

The role of Noise, Disorder and Heterogeneity in macroscopic activity

Jonathan Touboul

Mathematical Neuroscience Team, Collège de France &
Inria, Mycenae Team

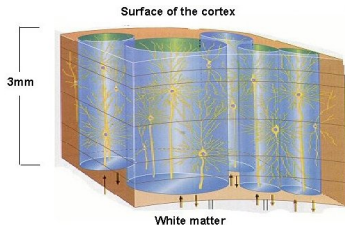
Between Theory and Applications: Mathematics in Action
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Brain & Neurons

Organization of the Brain

Global facts

- ▶ Highly complex system
- ▶ Neurons form spatially extended structures
- ▶ Transversally made of different layers,
- ▶ Sometimes organized in strongly connected columns,
- ▶ themselves spatially organized and interconnected,



<http://psych.unn.ac.uk/users/nick/>

Organization of the Brain

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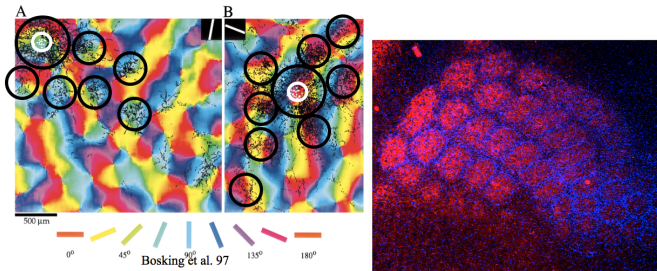
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Bosking et al 1997

Neural tissue is highly heterogeneous

Heterogeneities

Realistic networks display highly heterogeneous properties:

- ▶ **quenched heterogeneities in the interconnections:** static disorder related to: : the precise number of receptors and the extremely slow plasticity mechanisms
- ▶ **stochastic synaptic transmission:** efficiencies stochastically vary due to: : thermal noise, channel noise and the intrinsically probabilistic mechanisms of release and binding of neurotransmitter.
- ▶ **heterogeneous non-recurrent topologies**

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- ▶ **heterogeneous non-recurrent topologies**

How can we function?

At the microscopic scale:

- ▶ The brain is a highly **complex system**
- ▶ Each neuron has a **stochastic activity**
- ▶ and **randomly** affects postsynaptic neurons neurons

At the macroscopic scale, the brain produces **highly reproducible, appropriate and quick responses to stimuli.**

Question

What is the miracle of collectivity?

Synchronization

Neurons tend to **activate synchronously**. Global oscillations

- ▶ Serve important functions (G. Buzaki, W. Singer)
- ▶ Impairments yield pathological effects (e.g. epileptic seizures)
- ▶ These have been related to abnormal network heterogeneity (Aradi - Soltesz 2002, J. Physiol.)

Journal of Physiology (2002), 538.1, pp. 227–251
© The Physiological Society 2002

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www.jphysiol.org

Modulation of network behaviour by changes in variance in interneuronal properties

I. Aradi and I. Soltesz

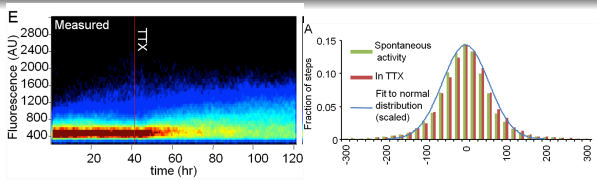
Department of Anatomy and Neurobiology, University of California, Irvine, CA 92697, USA

Three Phenomena of interest

Synchronization

Neurons tend to **activate synchronously**. Global oscillations

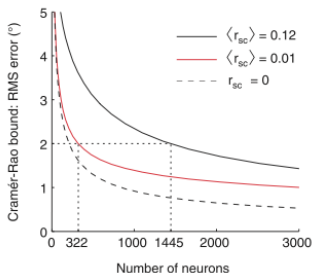
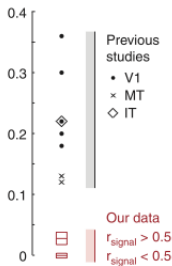
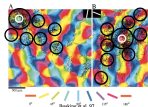
- ