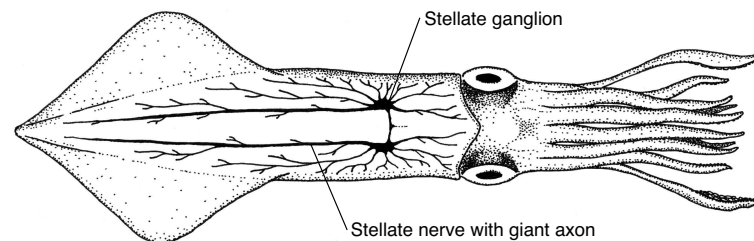


# Double coherence resonance in neuronal models driven by correlated noise

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# Introduction

**Coherence Resonance (CR)** : the effect induced by noise on an excitable oscillator, that leads to a regularization of the system response at an optimal noise intensity without any external drive. B. Lindner *et al.*, Phys Rep. 392 (2004) 321-424

- CR has been usually observed for **uncorrelated** inputs with respect to **noise intensity**  
Hu Gang *et al.*, PRL 71, 807 (1993) – A. Pikovsky & J. Kurths, PRL 78, 775 (1997)
- A **second type of CR** has been also observed with respect to the **level of correlation** :
  - lasers – Buldú *et al.*, PRE (2001)
  - digital circuits – Brugioni *et al.*, PRE (2005)
  - chemical reactions – Beato *et al.* PRE (2005)
  - neuronal models – Casado PLA (1997)

Our study:

- A FitzHugh-Nagumo (FHN) model subjected to a large number of stochastic **excitatory** and **inhibitory** post-synaptic inputs (PSPs) (small **positive** or **negative** kicks);
- Either excitatory or inhibitory Poissonian PSP trains are **correlated**.

By varying independently noise amplitude and correlation level, is it possible to observe a maximal coherence resonance ?



# Summary

- The FHN model and the stochastic stimulation protocol;
- Coherence resonance in brief;
- Influence of correlations on the coherent response;
- Double coherence resonance (DCR) with respect to noise and correlations;
- Heuristic explanations of the observed phenomena;
- Conclusions

# The FitzHugh-Nagumo Model

The FitzHugh-Nagumo (FHN) model is a two dimensional simplified neuronal model:

$$\begin{aligned}\dot{V} &= \phi\left(V - \frac{V^3}{3} - W\right) \quad ; \\ \dot{W} &= V + a_0 - I(t)\end{aligned}$$

where  $V$  is a voltage-like variable,  $W$  is a recovery variable and  $a_0$  is the bifurcation parameter.

For  $\phi = 100$  the **silent regime** is observed for  $a_0 > 1$ , while at  $a_0 < 1$  one has **periodic firing**. The external input is :

$$I(t) = \Delta W_0 \left[ \sum_{k=1}^{N_e} \sum_l \delta(t - t_k^l) - \sum_{m=1}^{N_i} \sum_n \delta(t - t_m^n) \right]$$

We examine the FHN model subject to  $N_E$  (resp.  $N_I$ ) trains of excitatory (resp. inhibitory) post-synaptic potentials, in the **balanced** case (i.e. for  $N_E = N_I \equiv N$ ) where  $\langle I \rangle \equiv 0$  for  $a_0 = 1.05$  and  $\Delta W_0 = 0.0014$ .



# High-input regime

- Instead of a continuous input  $I(t)$ , we consider  $N_E$  excitatory (EPSP) and  $N_I$  inhibitory postsynaptic inputs (IPSP), each corresponding to a voltage kick  $\Delta W_0 = 0.0014$ .
- These inputs originate from **uncorrelated** neurons emitting **Poissonian spike trains** with frequency  $\nu_0$ .
- This corresponds to a single excitatory (resp. inhibitory) Poissonian spike train with frequency  $\nu_E = N_e \times \nu_0$  (resp.  $\nu_I = N_I \times \nu_0$ ) for  $N_e \sim N_I \sim 100 - 1,000$ .

For these high frequencies the **net input spike count** within a (sufficiently large) temporal window  $\Delta T$  is essentially **Gaussian distributed** and it can be characterized by

$$\text{average} \quad \mu = \nu_0(N_E - N_I)\Delta T \quad ; \quad \text{variance} \quad V = \nu_0(N_E + N_I)\Delta T = \nu_0\sigma^2\Delta T$$

The response of the neuron is examined for a **zero** average external input

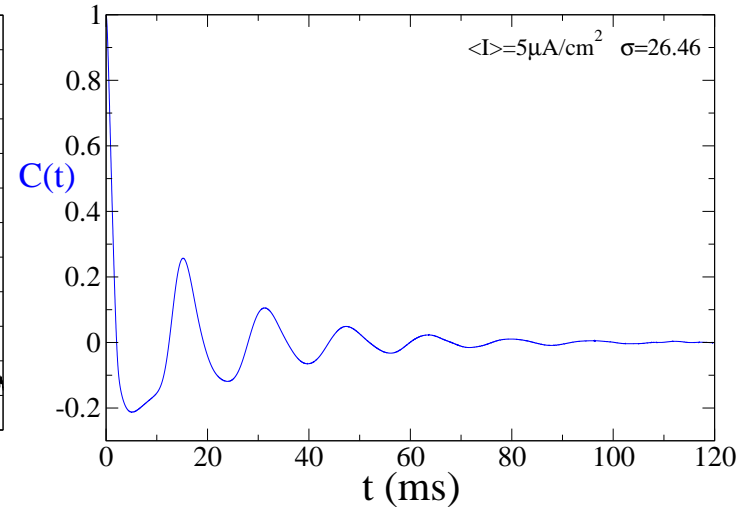
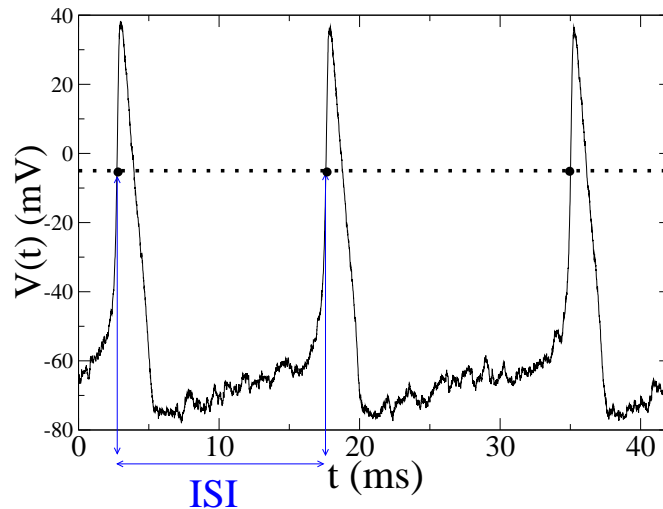
$$\langle I \rangle = \Delta W_0 \nu_0 (N_E - N_I) \equiv 0$$

by varying only the **standard deviation of the noise**  $\sigma = \sqrt{N_E + N_I}$

M.N. Shadlen & W.T. Newsome (1998)



# Statistical and dynamical indicators

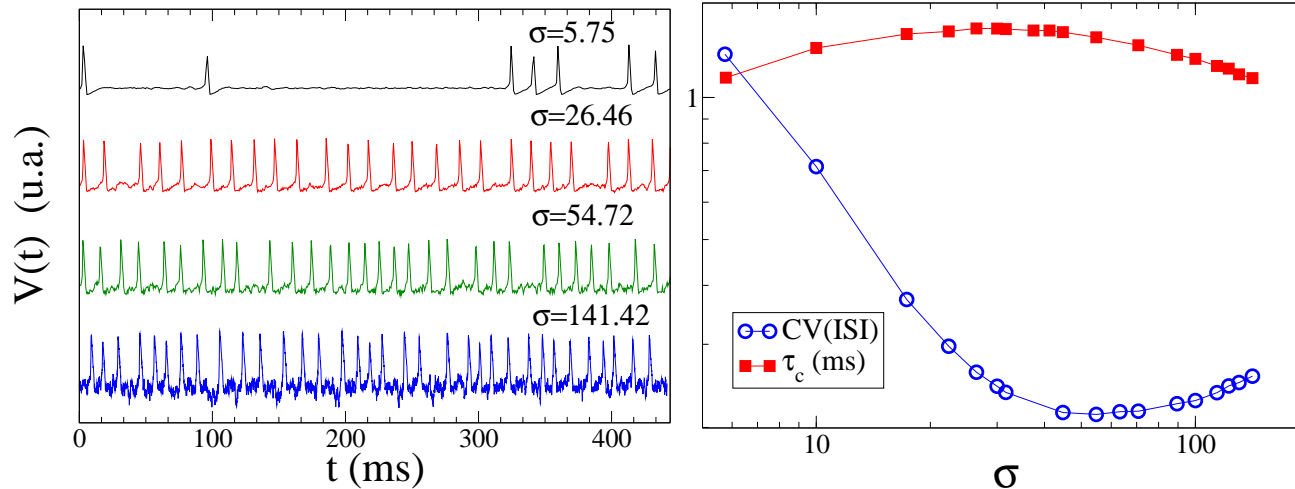


- ISI distribution  $\rightarrow P_{ISI}(t)$ ;
- $CV = \frac{Std(ISI)}{\langle ISI \rangle} \rightarrow$  coefficient of variation of the ISIs:  
 Poissonian distribution  $\rightarrow CV = 1$   
 regular sequence  $\rightarrow CV = 0$ ;
- $\tau_c = \int_0^\infty C^2(t) dt \rightarrow$  correlation time,  

$$C(\tau) = \frac{\langle V(t+\tau)V(t) \rangle - \langle V \rangle^2}{\langle V^2 \rangle - \langle V \rangle^2}$$

# Coherence Resonance

## Coherence of the emitted spike trains



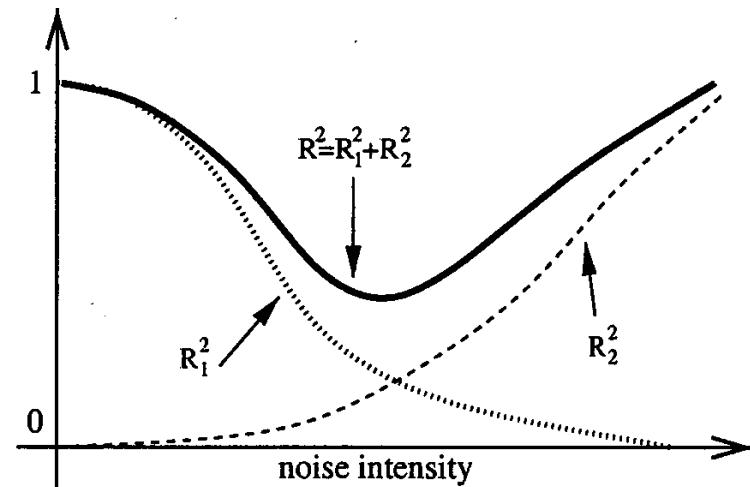
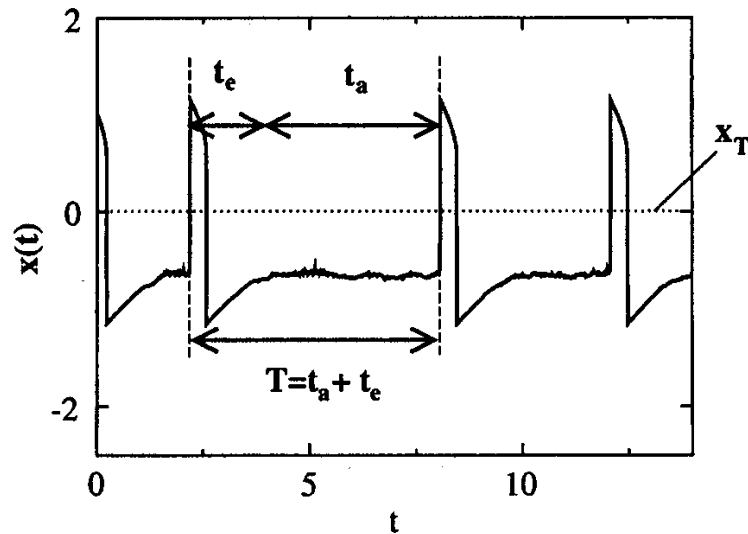
In the silent regime :

- **low noise**: Activation Process -  $P_{ISI}$  is Poissonian
- by increasing  $\sigma$  the firing rate increases, the spike train becomes more regular;
- a **maximal coherence level** is reached for an optimal  $\sigma$ -value;
- for **higher noise amplitudes** the response becomes again more irregular:  
**Brownian motion + drift** -  $P_{ISI}$  is an Inverse Gaussian.

Hu Gang et al., PRL 71, 807 (1993) – A. Pikovsky & J. Kurths, PRL 78, 775 (1997)



# Coherence Resonance



- The system is characterized by **two characteristic times**  $\rightarrow ISI \equiv T = t_a + t_e$  :
  - $t_a$  = **activation time**  $\rightarrow$  time needed to excite the system;
  - $t_e$  = **excursion time**  $\rightarrow$  duration of the spike (excited state).

- $CV(T)$  can be splitted in two contributions

$$CV(T)^2 = CV(t_a)^2 \frac{\langle t_a \rangle^2}{\langle T \rangle^2} + CV(t_e)^2 \frac{\langle t_e \rangle^2}{\langle T \rangle^2} = R_1^2(t_a) + R_2^2(t_e)$$

$R_1^2(t_a)$  **decreases** with  $\sigma$ , while  $R_2^2(t_e)$  **increases**  $\rightarrow$  **minimum** in  $CV(T)$

B. Lindner *et al.*, Phys Rep. 392 (2004) 321-424





# Correlations via shared inputs

- Correlations **ONLY** among either **excitatory** or **inhibitory** inputs are considered in the **balanced case**  $N_E = N_I \equiv N$ ;
- The **degree of correlation** among  $N$  distinct inputs  $\rho$  is given by the **average fraction of synapses** delivering kicks at **the same time**;
- The superposition of  $N$  **correlated** ( $\rho$ ) Poissonian spike trains with rate  $\nu_0$  gives rise to a sequence of kicks of variable amplitude  $\Delta W$  (**binomially distributed**) and with ISIs **Poissonian distributed** with rate  $\nu_x = \nu_0 / \rho$  (either  $x = e$  or  $x = i$ );
- The uncorrelated **excitatory** (resp. **inhibitory**) inputs are small kicks delivered at **high rate**  $\nu_U = N\nu_0$  (this is an almost continuous background);
- The correlated **inhibitory** (resp. **excitatory**) inputs are large amplitude events delivered at a **much lower rate**  $\nu_x \ll \nu_U$ ;

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- The correlated **inhibitory** (resp. **excitatory**) inputs are large amplitude events delivered at a **much lower rate**  $\nu_x \ll \nu_U$ ;
- The effect of the **uncorrelated inputs** leads to a **renormalization** of the bifurcation parameter:  $\bar{a} = a_0 \pm (N\nu_0 \Delta W_0)$ ;
- The effect of the **correlated inputs** is embodied in the **noise variance**

$$\sigma^2 = \Delta W_0^2 \nu_0 [\rho N^2 + (1 - \rho)N + N]$$

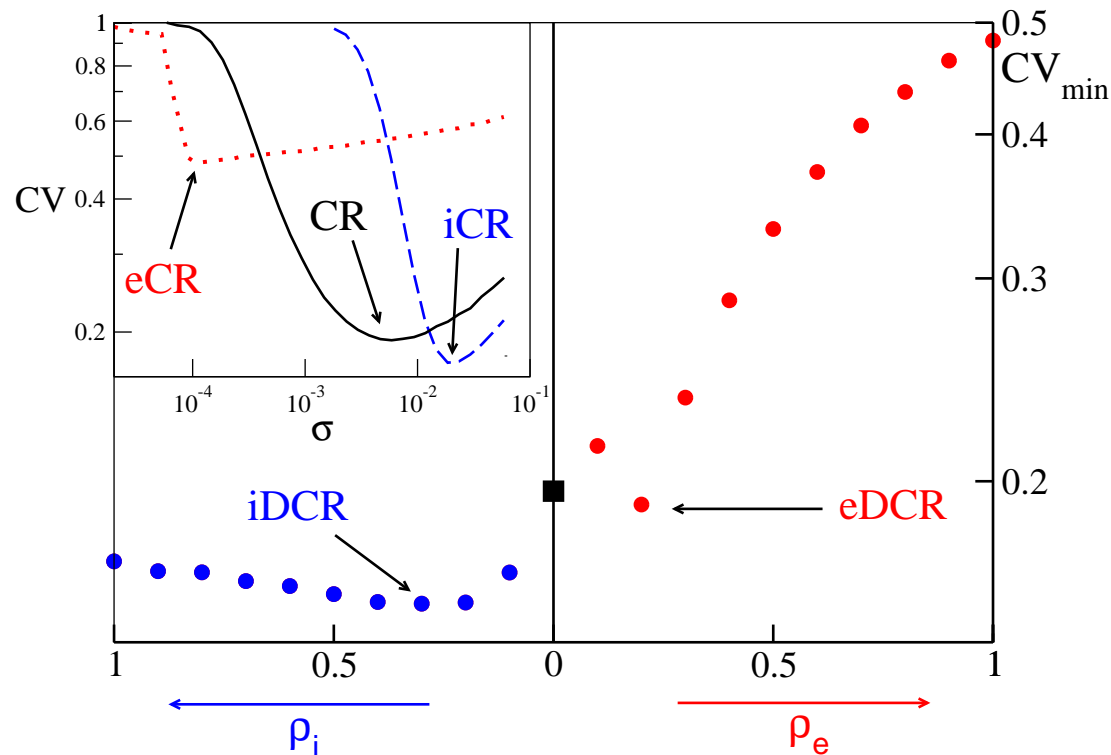
M.N. Shadlen & W.T. Newsome (1998) – E. Salinas & J. Sejnowski (2000)



# Response to correlated inputs

We have studied the response of the (balanced  $N_E = N_I$ ) Fitz-Hugh Nagumo model in the silent regime for excitatory (resp. inhibitory) correlated inputs by varying **INDEPENDENTLY** correlation  $\rho$  and noise variance  $\sigma^2$ .

