}\sum_{n=1}^{m_\delta} S(\tau - t_\delta^{(n)})\,\Big|\,M_\delta(T)=m_\delta\right]\right]$$

$$= E_{M_\delta}\left[\frac{1}{m_\delta}\sum_{n=1}^{m_\delta} E\left[S(\tau - t_\delta^{(n)})\,|\,M_\delta(T)=m_\delta\right]\right]$$

and

$$S(\tau - t_\delta^{(n)}) = \int_0^T \delta(t - t_\delta^{(n)})\, S(\tau - t)\, dt$$

$$\Rightarrow E\left[S(\tau - t_\delta^{(n)})\,|\,M_\delta(T)=m_\delta\right] = \int_0^T E\left[\delta(t - t_\delta^{(n)})\,\Big|\,M_\delta(T)\Big|_{=m_\delta}\right] S(\tau - t)\, dt$$

$$= \int_0^T \nu_\delta(t\,|\,M_\delta(T)=m_\delta)\, S(\tau - t)\, dt$$

$$\Rightarrow A_\delta(\tau) = E_{M_\delta}\left[\frac{1}{m_\delta}\sum_{n=1}^{m_\delta} \underbrace{\int_0^T \nu_\delta(t\,|\,M_\delta(T)=m_\delta)\, S(\tau - t)\, dt}_{\text{indep de } N}\right]$$

$$= E_{M_\delta}\left[\int_0^T \nu_\delta(t\,|\,M_\delta(T)=m_\delta)\, S(\tau - t)\, dt\right]$$

$$= \int_0^T E_{M_\delta}\left[\nu_\delta(t)\,|\,M_\delta(T)=m_\delta\right] S(\tau - t)\, dt$$

$$= \int_0^T \nu_\delta(t)\, S(\tau - t)\, dt.$$

Finalement

$$A_g(\tau) = (\nu_g * S)(\bar{\tau})$$

linear response

Therefore $A_g(\tau)$, the average form of the stimulus on a time interval $\bar{\tau}$, is the convolution of the frequency rate and of the signal.

The correlation function of v_j and s is:

$$C_j(\tau) = \frac{1}{T} \int_0^T v_j(t)\, s(t+\tau)\, dt$$

thus $\quad A_j(\tau) = T\, C_j(-\tau)$

Typically, the spike trigger average $C_j(\tau)$ is obtained by dividing by the average number of spikes within an interval of length T.

$$\Rightarrow \quad C_j(\tau) = \frac{T}{E(M_j(T))}\, C_j(-\tau) = \frac{A_j(\tau)}{E(M_j(T))}$$

$$\Rightarrow \quad \boxed{\; C_j(\tau) = \frac{C_j(-\tau)}{\langle v_j \rangle} \;}$$

Consider now the quantity

$$\langle R_\gamma(t_n) S(t-\tau)\rangle = \langle \sum_{n=1}^{M_\gamma(t)} S(t-t_\gamma^n) S(t-\tau)\rangle$$

$$= \langle \sum_{n=1}^{M_\gamma(t)} S(t-t_\gamma^n) S(t_\gamma^n-\tau)\rangle$$

where $\langle\ \rangle$ denotes the average w.r.t a Brownian stimulus
$\langle\ \rangle$ is stationary (law of the Brownian)

$$\langle R_\gamma(t) S(t-\tau)\rangle = \frac{1}{T}\int_0^T dt\ \langle \sum_{n=1}^{M_\gamma(t)} S(t-t_\gamma^n) S(t_\gamma^n-\tau)\rangle$$

$$= \langle \sum_{n=1}^{M_\gamma(t)} \frac{1}{T}\int_0^T S(t-t_\gamma^n) S(t_\gamma^n-\tau)\rangle$$

$$= \langle \frac{M_\gamma'(T)}{T} S(t_\gamma^* -\tau)\rangle$$

$$\sim \langle r_\gamma\rangle\langle S(t_\gamma-\tau)\rangle$$

Generalisation: Wiener expansion - Volterra series

We assume that the response is a definite functional of the stimulus:

$$R(t) = H[S](t)$$

The Volterra series reads:

$$R(t) = H_0 + \int_0^{+\infty} d\tau_1 \, H_1(\tau_1) \, S(t-\tau_1)$$
$$+ \int_0^{+\infty}\int_0^{+\infty} d\tau_1 \, d\tau_2 \, H_2(\tau_1,\tau_2) \, S(t-\tau_1) S(t-\tau_2)$$
$$+ \, - \, - \, -$$

The H_n are called Volterra kernels. The integrals holds on $[0, +\infty[$ due to causality $(t-\tau \leq t)$. Note that H functions are symmetric with respect to permutation of arguments.

$$H_2(\tau_1, \tau_2) = H_2(\tau_2, \tau_1)$$
$$H_3(\tau_1, \tau_2, \tau_3) = H_3(\tau_1, \tau_3, \tau_2) = H_3(\tau_2, \tau_3, \tau_1) = \, - \, - \, -$$
$$- \, - \, - \, - \, - \, -$$

Assume that S is now a Gaussian white noise. Denote by $\langle \ \rangle$ the average with respect to the white noise distribution.

$$\langle S(t) \rangle = 0 \; ; \; \langle S(t_1) S(t_2) \rangle = \delta(t_1 - t_2) \; ;$$
$$\langle S(t_1) S(t_2) S(t_3) \rangle = 0$$
$$\langle S(t_1) S(t_2) S(t_3) S(t_4) \rangle = \delta(t_1-t_2)\delta(t_3-t_4)$$
$$+ \delta(t_1-t_3)\delta(t_2-t_4)$$
$$+ \delta(t_1-t_4)\delta(t_2-t_3)$$

$$\langle S(t_1)\, S(t_2)\, S(t_3)\, S(t_4)\, S(t_5)\rangle = 0 \quad \text{etc} \sim.$$

Averaging $R(t)$ with respect to the noise we obtain:

$$\langle R(t)\rangle = H_0 + \int_0^{+\infty} d\tau_1\, H(\tau_1)\, \langle S(t-\tau_1)\rangle\, d\tau_1$$

$$+ \iint_0^{+\infty} d\tau_1\, d\tau_2\, H(\tau_1,\tau_2)\, \langle S(t-\tau_1) S(t-\tau_2)\rangle\, d\tau_2$$

$$+ \int_{\mathbb{R}_+^3} d\tau_1\, d\tau_2\, d\tau_3\, H(\tau_1,\tau_2,\tau_3)\, \langle S(t-\tau_1) S(t-\tau_2) S(t-\tau_3)\rangle$$

$$+ \int_{\mathbb{R}_+^4} d\tau_1\, d\tau_2\, d\tau_3\, d\tau_4\, H(\tau_1,\tau_2,\tau_3,\tau_4)\, \langle S(t-\tau_1) S(t-\tau_2) S(t-\tau_3) S(t-\tau_4)\rangle$$

$$+ \; \text{---}$$

$$= H_0 + \int_{\mathbb{R}_+^2} d\tau_1\, d\tau_2\, \underset{2}{H}(\tau_1,\tau_2)\, \delta(\tau_1-\tau_2) + \int_{\mathbb{R}_+^4} d\tau_1\, d\tau_2\, d\tau_3\, d\tau_4 \; \underset{4}{H}(\tau_1,\tau_2,\tau_3,\tau_4) \begin{bmatrix} \delta(\tau_1-\tau_2)\delta(\tau_3-\tau_4)+ \\ \delta(\tau_1-\tau_3)\delta(\tau_2-\tau_4)+ \\ \delta(\tau_2-\tau_3)\delta(\tau_1-\tau_4) \end{bmatrix}$$

$$+ \; \text{---}$$

$$= H_0 + \int_{\mathbb{R}_+} d\tau_1\, \underset{2}{H}(\tau_1,\tau_1) + \int_{\mathbb{R}_+^2} \left[H_4(\tau_1,\tau_1,\tau_2,\tau_2) + \underset{4}{H}(\tau_1,\tau_2,\tau_1,\tau_2)\, d\tau_1\, d\tau_2 \right] d\tau_1\, d\tau_2$$

$$+ \int_{\mathbb{R}_+^2} H_4(\tau_1,\tau_2,\tau_1,\tau_2)\, d\tau_1\, d\tau_2$$

$$+ \; \text{---} \quad = G_0$$

Likewise one can show that.

$$\langle R(t)\, S(t-\tau_1)\, S(t-\tau_2)\rangle = g_2(\tau_1, \tau_2)$$

etc ---

Finally, one can show that the following Wiener expansion holds, for any signal $S(t)$

$$R(t) = G_0 + G_1[S(t)] + G_2[S(t)] + \cdots$$

with

$$G_1[S(t)] = g_1 * S(t)$$

$$G_2[S(t)] = \int_{\mathbb{R}_+^2} g_2(\tau_1, \tau_2)\, S(t-\tau_1)\, S(t-\tau_2)\, d\tau_1 d\tau_2$$
$$\longrightarrow \int g_2(\tau, \tau)\, d\tau$$

$$G_3[S(t)] = \int_{\mathbb{R}_+^3} g_3(\tau_1, \tau_2, \tau_3)\, d\tau_1\, d\tau_2\, d\tau_3$$
$$-3 \int g_3(\tau_1, \tau_1, \tau_2)\, S(t-\tau_2)\, d\tau_1 d\tau_2$$

etc ---

This provides the average value of $\langle R(t) \rangle$ under the brownian stimulus. Note that it is time independent, as expected from stationarity.

Consider now the average:

$$\langle R(t) S(t-\tau) \rangle = \cancel{H_0} \langle S(t-\tau) \rangle + \int_0^{+\infty} H_1(\tau_1) \langle S(t-\tau) S(t-\tau_1) \rangle d\tau_1$$

$$+ \int_{\mathbb{R}_+^2} H_2(\tau_1, \tau_2) \langle S(t-\tau) S(t-\tau_1) S(t-\tau_2) \rangle d\tau_1 d\tau_2$$

$$+ \int_{\mathbb{R}_+^3} H_3(\tau_1, \tau_2, \tau_3) \langle S(t-\tau) S(t-\tau_1) S(t-\tau_2) S(t-\tau_3) \rangle d\tau_1 d\tau_2 d\tau_3$$

$$+ \cdots$$

$$= 0 + H_1(\tau) + 0 + \int \begin{pmatrix} H_3(\tau, \tau_2) \\ + H_3(\tau_2, \tau) \\ + H_3(\tau_2, \tau) \end{pmatrix} d\tau_2 + 0 + \cdots$$

$$= H_1(\tau) + 3 \int H_3(\tau, \tau_2) d\tau + \cdots$$

$$= g_1(\tau)$$

with $\boxed{g_1(\tau) = \langle R(t) S(t-\tau) \rangle}$

3) Statistical models.

We would now like to address the question of spike train statistics in the realm of dynamical systems theory and statistical physics.

Consider therefore a spiking model of neuron (see section I.1.2) for examples), possibly with noise. This model dynamics will naturally produce words and word probability can be computed e.g. by :

$$P(R) = \lim_{T \to +\infty} \frac{1}{T} \sum_{t=1}^{T} \mathcal{X}_t(R), \qquad (4.3\text{-}1)$$

where $\mathcal{X}_t(R) = 1$ iff the word R occurs at time T. Note that this definition assumes that dynamics is stationary. Otherwise, e.g. if the entropy is time dependent then P depends on time and

$$P_t(R) = \lim_{T \to +\infty} \frac{1}{T+t} \sum_{\Delta=-T}^{t} \mathcal{X}_\Delta(R), \qquad (4.3\text{-}2)$$

(Here time is assumed to be discrete as required for a proper definition of rasters).

Let us focus here on static entries (as we implicitly did in the previous section).

The estimation of $P(R)$ from data is extremely difficult for large words which have typically a small probability of occurrence and requires long time sequences to provide reliable numerical estimates. Moreover P contains all information on spike statistics, with, maybe, redundancies. Typically, people use (4.3-1) to compute statistical indicators such as :

$$V_i = \lim_{T \to +\infty} \frac{1}{T} \sum_{t=1}^{T} \mathcal{X}_t \left(\begin{matrix} 0 \\ \vdots \\ 1 \\ \vdots \\ 0 \end{matrix} \right) \!\! \to i \; , \qquad \text{(Frequency rate of neuron } i \text{)}$$

$$V_{ij} = \lim_{T \to +\infty} \frac{1}{T} \sum_{t=1}^{T} \mathcal{X}_t \left(\begin{matrix} 0 \\ \vdots \\ 1 \!\!\leftarrow i \\ \vdots \\ 1 \!\!\leftarrow j \\ 0 \end{matrix} \right) \; , \qquad \text{(Probability that } i, j \text{ fire simultaneously),}$$

$$V_{ij}(\tau) = \lim_{T \to +\infty} \frac{1}{T} \sum_{t=1}^{T} \mathcal{X}_t \left[\begin{matrix} 0 & & 0 \\ \vdots & & \vdots \\ \textcircled{1} & & 0 \\ \vdots \, i & & 0 \\ 0 & j & \textcircled{1} \\ & 0 \end{matrix} \right] \; , \qquad \text{Probability that } i \text{ fires then } \tau \text{ timesteps later } j \text{ fires}$$

4.3.1) The maximal entropy principle

In principle knowing all moments of the distribution P allow to compute its characteristic function (whenever it is analytic) and hence to know P. Unfortunately, arbitrarily, it is not possible to compute all moments from experiment.

Assume therefore that we have computed some of these e.g rates, spike synchronization probability, more generally assume that we are given the average value of a set of K observables φ_l, $l = 1..K$, $\varphi_l \equiv \varphi_l(\omega)$, where ω is a raster. As an example

$$\text{if } \varphi_l(\omega) = \omega_i(t) \quad \text{then} \quad \langle \varphi_l \rangle = V_i(t), \text{ the frequency rate, etc}$$

The question is: "Is there a probability distribution which matches the experimental value of observables,

$$\boxed{P(\varphi_l) = \langle \varphi_l \rangle, \quad \forall l} \qquad (4.3.1\text{-}1)$$

without any further assumption.

The answer is given by statistical physics see Jaynes

One has to search a probability P which maximizes statistical entropy under the constraints. Equivalently, one has to maximize

$$\boxed{H[P] + \sum_l \lambda_l \, P(\varphi_l),} \qquad (4.3.1\text{-}2)$$

where λ_l are called Lagrange multipliers, and $H(P)$ is given by

$$\boxed{H(P) = - \sum_\omega P(\omega) \log P(\omega)} \qquad (4.3.1\text{-}3)$$

Rq Here, for simplicity, we have considered a finite set of words ω. Extension to infinite words will be discussed below.

Then, there is a solution, called a Gibbs distribution given by:

$$\boxed{\text{Gibbs distribution}}$$

$$H(P) = -\sum_\omega P_\omega \log P_\omega \quad ; \quad P_\omega = P(\omega)$$

$$P(\varphi_\ell) = \sum_\omega P_\omega \, \varphi_\ell(\omega).$$

Maximize $G(P) = H(P) + \sum_{\ell=1}^{K} \lambda_\ell P(\varphi_\ell) \quad \Longleftrightarrow$

i) $\dfrac{\partial G}{\partial P_\omega} = \dfrac{\partial H}{\partial P_\omega} + \sum_{\ell=1}^{K} \lambda_\ell \dfrac{\partial P(\varphi_\ell)}{\partial \omega} = -\log P_\omega - 1 + \sum_{\ell=1}^{K} \lambda_\ell \varphi_\ell(\omega) = 0 \quad \forall \omega$

$\Longleftrightarrow \quad P_\omega = \exp\left(\sum_{\ell=1}^{K} \lambda_\ell \varphi_\ell(\omega)\right) \exp(-1)$

$+ \; P$ must be normalised $\quad \Longrightarrow \quad \sum_\omega P_\omega = 1 \quad \Longrightarrow$

Set $Z = \sum_\omega \exp\left(\sum_{\ell=1}^{K} \lambda_\varphi \varphi_\ell(\omega)\right) \; \cancel{e^{-1}}$ disappears the normalisation.

$\Longrightarrow \quad \boxed{P_\omega = \dfrac{1}{Z} \exp\left(\sum_{\ell=1}^{K} \lambda_\ell \varphi_\ell(\omega)\right)}$

ii) $\dfrac{\partial^2 G}{\partial P_\omega \, \partial P_{\omega'}} = -\dfrac{1}{P_\omega} \delta_{\omega\omega'} < 0.$

Prop Set $F = \log Z$.

$G(P) = -\sum_\omega P_\omega \left(-\log Z + \sum_{\ell=1}^{K} \lambda_\varphi \varphi_\ell(\omega)\right) + \sum_{\ell=1}^{K} \lambda_\varphi P(\varphi_\ell)$

$= \log Z - \sum_{\ell=1}^{K} \lambda_\varphi P_\ell(\varphi_\ell) + \sum_{\ell=1}^{K} \lambda_\varphi \, P(\varphi_\ell)$

Theo $\boxed{F = \log Z = G(P) = H(P) + \sum_{\ell=1}^{K} \lambda_\ell P(\varphi_\ell)}$

$$\frac{\partial F}{\partial \lambda_\ell} = \frac{1}{Z}\frac{\partial Z}{\partial \lambda_\ell} = \sum_w \varphi_\ell(w) \exp \frac{\sum_{\ell=1}^{K} \lambda_\ell \varphi_\ell(w)}{Z} = P(\varphi_\ell);$$

$$\frac{\partial^2 F}{\partial \lambda_\ell \partial \lambda_{\ell'}} = \frac{\partial}{\partial \lambda_\ell} \cdot \left(\frac{1}{Z}\frac{\partial Z}{\partial \lambda_\ell} \right) = -\frac{1}{Z^2}\left(\frac{\partial Z}{\partial \lambda_\ell}\frac{\partial Z}{\partial \lambda_{\ell'}}\right) + \frac{1}{Z}\frac{\partial}{\partial \lambda_{\ell'}} \cdot \left(\sum \varphi_\ell \, e^{\sum_\ell \lambda_\ell \varphi_\ell} \right)$$

$$= - P(\varphi_\ell)P(\varphi_{\ell'}) + \sum_w \varphi_\ell(w)\varphi_{\ell'}(w) \; \frac{e^{\sum \lambda_\varphi \varphi_\ell(w)}}{Z}$$

$$\Rightarrow \boxed{\frac{\partial^2 F}{\partial \lambda_\ell \partial \lambda_{\ell'}} = P(\varphi_\ell \varphi_{\ell'}) - P(\varphi_\ell)P(\varphi_{\ell'})}$$ Correlation function.

NB

Set $\mathcal{N} = \sum_w 1$ (total number of words), then:

$$\frac{Z}{\mathcal{N}} = \sum_w \frac{1}{\mathcal{N}} \exp \sum_{\ell=1}^{K} \lambda_\varphi \varphi_\ell(w) = E_{\frac{1}{\mathcal{N}}} \left[\exp \sum \lambda_\varphi \varphi_\ell(w) \right]$$

where the expectation is taken with respect to the uniform measure. Thus, $\frac{Z}{\mathcal{N}}$ is a generating function and $\log Z$ a log generating function

Remarque

The limit $\mathcal{N} \to +\infty$ is _not_ straightforward
  (this is an euphemism).

$$\boxed{P_E(\omega) = \prod_{i=1}^{N} P_t(\omega_i)} \quad (4.3.2-1)$$

with $\quad P_t(\omega_i) = \exp \lambda_{i,t}\,\omega_i \, / \,(1 + \exp \lambda_{i,t}) = \dfrac{e^{\lambda_{i,t}}}{S_{i,t}}$

Note indeed that $\quad Z_t = \displaystyle\sum_{\omega_i(t)=0,1} \exp \sum_{i=1}^{N} \lambda_{i,t}\omega_i(t) = \sum_{\omega_i(t)=0,1} \prod_{i=1}^{N} e^{\lambda_{i,t}}$

$$= \prod_{i=1}^{N} \sum_{\omega_i(t)=0,1} e^{\lambda_{i,t}\omega_i(t)} = \prod_{i=1}^{N} \left(1 + e^{\lambda_{i,t}} \right)$$

Eq. (4.3.2-1) signifies that, in the Poisson model, spikes coming from different neurons are considered as being <u>independent</u>.

This model is called <u>inhomogeneous Poisson</u> when rates depend and <u>homogeneous Poisson</u> otherwise.

Note that $\quad \nu_i(t) = \dfrac{e^{\lambda_{i,t}}}{S_{i,t}} = P_t(t) \implies \lambda_{i,t} = \log \dfrac{e^{\nu_i(t)}}{1 - \nu_i(t)}$

thus

$$\boxed{P_E(\omega) = \prod_{i\,|\,\omega_i(t)=1} \nu_i(t) \cdot \prod_{i\,|\,\omega_i(t)=0} \left(1 - \nu_i(t)\right)} \quad (4.3.2-2)$$

Likewise, the probability of <u>larger words</u> is given by:

$(4.3.2$

$$\boxed{P(\omega = \omega(t_1)\dots\omega(t_n)) = \prod_{\ell=1}^{n} \left(\prod_{i\,|\,\omega_i(t_\ell)=1} \nu_i(t_\ell) \prod_{i\,|\,\omega_i(t_\ell)=0} (1 - \nu} \right.}$$

Consider the event <u>"Neuron i has fired at times $t_i^{(1)} \dots t_i^{(n)}$ wi</u> a time window of length T. The corresponding probability is:

$$P(t_i^{(1)} \dots t_i^{(n)}) = \prod_{\ell=1}^{n} \nu_i(t_i^{(\ell)}) \prod_{t \neq t_i^{(\ell)}} \left[1 - \nu_i(t) \right]$$

$$= \exp \sum_{t \neq t_i^{(\ell)}} \log(1 - \nu_i(t)) \prod_{\ell=1}^{n} \nu_i(t_i^{(\ell)})$$

Recall that we have sampled at a rate δt and that ν_i d for $\nu_i \,\delta t$. Thus, to get the "continuous time" limit of this one has to take $\delta t \to 0$. In this case P becom a probability density.

$$P(w) = \frac{1}{Z} \exp + \sum_{\ell=1}^{K} \lambda_\ell \, \Psi_\ell(w) \qquad (4.3.1\_4)$$

with $\quad Z = \sum_{w} \exp \sum_{\ell=1}^{K} \lambda_\ell \, \Psi_\ell(w)$, the partition function.

Exercise : Redo the proof, show that $F = -\log Z$, is the generating function of cumulants (see sheet for corrections).

Time dependent model :-

This form affords an extension when P depends on the parameters λ_ℓ:

$$P_t(w) = \frac{1}{Z_t} \exp \sum_{\ell=1}^{K} \lambda_{\ell_t} \, \Psi_\ell(w). \qquad (4.3.1\_5)$$

Here the observable average value may depend on time. Having such a Gibbs distribution amounts to assuming that we have measured the time dependent average of each Ψ_ℓ, $\overline{\Psi_{\ell,t}}$ and that $P_t(w)$ is such that :

$$P_t(\Psi_\ell) = + \frac{\partial \log Z_t}{\partial \lambda_\ell(t)} = \overline{\Psi_{\ell,t}} \qquad (4.3.1\_6)$$

Here we have assumed that the set of words is not evolving with time.

4.3.2) The Poisson model

There are different ways of introducing this model. Here we follow the tracks of maximal entropy principle.

Assume that we have only measured firing rates (with the possibility that they depend on time). Then $P_t(w)$ reads :

$$P_t(w) = \frac{1}{Z_t} \exp \sum_{i=1}^{N} \lambda_{i,t} \cdot \omega_i(t),$$

and $\quad \nu_i(t) = \dfrac{\partial \log Z_t}{\partial \lambda_{i,t}}$.

Hence here the basic words are only spiking patterns. The prob of larger words is given by eq. $(4.3.2\_3)$

In this case, the probability $P_t(w)$ factorizes :

$$t_i^{(1)} \cdots t_i^{(n)}) \, \delta t^n = \exp \sum_{t \neq t_i^{(\ell)}} \log(1 - \nu_i'(t)\delta t) \prod_{\ell=1}^{n} \nu_i'(t_i^{(\ell)}) \, \delta t^n$$

$$P(t_i^{(1)} \cdots t_i^{(n)}) \sim \exp -\sum_{t = t_i^{(\ell)}} \nu_i'(t)\delta t \prod_{\ell=1}^{n} \nu_i'(t_i^{(\ell)})$$

In the limit, the sum becomes the integral $\int_0^T \nu_i'(t)\,dt$ and one ends up with a classical equation in the literature:

$$\boxed{P(t_i^{(1)} \cdots t_i^{(n)}) = \exp -\int_0^T \nu_i'(t)\,dt \prod_{\ell=1}^{n} \nu_i'(t_i^{(\ell)})} \quad (4.3.2-4)$$

In the same way the probability of having exactly n spikes for neuron i within a time window of length T is:

$$P_T[n] = \sum_{\substack{\text{All subsequences of times} \\ t_i^{(1)} \cdots t_i^{(n)} \text{ in a window} \\ \text{of length } n}} P(t_i^{(1)}, \cdots, t_i^{(n)}) \longrightarrow \underline{\text{Absolutely requires time discretization.}}$$

In the case of an homogeneous Poisson process we have

$$P_T[n] = C_{T/\delta T}^{n} \left(\nu_i \cdot \delta t\right)^n (1 - \nu_i \delta t)^{\underbrace{\frac{T}{\delta T} - n}_{\text{number of bins}}} \quad \text{(binomial law)}$$

If δt is small (if the code is very sparse) $\underline{\nu_i \delta t \text{ is small}}$.

If T is large one obtains the limit of a Binomial law when $\nu_i \delta t \to 0$ and $T \to +\infty$

$$\lim_{\delta t \to 0} (1 - \nu_i \delta t)^{\frac{T}{\delta t} - n} = \exp\left(\frac{T}{\delta t} - n\right) \log(1 - \nu_i \delta t) \sim \exp -\nu_i T$$

$$C_{T/\delta t}^{n} = \frac{1}{n!} \frac{(T/\delta t)!}{(T/\delta t - n)!} = \frac{1}{n!} \cdot \frac{(T/\delta t)^{(T/\delta t)} e^{-T/\delta t}}{(T/\delta t - n)^{(T/\delta t - n)} e^{-(T/\delta t - n)}}$$

$$= \frac{1}{n!} (T/\delta t)^n \left(\frac{T/\delta t}{T/\delta t - n}\right)^{T/\delta t - n} = \frac{1}{n!} \left(\frac{T}{\delta t}\right)^n \Longrightarrow$$

$$\boxed{P_T(n) \sim \frac{1}{n!} (\nu_i T)^n \exp -\nu_i T} \qquad \underline{\text{Poisson distribution}}$$

$$(4.3.3-5)$$

4.3.3) The Ising model

Assume now that we are given both experimental values of rates and spike coincidence probabilities : $\nu_i(t)$ and $\nu_{ij}(t)$.
The corresponding Gibbs distribution reads :

$$(4.3.3-1)$$

$$P_t(\omega) = \frac{1}{Z_t} \exp \sum_{i=1}^{N} h_i(t)\,\omega_i(t) + \sum_{i<j} J_{ij}(t)\,\omega_i(t)\,\omega_j(t)$$

Here again elementary words are spiking patterns.

Clearly, P_t has the same form as an Ising model, as emphasized by :
Schneidman,

The multipliers $h_i(t)$, $J_{ij}(t)$ are provided by the relation

$$\frac{\partial \log Z_t}{\partial h_i(t)} = \nu_i(t) \quad ; \quad \frac{\partial \log Z_t}{\partial J_{ij}(t)} = \nu_{ij}(t)$$

Current investigations are attempting to compute these multipliers by Monte Carlo methods.

The probability of larger words is still given by a product

$$P_t(\omega(t_1)\dots\omega(t_n)) = \prod_{\ell=1}^{n} P_{t_\ell}(\omega(t_\ell)).$$

Here contrarily to the Poisson case, neurons are dependent (but spiking pattern at different times are still independent).

The analogy with Ising model is not only formal. Since the probability distribution has the same form, same properties (including phase transitions as $N \to +\infty$) should hold. But one has to interpret the properties in the realm of neurons dynamics. A few remarks:

* h_i, J_{ij} are fully determined by the underlying neuron dynamics and by possible entries. It would be nice to characterize explicitely this dependence.

* h_i, J_{ij} are not homogeneous. Thus the model is closer to a spin glass (though J_{ij}'s are not independent)

than it's the standard Ising model.

* Phase transitions correspond to abrupt change in the underlying dynamics due e.g. to stimuli. Such bifurcations have already been encountered in previous sections. We shall meet some others when dealing with synaptic plasticity.

Instead of analysing a huge dynamical system with many degrees of freedom and even more parameters, the phase transition point of view amounts to replacing the bifurcation analysis by the change in statistical properties, manifested by _____ parameters. In the "Ising" model Ansatz the parameters are h_i (multiplier related to neurons activity)

and J_{ij} (multiplier related to neurons synchrony).

In particular a sharp change in synchrony at a certain time period corresponds to a sharp increase of $J_{ij}(t)$ and requires conditions on the J_{ij}'s.

Dynamique
Reverse correlation
La Double

4.3.4) Generalisations - How to validate a statistical model

Generalisations are provided by eq. (4.3.1.4). Theoretical everything is possible, but empirically, the computation of the average values of $\varphi_\ell(w)$ of this function involve a lot of events is difficult.

Finally, the main question: "How to degenerate between these models? Is there one which is best than the others?

The choice of observables φ_ℓ fixes the maximal length of words that we need, as well as the form of the Gibbs distribution. Given such a choice, we have a set of basic words whose empirical probability can be computed

$$\Pi(w) = \frac{1}{T} \sum_{t=1}^{T} \chi_t(w) .$$

As we saw, a way to quantify the resemblance between 2 probabilities is to minimize the KL divergence (4.2.2-4). Here

$$D(\Pi ; P) = -\sum_w \Pi(w) \log \Pi(w) + \sum_w \Pi(w) \log P(w)$$

$$= -H(\Pi) + \log Z + \sum_w \Pi(w) \sum_\ell \lambda_\ell \varphi_\ell(w)$$

$$= -H(\Pi) + F + \sum_\ell \lambda_\ell \Pi(\varphi_\ell)$$

$H(\Pi)$, the entropy of the empirical measure is a constant. Thus minimizing D amounts to maximizes $F + \sum_\ell \lambda_\ell \Pi(\varphi_\ell)$. Namely:

$$\boxed{\frac{\partial F}{\partial \lambda_\ell} = \Pi(\varphi_\ell)} \qquad (4.3.4\_1)$$

and

$$\boxed{\frac{\partial^2 F}{\partial \lambda_\ell \partial \lambda_{\ell'}} \geqslant 0} \qquad (4.3.4\_2) .$$

Eq (4.3.4_1) is precisely (4.3.1_6). Thus one imposes the coincidence between the theoretical value of $\langle \varphi_\ell \rangle$ and the empirical value. Likewise (4.3.4_2) is a correlation matrix, which up

...tivity.

Now, if we want to compare several models (corresponding to different choices of $\varphi_{\ell,0}$) we have to:

i) Find the set of λ_ℓ's $\overset{\lambda_\ell^*}{}$ which match eq. (13.4.1)

ii) Compute the quantity $-F + \sum_{\ell} \lambda_\ell^* \, \Pi(\varphi_\ell)$

iii) Among all models, find the one (if any) which <u>minimizes</u> this quantity

This requires the <u>knowledge of F</u>. For 2 models M_1, M_2 corresponding to observables $\varphi_\ell^{(1)}, \varphi_\ell^{(2)}$ we say that <u>1 is better</u> than 2 iff:

$$\sum_{\ell_1=1}^{K_1} \lambda_{\ell_1}^* \, \Pi(\varphi_{\ell_1}^{(1)}) - F_1 \leq \sum_{\ell_2=1}^{K_2} \lambda_{\ell_2}^* \, \Pi(\varphi_{\ell_2}^{(2)}) - F_2$$

The main difficulty here is to <u>compute F</u>.

It can be computed as the <u>largest eigenvalue</u> of a transition matrix, call the Ruelle-Perron-Frobenius operator in <u>dynamical</u> <u>systems</u> theory. Here F can be computed "exactly" for many models with however <u>severe</u> restrictions on the <u>world</u> size, in order to implement <u>numerically</u> the computation of F.
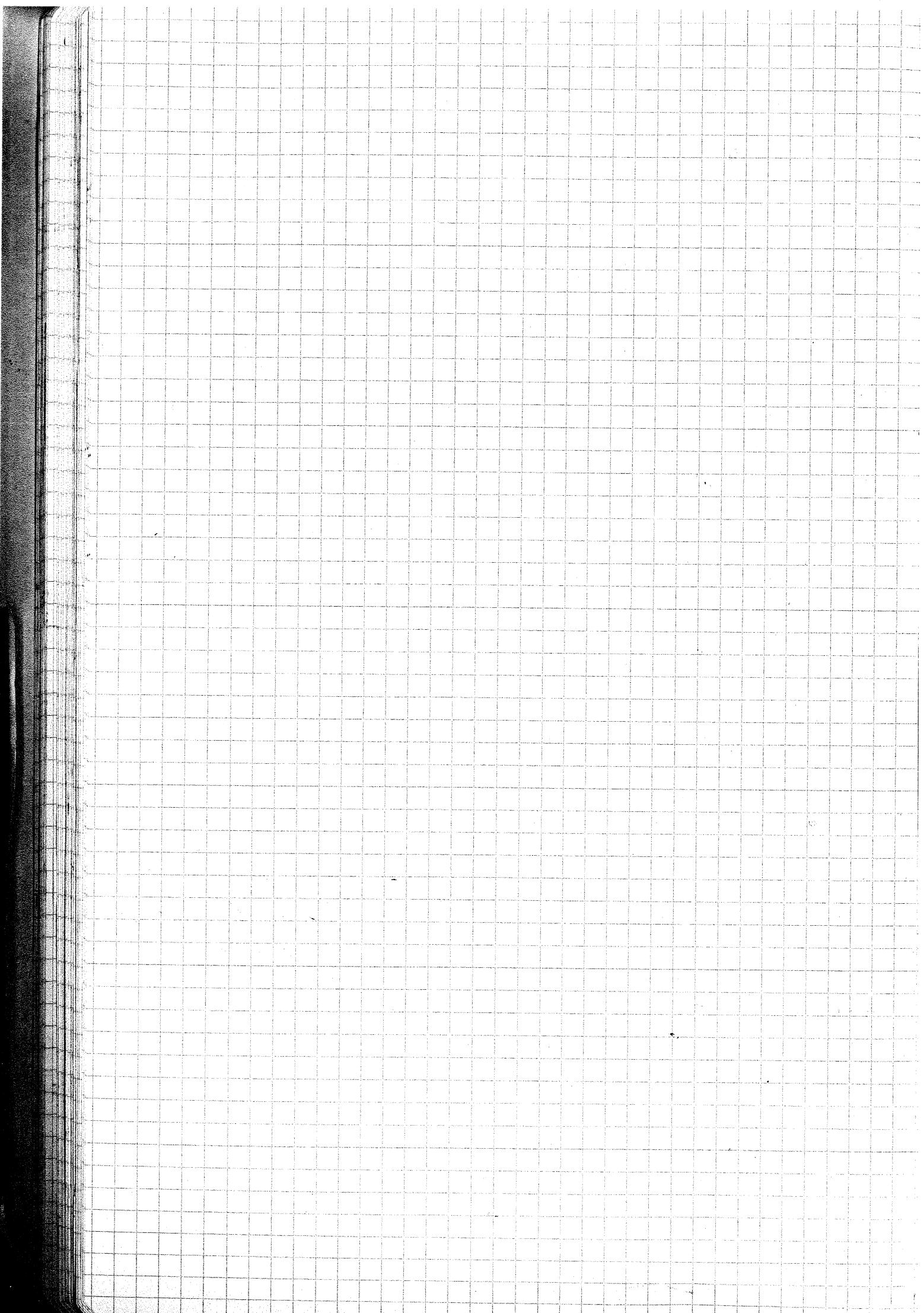
Fly flight path

straight segments interrupted
by sharp turns
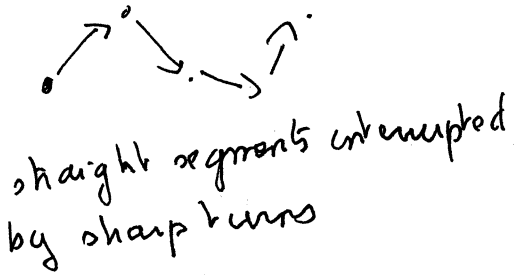
The ability of the fly to maintain
a steady course depends on sensory,
particular visual feedback.

A change in visual input can trigger
a change in flight path with a
latency of just 30 ms.

Experiment
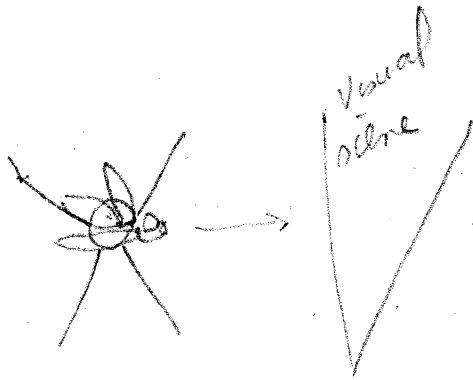
Fly control by tethering the fly so
that it hangs, wings flapping, from
a torsion balance. If the visual
environment of the fly rotates, the
fly generates a torque, to compensate
the rotational motion. One can close
the sensory-motor loop artificially by
giving the visual environment an added
the measured torque, as would happen
velocity proportional to the negative of the fly will spontaneously fixate an object,
of the fly were free to turn. ⇒ The fly will spontaneously fixate an object,
creating the image of flying straight toward that object.

Pb: The fly is able to turn by 10° in 100 ms, ~~but~~ the airflow over its
body is extremely unsteady. (speed, wind, etc...) ⇒ The fly has to adapt its torque
to external condition ⇒ no rigid mechanism: the fly must learn and
constantly update the rule appropriate to its current flight dynamics.

Visual system : photoreceptor cells → processing → movement sensitive
                                                    neurons
                                          ⌐→ wide field motion
                                          └→ narrow field
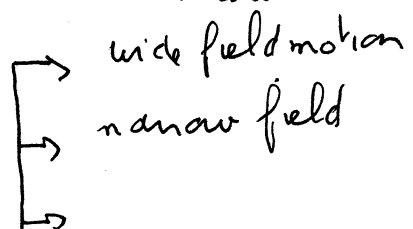
focus on neuron H_1 (one for each eye), sensitive to wide field motion.
Possible to record continuously from H_1 for periods of many days.

Experiment: the fly look as a
moving pattern presented on a
display oscilloscope. (refreshed
800 times per second)
The signal wave form $\sigma(t)$ is the
time dependent angular velocity of
the motion, with the spatial structure of
the pattern held fixed.

$\sigma(t)$
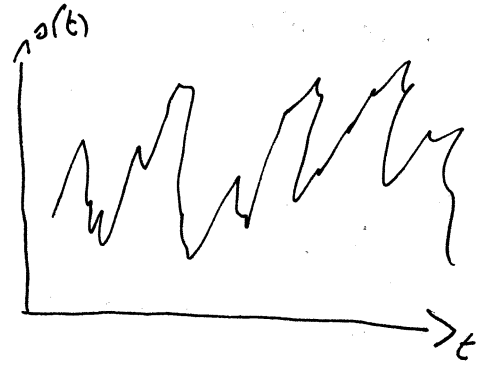
$\Rightarrow$ One registers spikes times $\{t^{(n)}\}$ $\Rightarrow$ Provides $P[\{t^{(n)}\}|\sigma(\tau)]$.

Remark.

Let us first consider the number of spikes, n, in a 200 ms window,
and the average angular velocity of motion across the fly's visual field,
σ, in a corresponding window (measured in units of the fly photoreceptor (ommatidia)).

$\Rightarrow$ Joint probability $P(n, \sigma)$ from which one can either
construct $P(n|\sigma)$ or $P(\sigma|n)$, as well as $P(n)$ and $P(\sigma)$.
One infers then $E(\sigma|n)$ (best estimate of the average speed given that
n has been observed), and $E(n|\sigma)$ (average rate as a response to a
stimulus with average rate σ). See figure for more details.

Foundations
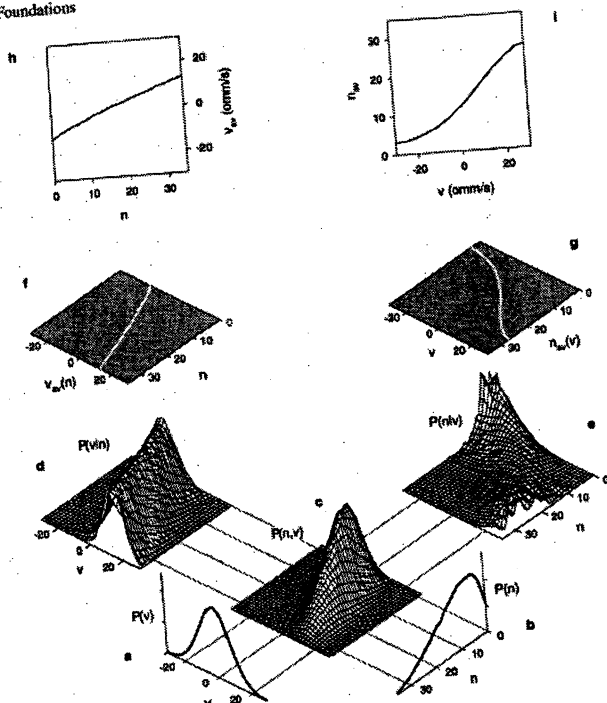
Figure 2.2

Illustration of Bayes' rule applied to experimental data obtained from an experiment on a motion sensitive cell (H1) in the blowfly. The fly viewed a spatial pattern displayed on an oscilloscope screen, and this pattern moved randomly, diffusing across the screen. At the same time, spikes from H1 were recorded. The figure depicts the statistical relations between a stimulus variable, v, and a spike count, n. v is the value of the stimulus velocity averaged over a 200 ms time window. It is measured in units of the fly's photoreceptor spacing (ommatidia) per second, or omm/s. One ommatidial distance is about $1.3°$ of visual angle. n is the number of spikes counted in a 200 ms window, delayed 20 ms with respect to the stimulus-averaging window. The choice of these variables is made here for the purpose of illustration, not because we think that the fly uses these categories—flying at a speed of ~ 1 m/s, the fly would surely crash if it averaged for 200 ms before making a decision. (a) Probability density $P(v)$ for all the 200 ms windows in the experiment, taken in an overlapping way at 2 ms increments. (b) Probability $P(n)$ of finding n spikes in a 200 ms window, computed in the same way. (c) Joint probability density $P(n, v)$ for n and v; $P(v)$ and $P(n)$ are the two marginal distributions of $P(n, v)$. As can be seen, $P(n, v) \neq P(n) \cdot P(v)$, which means that there is indeed a correlation between stimulus and response. We can look at this correlation in two ways, either forward or reverse. The reverse description is summarized in $P(v|n)$ shown in (d). This is a family of distributions of v, parameterized by the observed response n. In other words, for each n we have a different distribution of v, and if we know that the count in a certain window is $n = n_0$, the distribution of velocities that could have given rise to that count is given by the slice $P(v|n_0)$ out of the family of conditional distributions $P(v|n)$. In the forward description we ask what values of n could be induced by a given value of v. This is described by the conditional distribution $P(n|v)$ shown in (e). The white lines in panels (f) and (g) show the average values of v given n, and of n given v respectively. These data are replotted in a standard orientation in (h) and (i). The average value $v_{av}(n)$ in (f) and (h) gives the best estimate of the stimulus given that a response n is observed (see section A.7); this is akin to the problem an observer of the spike train must solve. The average $n_{av}(v)$ in (g) and (i) gives the average response as a function of the stimulus, corresponding to the forward description. As explained in the text, the reverse estimator can be quite linear, even when the forward description is clearly nonlinear.

Spike- triggered average.

Fix one spike arrival time and look at the stimulus before that spike arrives. Averaging over events provides the spike triggered average, or spike response

(See figure for details)

<u>Dictionary for the neural code</u>

Knowing $P[\{t^{(n)}\} | \sigma(\tau)]$ infer $P[\sigma(\tau) | \{t^{(n)}\}]$.

Take a snapshot of the spike train at some observation time t_{obs}.
At this instant, a time t_0 has elapsed since the last spike, while the second to last spike occured at time t_{-1}, etc.
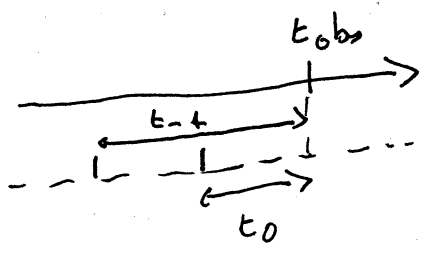
<u>Call</u> $R = \{t_{-n} \cdots t_{-1}, t_0\}$. ($n$ small)

Assume that experiment has occured on a very long time $\Rightarrow$ the spike bloc R has occured many times, corresponding to observation times $t_{obs}^{(1)} \cdots t_{obs}^{(\ell)}$.

Looking backward in time for each $t_{obs}^{(\ell)}$, one can least some particular wave forms $\sigma(t_{obs}^{(\ell)} - \tau) \Rightarrow$ provides the R-response conditional ensemble $P[\sigma(t_{obs} - \tau) | R]$.

This probability distribution is unknown but one can measure its first moments ($n = 1 \cdots 4$). In the experiments on the fly, one finds that, for many examples of responses R, this distribution is a <u>Gaussian</u>, characterized by the <u>mean velocity vector</u> $w_R(\tau)$ and <u>covariance matrix</u> $c_R(\tau_1, \tau_2)$ (N.B. the stimulus is random with a stationary distribution, so that $P[\sigma(t_{obs} - \tau) | R]$

$= P[\sigma(-\tau) | R]$.

Examples are given in Fig... The following notation is used. The superscript $-$ and $'$ signify, respectively, the absence or the presence of spikes. For example '5'10$^-$ means interspike interval of 5ms, followed by a 10ms interval without spike.

clearly, more complex correlations on the spatial and temporal... more complex conditional mean waveforms. For example the conditional mean waveform changes drastically with the interspike interval. For long interval one can distinguish 3 phases in the average velocity waveform: 2 positive peaks occurring 25 ms before each of 2 spikes, and a trough between them. As the interval becomes shorter, those 2 interval merge. This transition occurs for intervals with a length of the order of the photoreceptor integration time. ⟹ structure in stimulus event on time scale below the photoreceptor integration time cannot be detected.
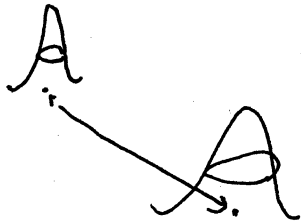
Measure of proximity between responses.

Since $P(o(t)|R)$ are gaussian one can measure the length of the vector that points from the center of one distribution to the center of the other, appropriately normalized by the covariance matrix (see figure for the measure of discrimination)

Conclusion: Once a spike has fired, the precision with which the observer must remember its position should be high shortly after the spike has occured.

Eigenvalues decomposition. The decomposition of covariance matrices in eigenvalues and related eigenvectors allows to determine the combinations of stimuli that vary independently, whereas eigenvalues measure the variance of each of these independent directions. These eigenvalues are very close to those of the prior ensemble, $P(o(t))$,
BUT two ⟹ narrowing of the probability distribution along 2
smaller eigendirections. See Fig.

TABLE 2. SYMBOLIC AND PICTORIAL NOTATIONS FOR STRETCHES OF NEURONAL RESPONSE ACTING AS CONDITIONS IN COMPUTING THE RESPONSE-CONDITIONAL SUMS (RCSs), TOGETHER WITH THE STRATEGY FOR THEIR COMPUTATION

notation		
symbolic	pictorial	computation
RCS $('t_{-1}'t_0^-)$		directly from experiment
RCS $(^-t_{-1}'t_0^-)$		$\displaystyle\sum_{\alpha > t_{-1}} \text{RCS}('\alpha't_0^-)$
RCS $('t_0^-)$		$\displaystyle\sum_{\alpha > 0} \text{RCS}('\alpha't_0^-)$
RCS $(^-t_0^-)$		$\displaystyle\sum_{\alpha > t_0} \text{RCS}('\alpha^-)$
RCS (0^-)		$\displaystyle\sum_{\alpha > 0} \text{RCS}('\alpha^-)$
RCS $('t_{-1}'t_0')$		directly from experiment
RCS $(^-t_{-1}'t_0')$		$\displaystyle\sum_{\alpha > t_{-1}} \text{RCS}('\alpha't_0')$
RCS $('t_0')$		$\displaystyle\sum_{\alpha > 0} \text{RCS}('\alpha't_0')$
RCS $(^-t_0')$		$\displaystyle\sum_{\alpha > t_0} \text{RCS}('\alpha')$
RCS $(0')$		$\displaystyle\sum_{\alpha > 0} \text{RCS}('\alpha')$
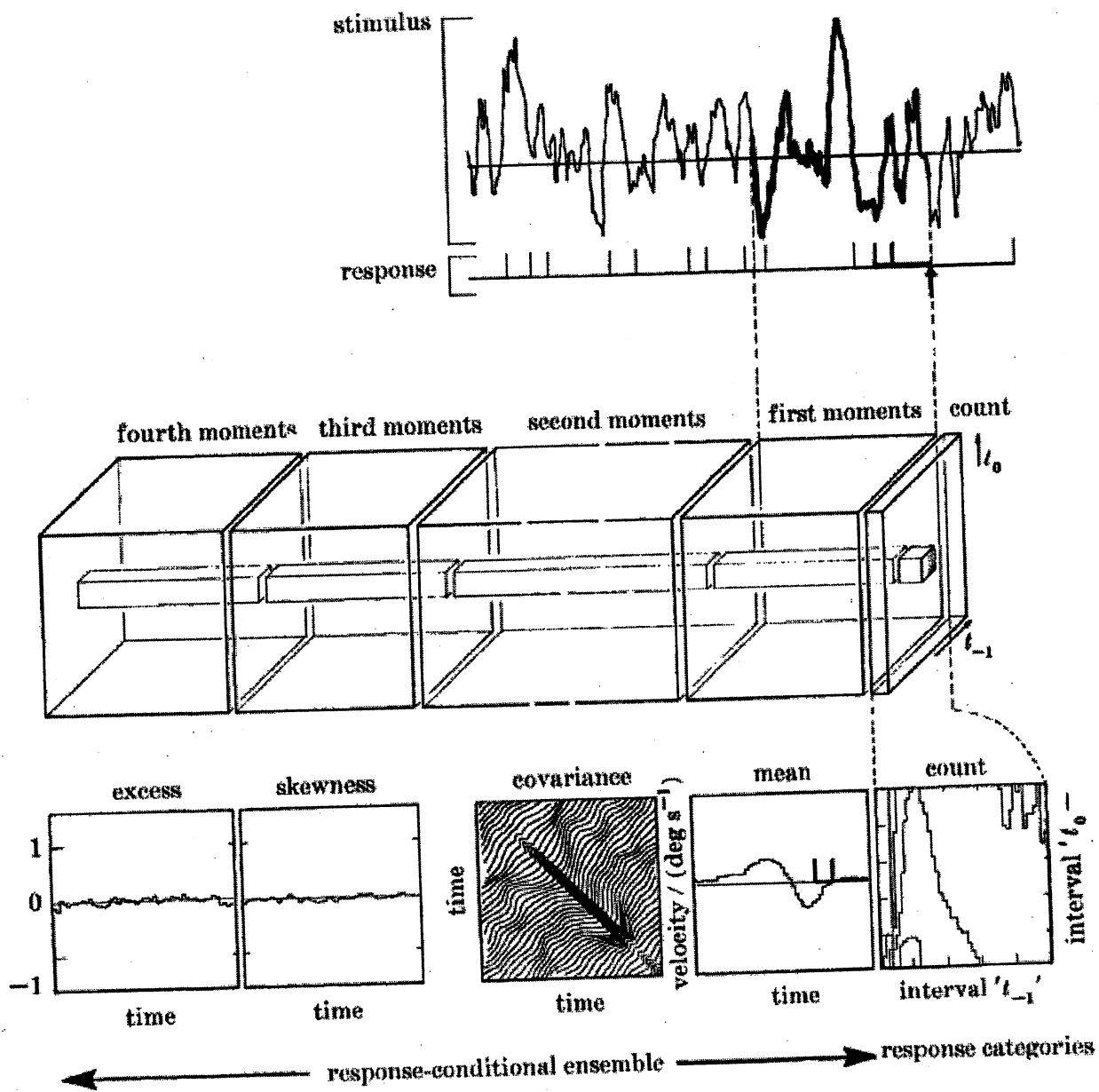
FIGURE 1. Explanation of the procedure followed in off-line analysis. The two traces at the top show a random stimulus (in this case the angular velocity in rigid movement of a wide-field pattern) together with the neuron's response, both as functions of time. In the large block at the centre, the first through fourth moments of the stimulus waveform are summed, conditional on different neuronal firing patterns. The bottom trace presents an example of the end result for one response condition after the full experiment has been analysed.
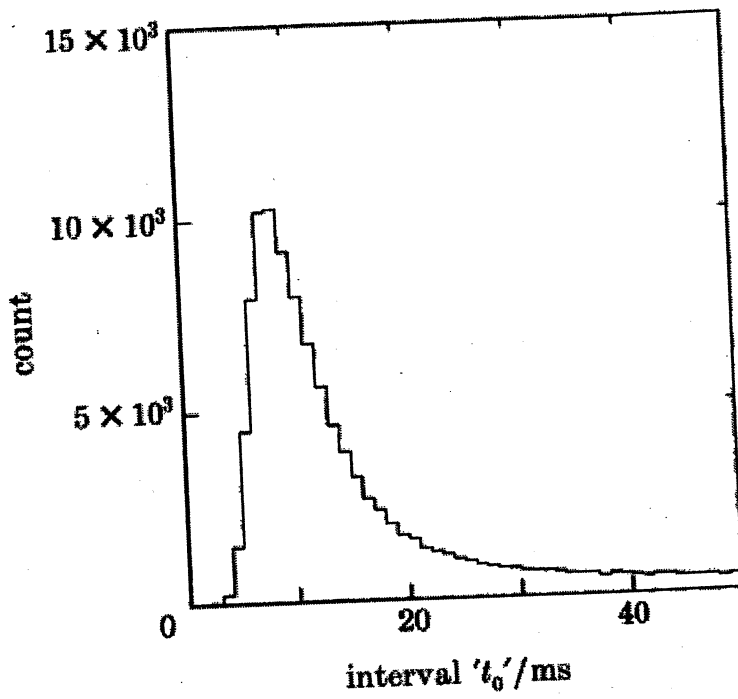
FIGURE 2. Count histogram of the occurrences of closed spike intervals ['t_0']
over the entire experiment. The bin width is 1 ms.
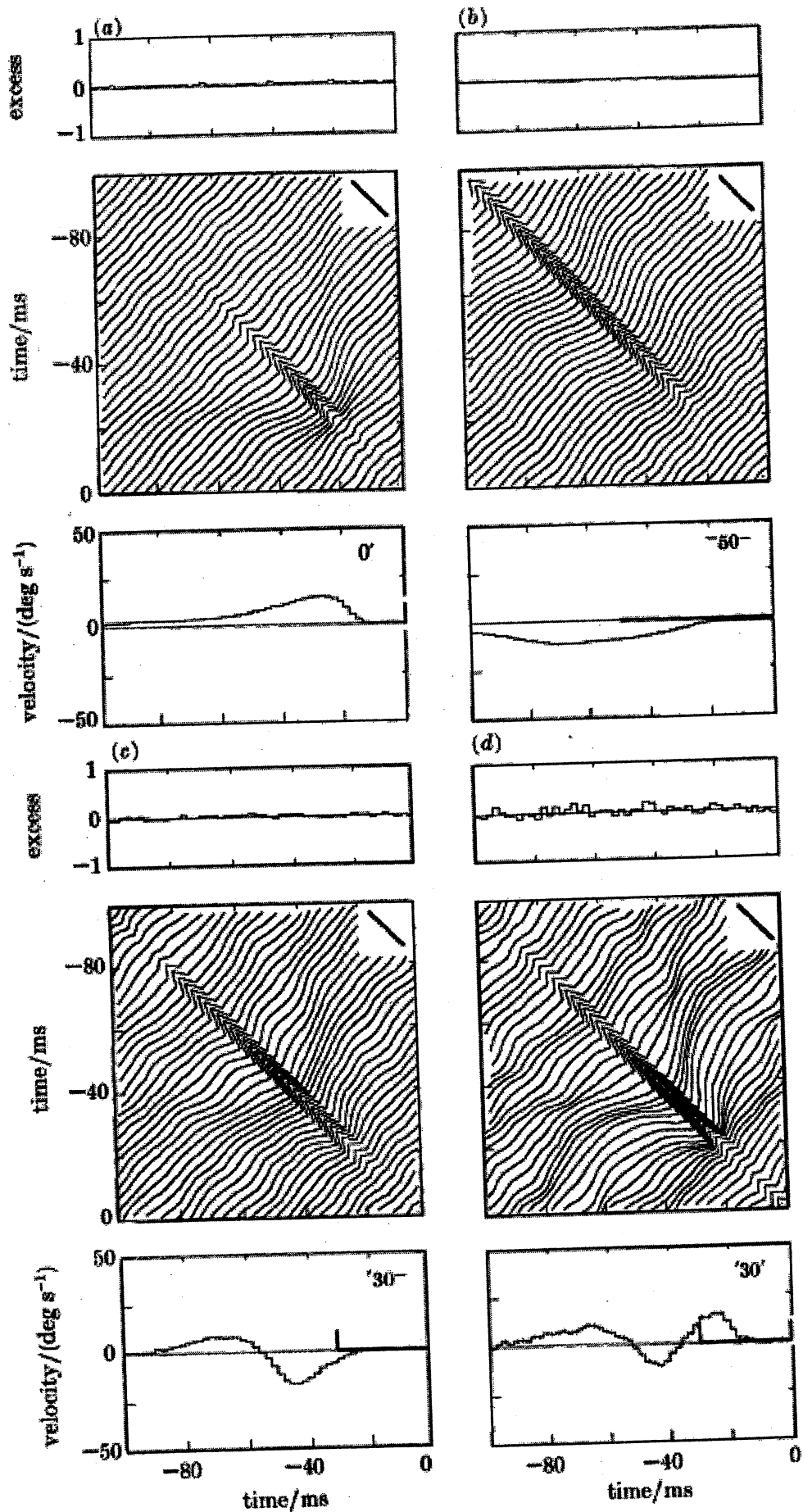
FIGURE 5 e–h. For description see page 398.
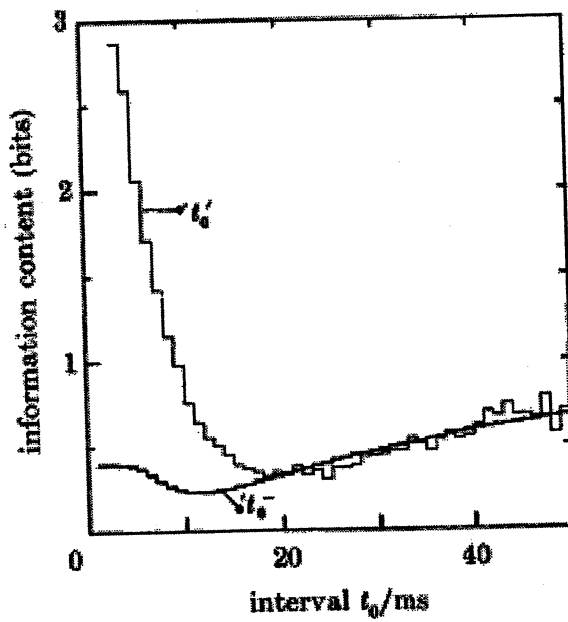
FIGURE 7. Information content of open intervals (heavy line) and closed intervals (thin line) as a function of interval length.
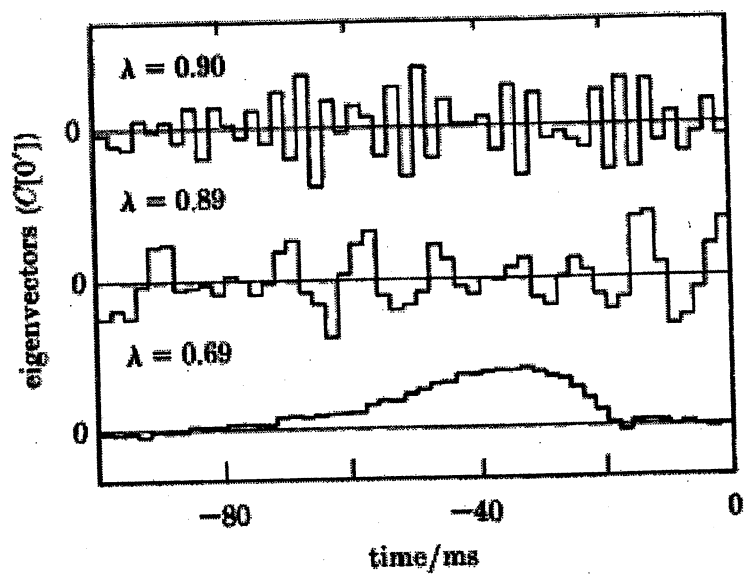
FIGURE 8. Eigenvectors corresponding to the three lowest eigenvalues of the covariance matrix conditional on a single spike.
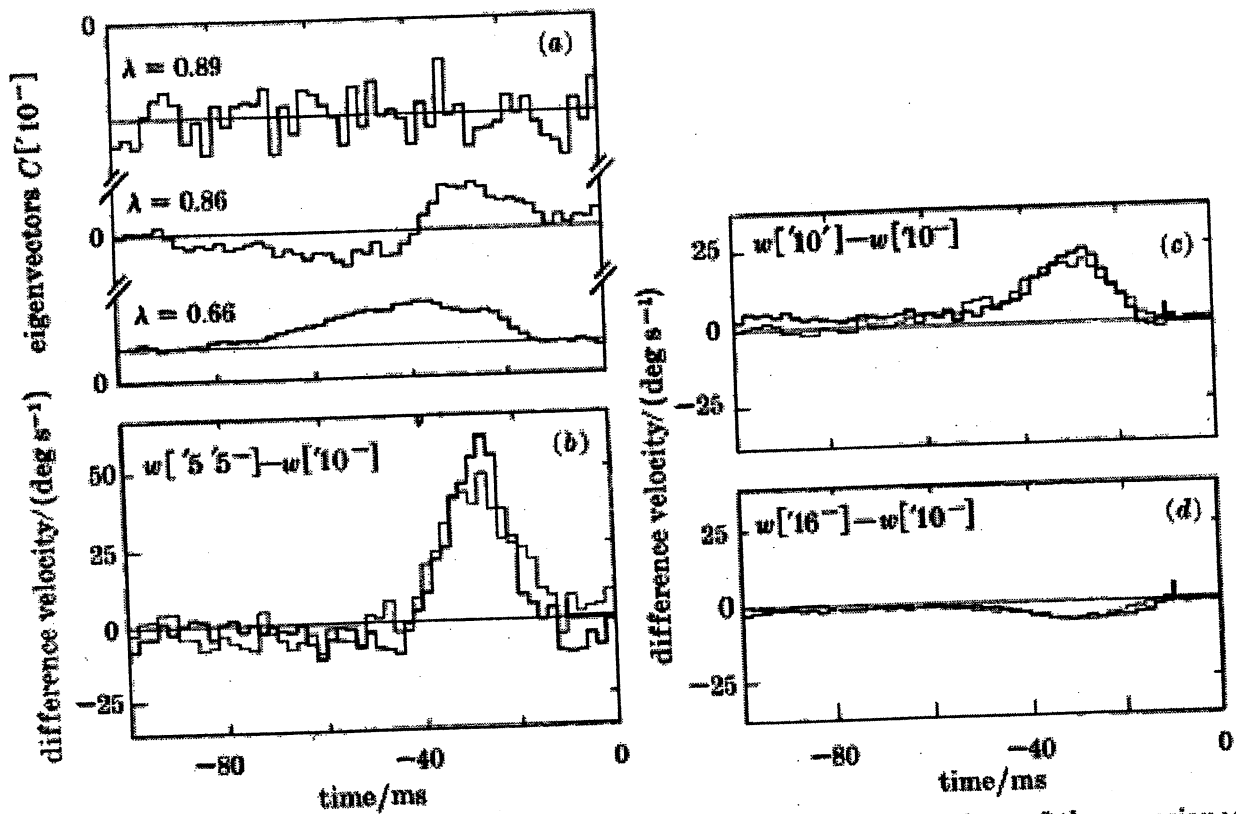
FIGURE 10. (a) Eigenvectors corresponding to the three lowest eigenvalues of the covariance matrix conditional on a 10 ms open interval ['10⁻]. (b–d) Heavy lines are the differences among the mean waveforms w['5'5⁻]−w['10⁻], w['10']−w['10⁻], and w['16⁻]−w['10⁻], respectively. Thin lines are the fits to these difference waveforms using the first two eigenvectors in (a).
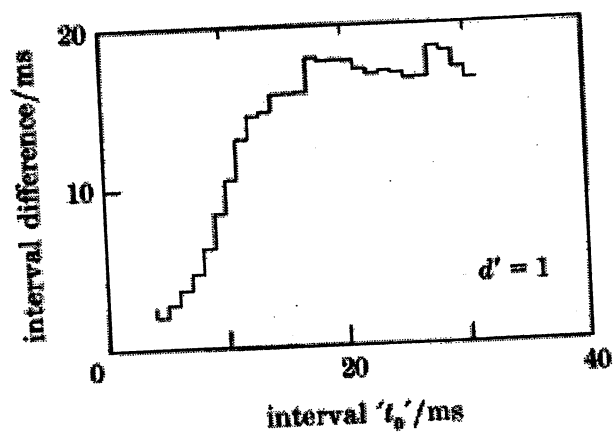
FIGURE 11. Difference interval as a function of the interval length for which the corresponding mean waveforms can be discriminated with $d' = 1$. See text for details.