- Coherence Resonance (CR) is observed for any **excitatory** (resp. **inhibitory**) level of correlation at finite noise amplitude.
- Double Coherence Resonance (DCR) : an absolute CR with respect to noise and correlation can be identified for **excitatory** (resp. **inhibitory**) correlated inputs.



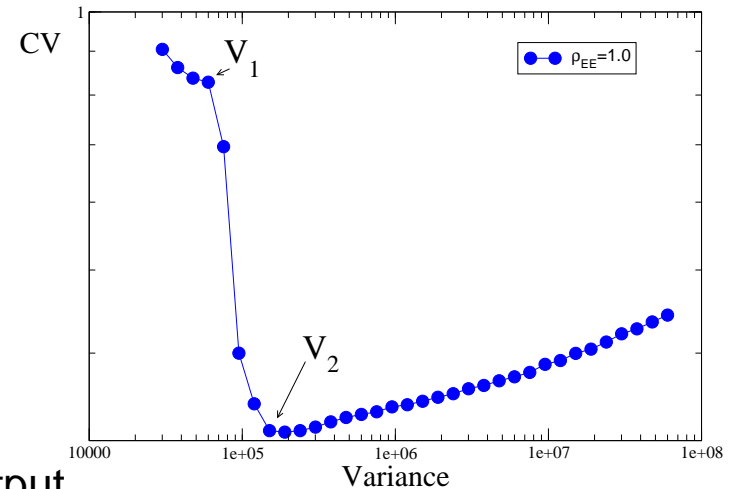
# Strong excitatory correlations

The coherence phenomenon is now determined only by the **kick amplitude** and not by the properties of the asymptotic stochastic processes, since in the present case the output can be always described as a **Poissonian process with a refractory time**:

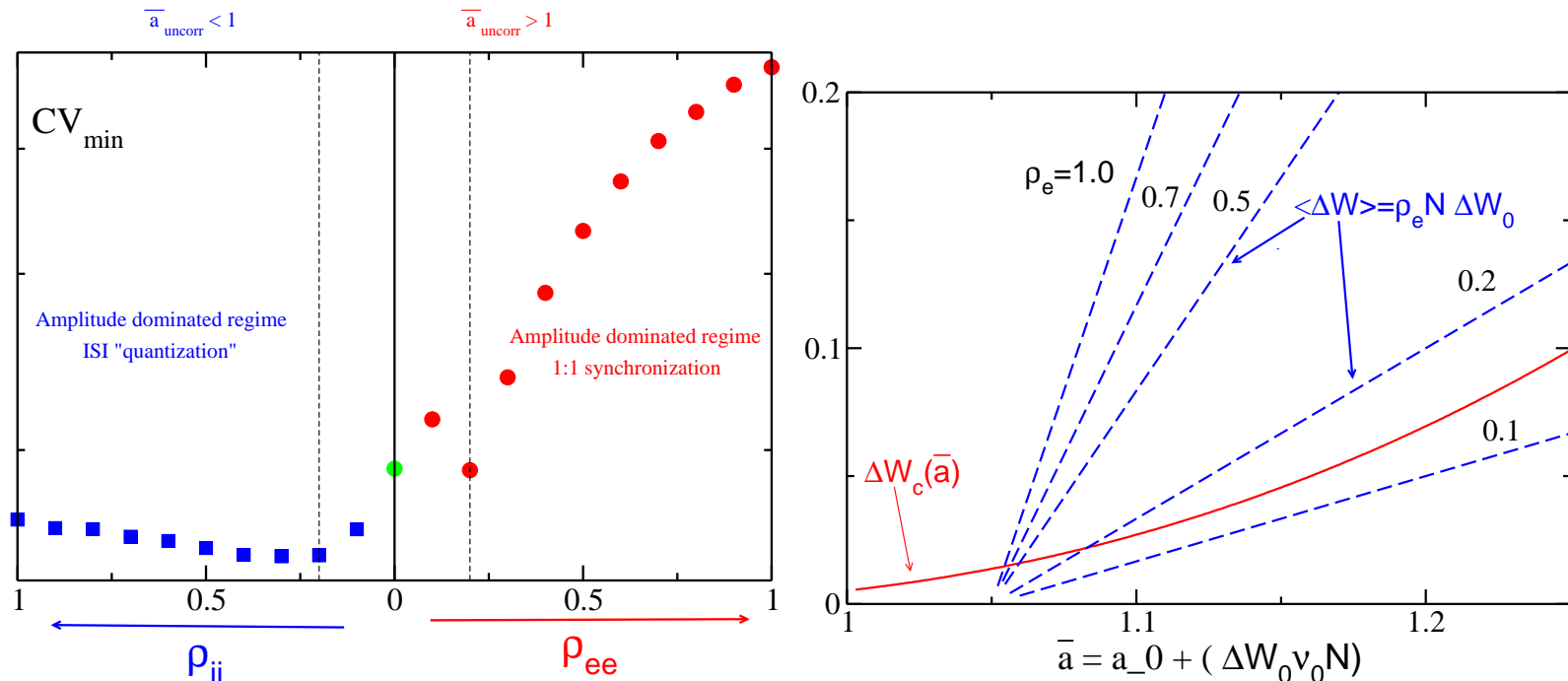
$$CV = 1 - T_{ref}\bar{\nu}$$

For increasing variance ( $N$ ) the **amplitude** of the **correlated** kicks **increases**. while the effect of the **uncorrelated (inhibitory)** trains drives the system towards the **silent regime**.

- for  $Variance < V_1 \rightarrow$  **Activation Process**
- for  $V_1 < Variance < V_2$   
1 kick may be sufficient to elicit a spike
- for  $Variance \geq V_2$   
Each kick elicits always a spike apart during the refractory period
  - 1 : 1 **synchronization** between input and output
  - $\bar{\nu} = \nu_0 / \rho_e$  ;
  - By further increasing  $Variance \rightarrow T_{ref}$  decreases

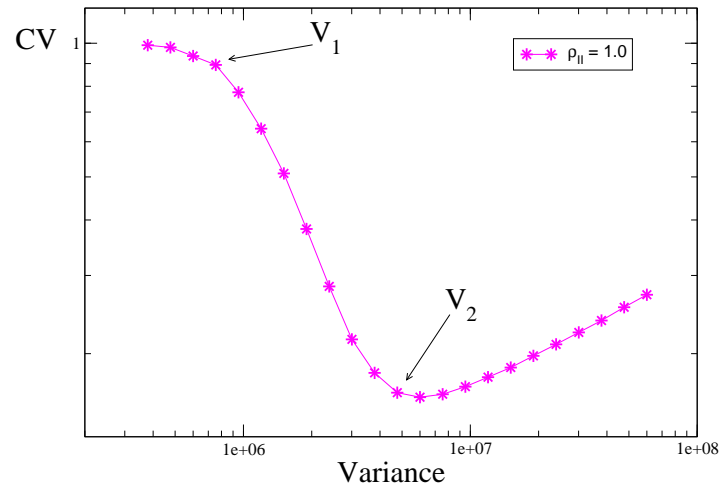


# Excitatory DCR



- for  $\rho_e \geq \bar{\rho}_e$ , 1:1 synchronization is always achieved for kick amplitudes  $\geq \Delta W_c$ 
  - therefore  $CV_{min} = 1 - T_{ref} v_0 / \rho_e$
  - the  $CV_{min}$  is attained at essentially the same  $\Delta W_c$ ,  $T_{ref}$  does not vary too much.
- for  $\rho_e < \bar{\rho}_e$ , the system is no more strictly forced by the driving kicks:
  - at the minimum the firing rate is smaller  $\bar{v} < v_0 / \rho_e$ .

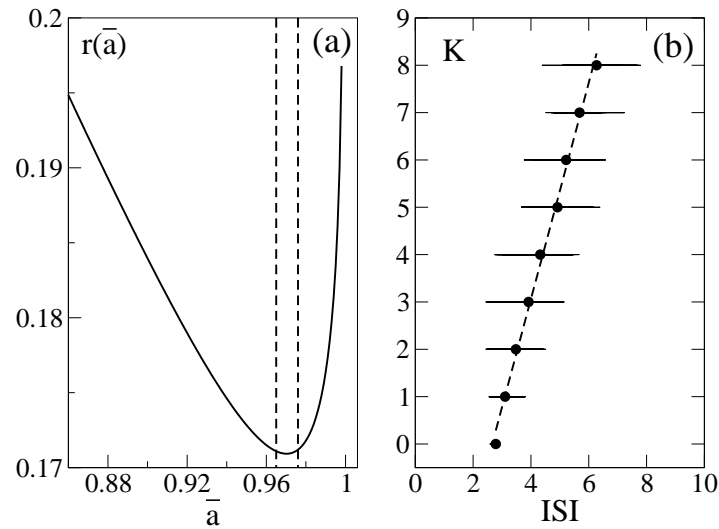
# Strong inhibitory correlations I



- for  $Variance < V_1$  Silent regime - Activation Process -  $CV \simeq 1$
- for  $V_1 < Variance < V_2$ 
  - The uncorrelated excitatory inputs lead the system towards the repetitive firing regime  $\bar{a} < 1$
  - Despite the increase of their amplitude the inhibitory kicks are not too effective
  - The signal becomes more regular  $CV$  decreases
- for  $Variance > V_2$  Each inhibitory kick induces a certain delay in the spike time of the neuron - A multimodal structure appears in the ISI distribution

Frequency of the correlated kicks ( $\nu_0$ )  $\ll$  Frequency of the uncorrelated kicks ( $N\nu_0$ )

# Strong inhibitory correlations II

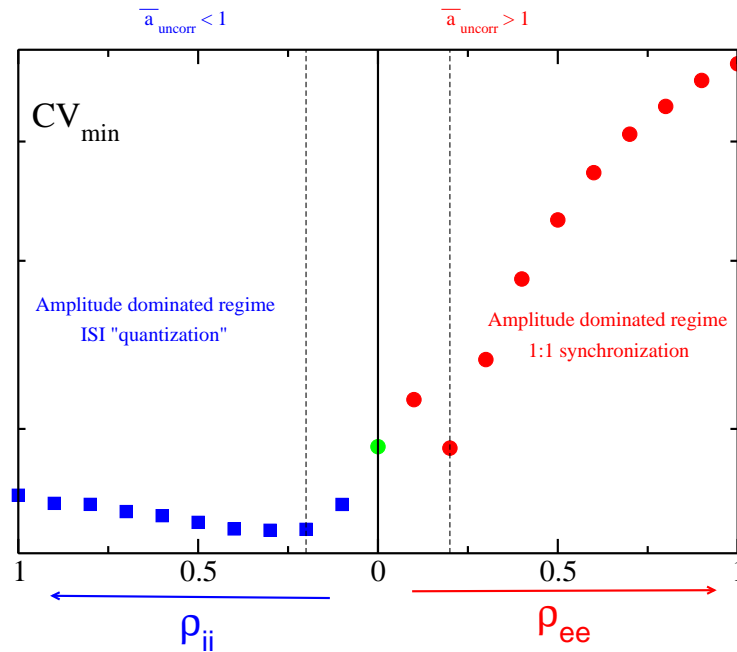


The fraction of time  $r(\bar{a})$  a FHN neuron is sensitive to the arrival of a kick before a spike emission for the deterministic case has a minimum:

$$r(\bar{a}) = 1 - T_{ref}(\bar{a})/T_f(\bar{a})$$

Noticeably, the  $CV_{min}$  occurs for  $\bar{a} \sim 0.97$  for  $\rho_i > \bar{\rho}_i$ .