For simplicity (tractability) assume that the different responses $R_1 \cdots R_k$
what we have observed are conditionally independent.

$$P[R_1 \cdots R_k | o] = \prod_{i=1}^{k} P[R_i | o]$$

$$\Rightarrow \quad P[o | R_1 \cdots R_k] = \frac{P[R_1 \cdots R_k | o] P(o)}{P[R_1 \cdots R_k]} = \frac{\prod_{i=1}^{k} P[R_i | o] P(o)}{P(R_1 \cdots R_k)}$$

$$P[R_i | o] = \frac{P[o | R_i] P[R_i]}{P(o)} \quad \Rightarrow$$

$$P[o | R_1 \cdots R_k] = \prod_{i=1}^{k} \frac{P(R_i | o) P(R_i)}{P(o)} \frac{P(o)}{P(R_1 \cdots R_k)}$$

$$= \left(\frac{1}{P(R_1 \cdots R_k)} \prod_{i=1}^{k} P(R_i) \right) P(o) \times \left(\prod_{i=1}^{k} \frac{P[o | R_i]}{P(o)} \right)$$

$\underbrace{}$
code depends
only on the observed
sequence of responses

$\underbrace{}$
$P(o | R_i)$ are
Gaussian.

$$P(o | R_i) \sim \exp -\frac{1}{2} (o - w_{R_i})^T C_{R_i}^{-1} (o - w_{R_i})$$

Take $P(o) \propto \exp \left[-\frac{1}{2} o^T C_o^{-1} o \right]$ $\overbrace{}^{C^{-1}}$

$$\Rightarrow \quad P[o | R_1 \cdots R_k] \propto \exp\left(-\frac{1}{2} o^T \underbrace{\left[C_o^{-1} + \sum_{i=1}^{k} (C_{R_i}^{-1} - C_o^{-1}) \right]}_{} o \right.$$

$$\left. + \underbrace{\sum C_{R_i}^{-1} w_{R_i}}_{C^{-1} m} \right.$$

Gaussian $\Rightarrow$

Best estimate :

$$D_{est} = \left[\sum_{i=1}^{k} \left(C_{R_i}^{-1} - C_0^{-1} \right) + C_0^{-1} \right]^{-1} \sum_{i=1}^{k} C_{R_i}^{-1} W_{R_i}$$

$\Rightarrow$ Provide a way to reconstruct a "on line" by identification
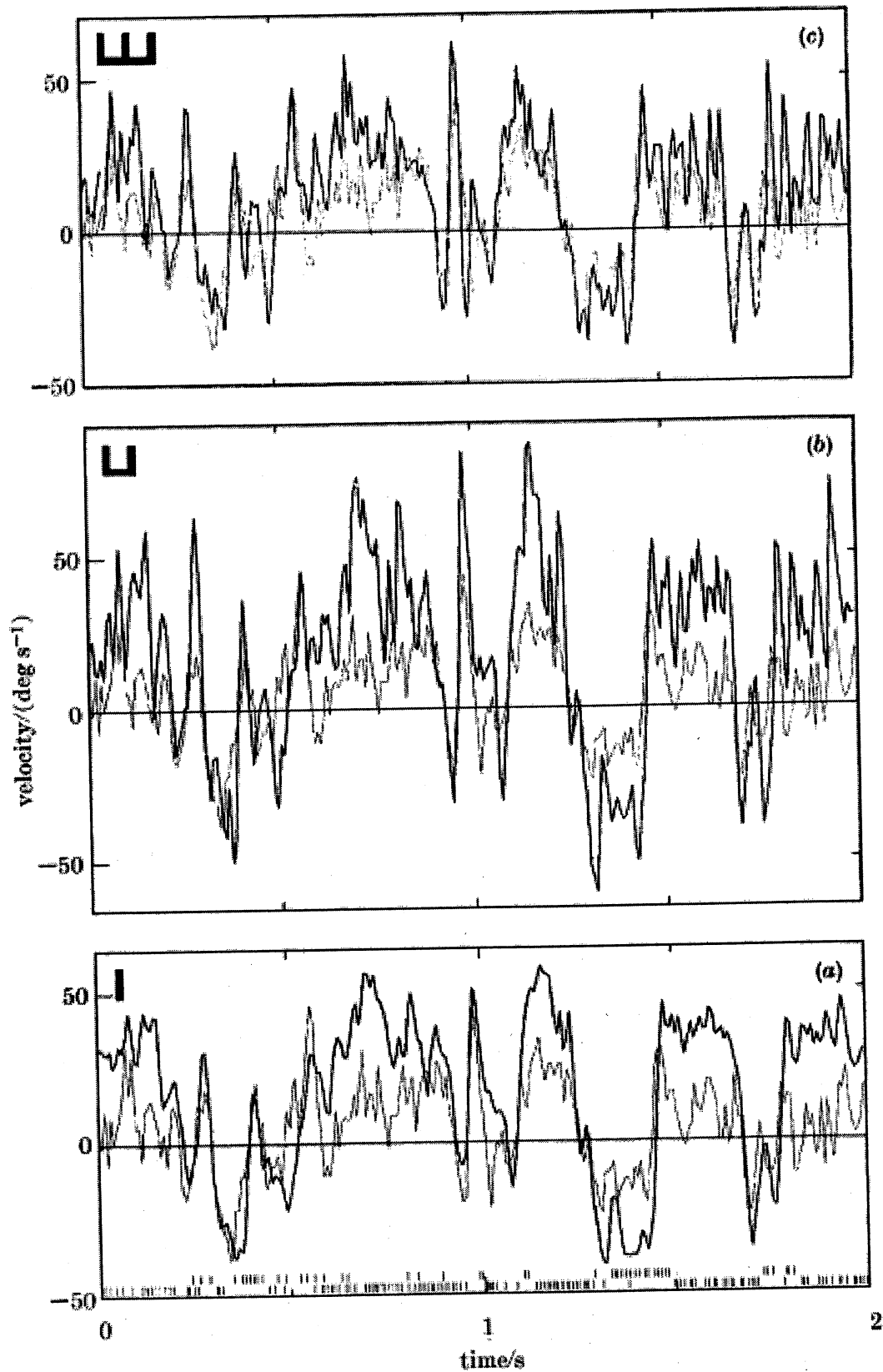of responses. (see figure)

FIGURE 12. Reconstructions of the stimulus waveform (heavy lines) together with the actual waveform (thin lines) for a 2 s time window. The reconstructions are made on the basis of combined neural responses, symbolized by the small vertical bars at the bottom of (a), during two opposite phases of the stimulus. In the reconstruction we assume that (a) single spikes, (b) spike pairs or (c) spike triplets are generated independently, as described in the text.

Synaptic plasticity.

Up to now in this chapter we have considered that the w_{ij}'s are fixed parameters and we have been able to analyze collective dynamics in several examples.

We now consider the case where synaptic weights evolve according synaptic plasticity mechanisms. That is, we consider a coupled evolution of the form:

$$
(5.1) \quad
\begin{cases}
X^{(\tau)}(t+1) = F_{\gamma^{(\tau)}}(X^{(\tau)}(t)) \\[2mm]
\delta W_{ij}^{(\tau)} = W_{ij}^{(\tau+1)} - W_{ij}^{(\tau)} = \varepsilon g\left(W_{ij}^{(\tau)}, [w_i]_{t-T_0}^t, [w_j]_{t-T_0}^t \right),
\end{cases}
$$

focusing here to discrete time dynamics. X is the state of neurons in the network. X_i, the state of neuron i, can be the membrane potential or a vector including other variables.