# Inhibitory DCR



- The  $CV_{min}$  in the correlation interval  $[\bar{\rho} : 1]$  occurs essentially for the same renormalized parameter value  $\bar{a} = a_0 - (N\nu_0\Delta W_0) \sim 0.97$
- Therefore the average inhibitory kick amplitude at the minima depends only on the correlation  $\langle \Delta W \rangle \propto \rho_i$
- For decreasing  $\rho_i$  the kicks disturb less:  $CV_{min}$  decreases
- For sufficiently small  $\rho_i < \bar{\rho}_i$  the frequency of the inhibitory kicks becomes more important than their amplitude.
- Lowering  $\rho_i \rightarrow 0$  leads to an increase of the frequency  $\nu_i = \nu_0/\rho_i$ , that renders the neuronal firing more irregular:  $CV_{min}$  increases again



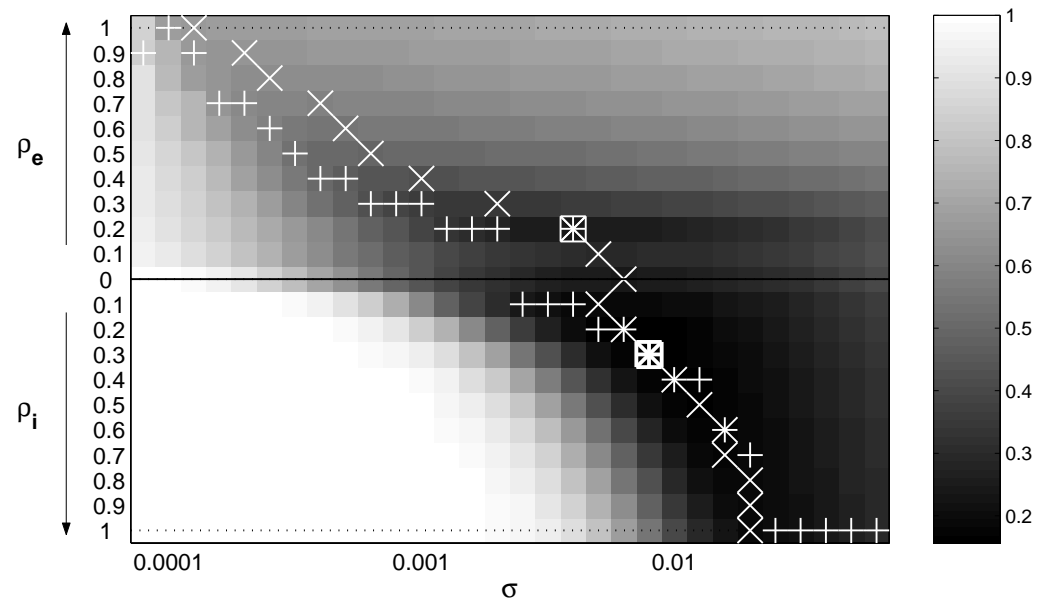


# Conclusions

- Absolute minima of CV corresponding to maximal coherence are observed at **finite noise and correlation** for both **inhibitory** and **excitatory** case.
- The extrema of  $CV_{min}$  indicate the change in the mechanisms inducing CR, from **amplitude dominated** to **usual mechanisms** related to the crossover from activated to (biased) diffusive processes.

A **DCR** with respect to **correlation** and **noise** intensity is a new phenomenon.

- $X$   $\rightarrow$  minima for fixed  $\rho$
- $+$   $\rightarrow$  minima for fixed  $\sigma$



# Conductance-based input

- The external current  $I(t)$  for the FHN is now rewritten as:

$$I(t) = g_e(t)(E_e - V) + g_i(t)(E_i - V)$$

where  $E_e$  (resp  $E_i$ ) is the excitatory (resp. inhibitory) reverse potential and  $g_e$  (resp.  $g_i$ ) is the the excitatory (resp. inhibitory) conductance.

- The excitatory conductance is defined as

$$g_e(t) = d_e \sum_{i=1}^N \sum_j \delta(t - t_i^j)$$

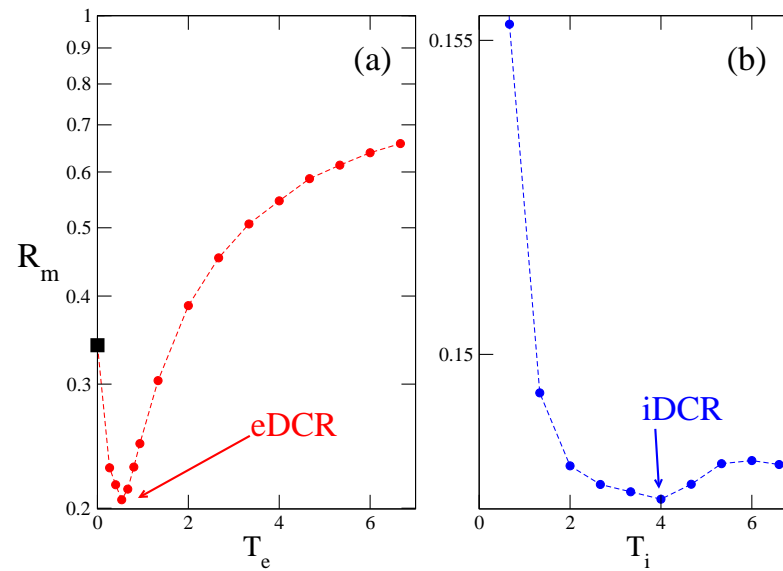
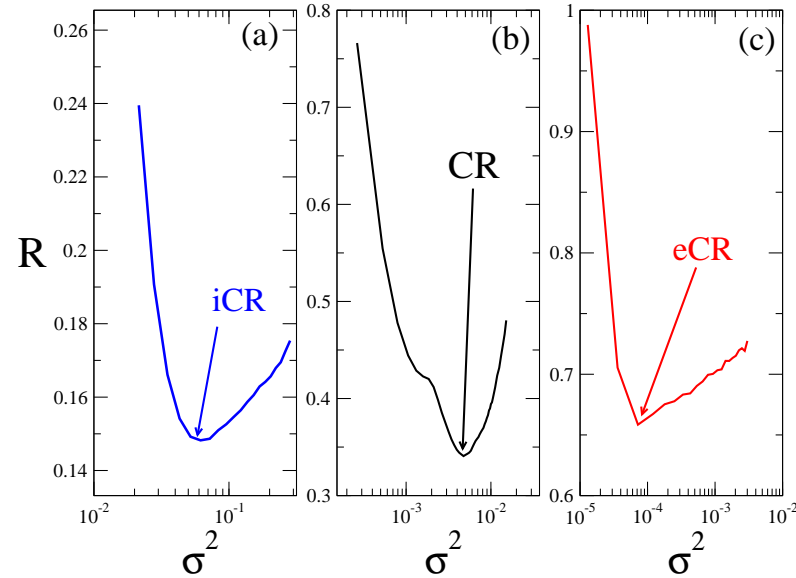
where  $d_e$  represents the strenght of the synapses and

- The set  $\{t_i^j\}$  counts over the Poisson-distributed excitatory pulses obtained as a super-position of  $N$  spike trains each characterized by a rate  $\nu_0$ , representing the  $N$  correlated or uncorrelated inputs. The overall (correlated or uncorrelated) spike trains are constructed exactly as before.

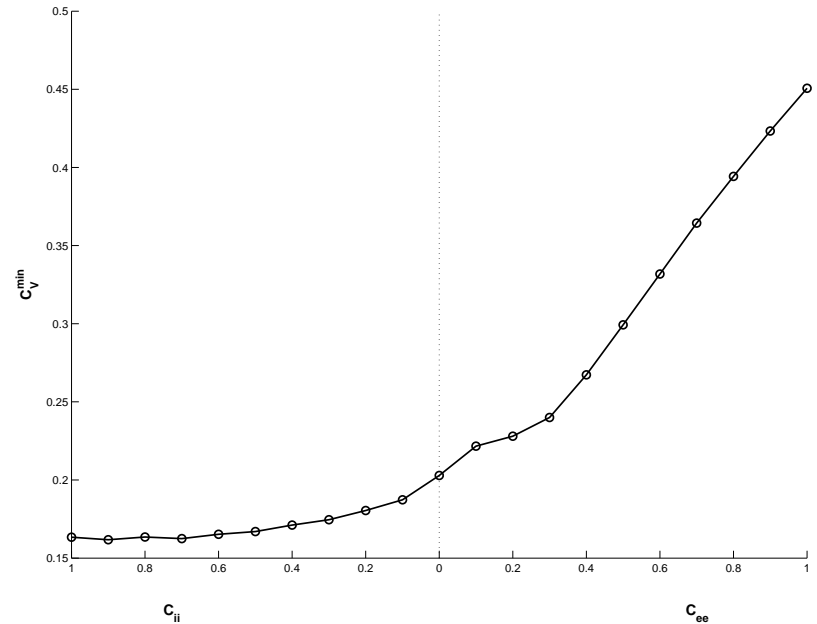
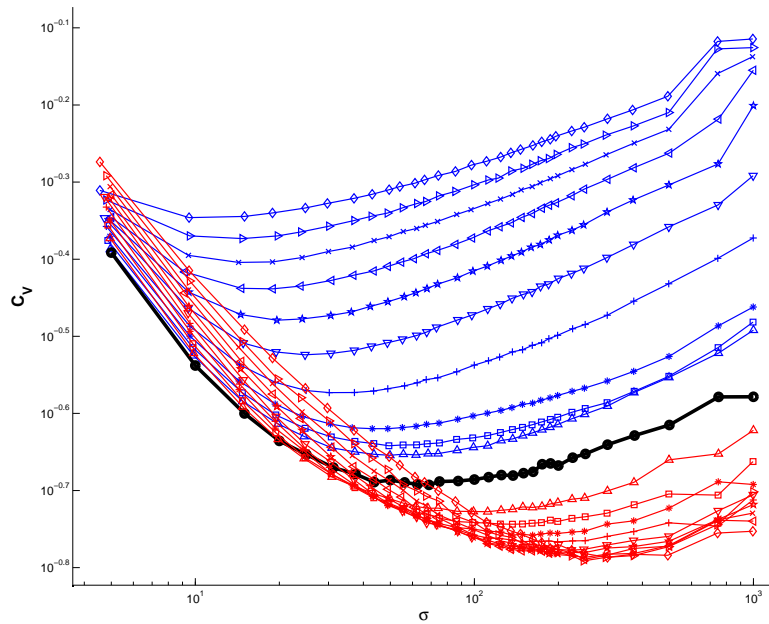
MJE Richardson, PRE (2004)



# Conductance-driven FHN



# Hodgkin-Huxley Model

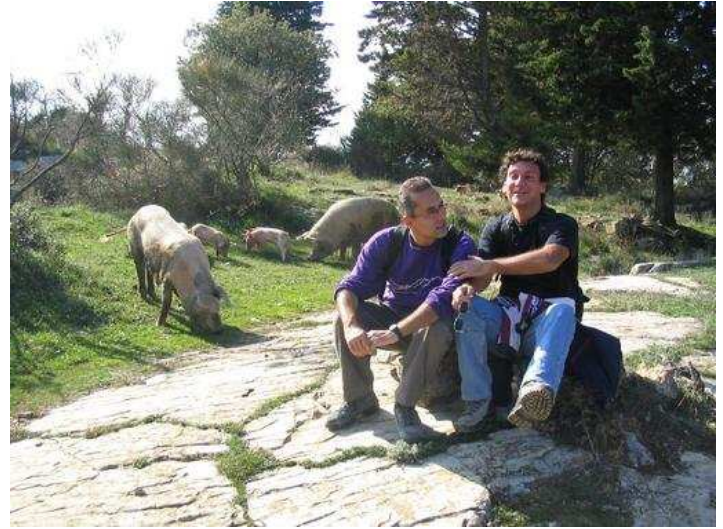


- eCR and iCR for any level of correlations, same mechanisms as in the FHN;
- no evidence of DCR
- why ? Maybe the chosen parameters  $\nu_0$  and  $\Delta W_0$  are not the right ones



# Credits

- **Stefano Luccioli** - Msc in Physics (2004-2005)
- Dynamics of realistic single neuronal models