We have to consider here 2 dynamics, possibly evolving on different timescales. Neurons dynamics evolve according to a dynamics indexed by a time variable t, while synapses evolve according to a timescale indexed by a time variable τ. We call "epoch" a phase of synaptic update.

$\gamma^{(\tau)}$ is a set of parameters including synaptic weights at epoch τ. Neurons dynamics depend on these parameters, hence the superscript τ on the neurons state. $\underline{\varepsilon\ is\ a\ small\ parameter.}$

(5.1) characterizes therefore a coupled dynamics where neurons dynamics depend on synaptic weights and synapse update depend on neurons state.

From now, we shall make the assumption that synaptic adaptation is slow compared to neurons dynamics. This has the following consequences:

We may consider that neurons dynamics evolve on a long time period, say sufficiently long to ensure that it has "reached" its omega limit set, this evolution occurring for constant $\gamma^{(\tau)}$. Then, the synaptic adaptation depends on the activity of neurons when dynamics is in the asymptotic regime.

A variation of weights, small because of the small parameter ε, induce a change in neurons dynamics. This change can be smooth (e.g. away from bifurcation point) or sharp at bifurcation point.

The image of the global evolution is to associate to each value of γ a point in the parameter space, corresponding to a given phase portrait. Synaptic plasticity corresponds to following a path in this space, where the path is determined by past neuron activity and integrates the past of the neural network.

W_3

Bifurcation manifold
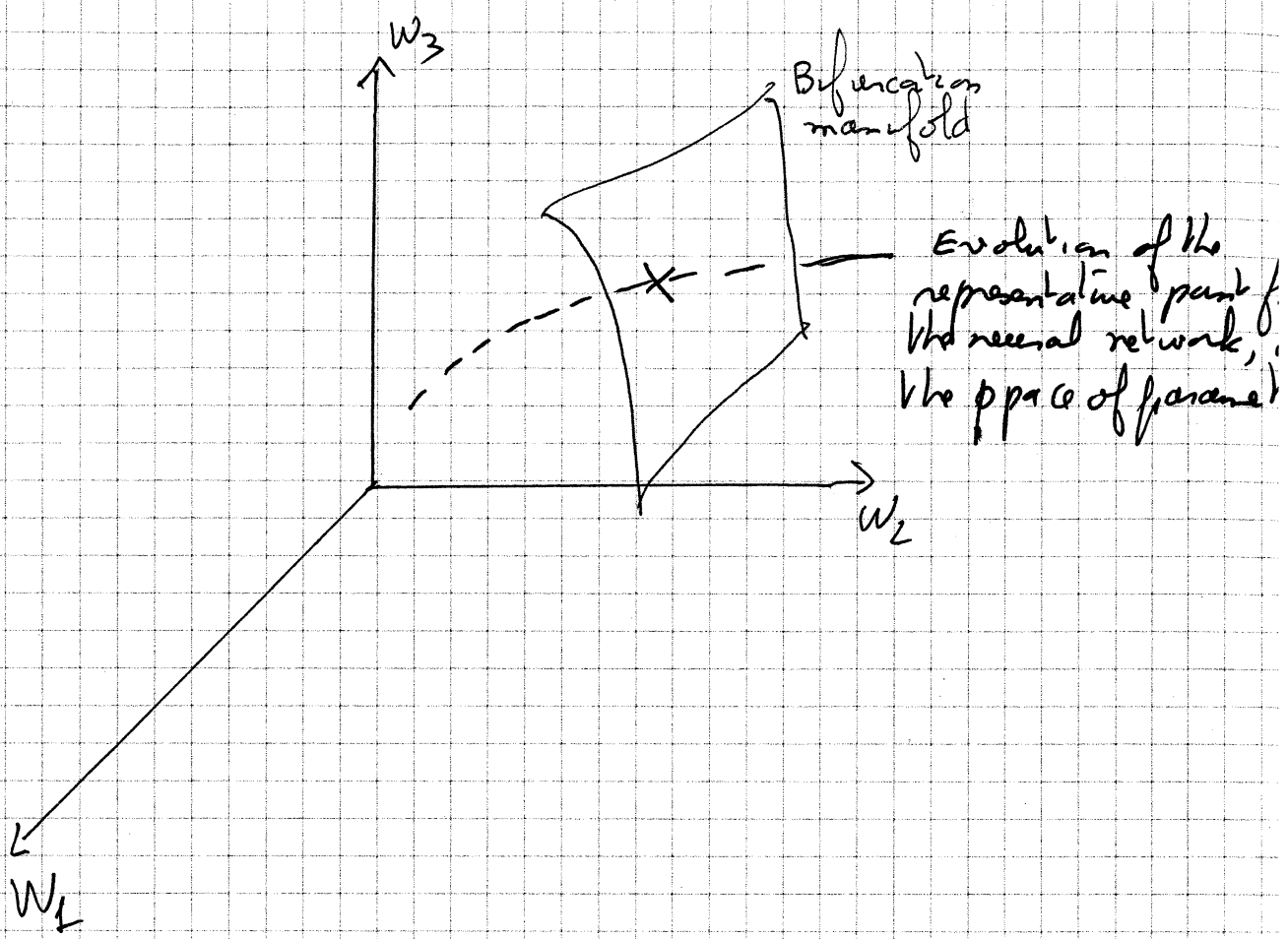
Evolution of the representative point of the neural network, the space of paramet[...]

W_2

W_1

Moving continuously, dynamics will have regular phase in evolut[...] (away from bifurcations point) punctuated by abrupt changes wh[...] the path crosses bifurcation manifolds. Here sharp transition [...] dynamics occur.

Dynamical effect of Hebbian learning in the CNT model

2.1) Description

As a first example let us consider the CNT model (   ). As we saw, considering random independent synaptic weights leads to a transition to chaos by quasi-periodicity as the reactivity of neurons, g, increases. Especially the largest Lyapunov exponent increases with g from stable fixed point, to a constant plateau corresponding to quasi periodicity transition, to a sharp increase, depending on neurons number N in the chaotic regime.
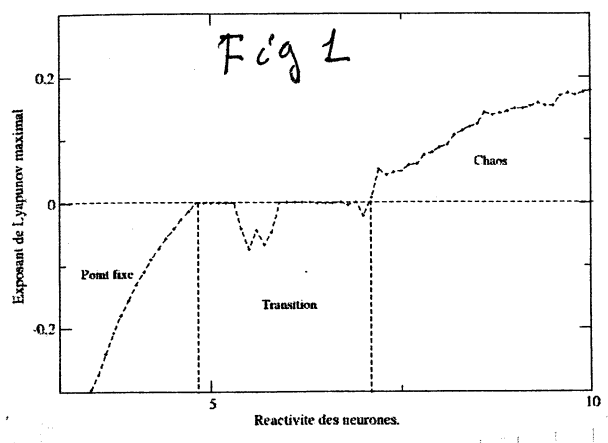
Having random independent synaptic weights corresponds to considering an initial network without structure, no memory. An information void system — A tabula rasa

Fig 1

In the chaotic regime dynamics is structurally stable. This especially means that a (weak) stimulus will not make a chaotic change in dynamics sharp chaotic, with small changes (continuous) in the attractor structure

Assume now that we add an Hebbian dynamics of synaptic weights. For example

$$W_{ij}^{(t+1)} = \lambda W_{ij}^{(t)} + (V_i^{(t)} - d_i)(V_j^{(t)} - d_j) H(V_j^{(t)} - d_j)$$

corresponding to a soft bound rule ($\lambda \in [0, 1[$) with activity threshold d_i, d_j and a term ensuring that change occurs only if neuron j (pre synaptic) is active. H being the Heaviside function.

Before plasticity

without stimulus   with stimulus

After plasticity

Fig 2.
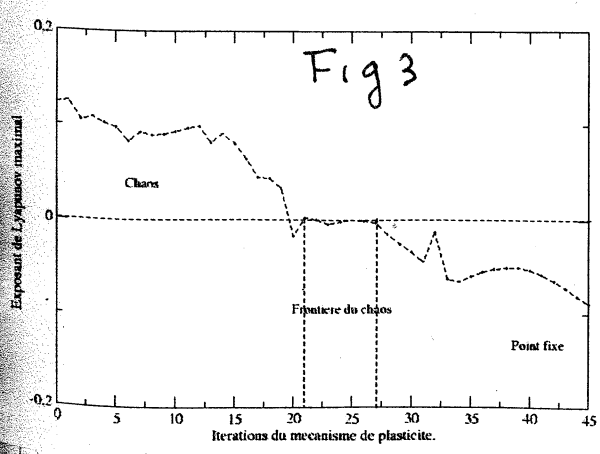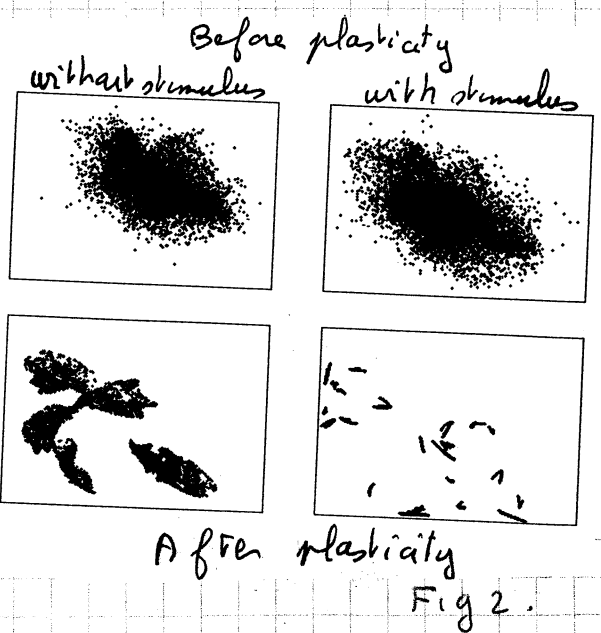
The effect is represented on Fig 3. Dynamics complexity decreases in a an inverse quasi periodicity route, up to a stable fixed point dynamics

This effect occurs as well in presence of a fixed stimulus. But at the edge of chaos there is a very interesting effect illustrated in Fig 2, bottom line.

Fig 3

The presentation of the stimulus induces a bifurcation in dynamics. This effect is robust, selective and acquired (see Dauce 1998).

But it occurs on a very small window of synaptic plasticity evolution when the system is at the edge of chaos. Other type of plasticity such as intrinsic plasticity could lead to a larger stabilisation at the edge of chaos.

5.2.2) Dynamical analysis