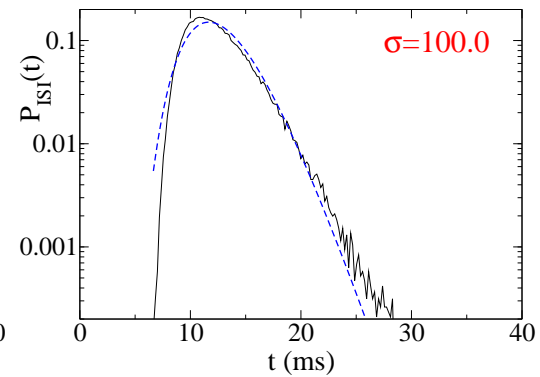
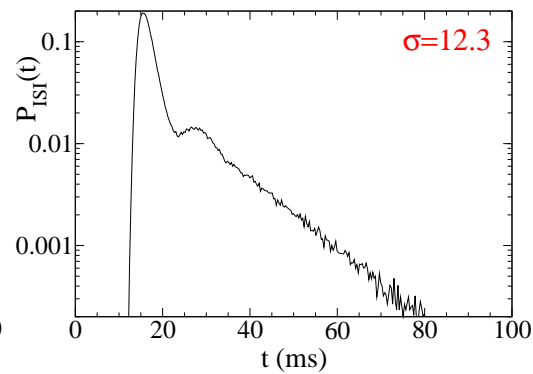
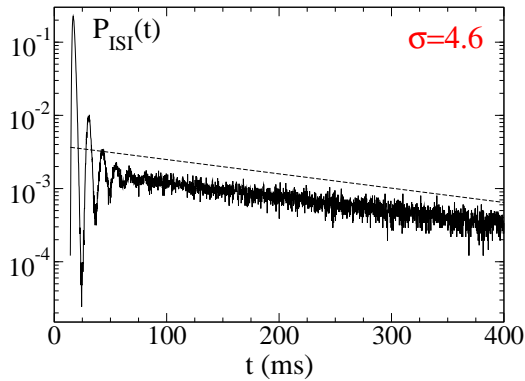
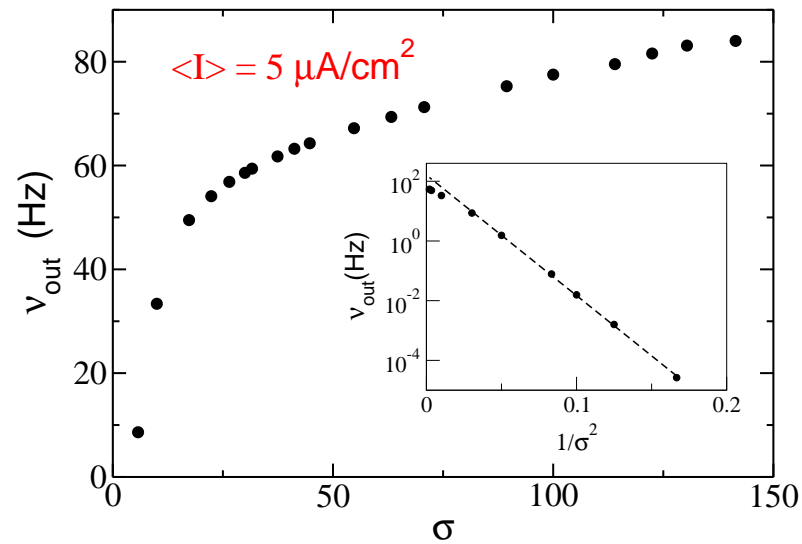
- **Thomas Kreuz** - Marie Curie Fellow (2005-2006)
- Dynamical Entropies in Assemblies of Neurons



<http://www.fi.isc.cnr.it/users/alessandro.torcini/neurores.html>

# Response of the silent neuron

The HH neuron is in the silent state, i.e. the average input current  $\bar{I}$  is smaller than  $I_{SN}$ .



# Response of the silent neuron

## Firing activated by noise

Two mechanisms compete:

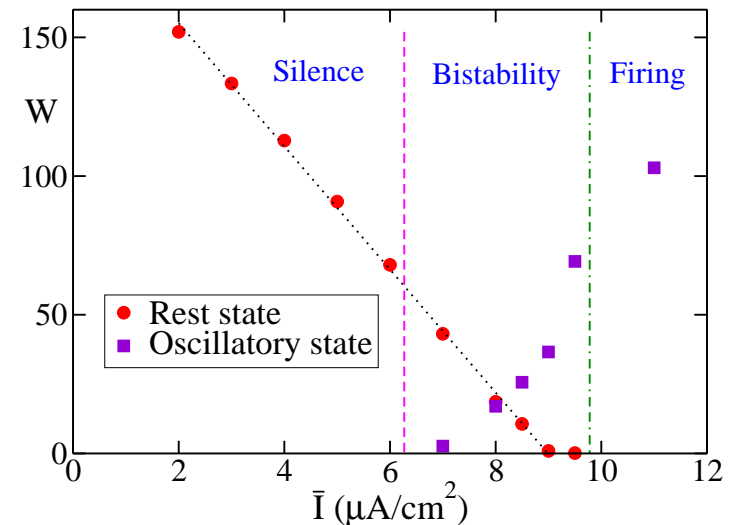
- the HH dynamics tends to relax towards the rest state;
- noise fluctuations lead the system towards an excitation threshold.

The dynamics of  $V(t)$  resembles the overdamped dynamics of a particle in a potential well under the influence of thermal fluctuations, and the firing times can be expressed in terms of the Kramers expression (for sufficiently small noise)

$$t_a \propto e^{W_S/\sigma^2}$$

the time distribution is Poissonian ( $CV = 1$ ).

- for  $\sigma < \sqrt{W_S}$  → Activation Process
- for  $\sigma > \sqrt{W_S}$  → Diffusive Dynamics



# Response of the silent neuron

## High noise limit

The effect of noise fluctuations on the neuron dynamics is twofold:

- a constant current  $\bar{I}$  driving the system;
- a stochastic term with zero average.

The dynamics of  $V(t)$  can therefore be described in terms of a Langevin process with a drift and the distribution of the first passage times is given by the inverse Gaussian distribution:

$$f(t) = \frac{\alpha}{\sqrt{2\pi\beta t^3}} e^{-\frac{(t-\alpha)^2}{2\beta t}}$$

In this case the coefficient of variation should be given by

$$CV \propto \frac{\sigma}{(\bar{I} + I_0)\sqrt{\langle ISI \rangle}}$$

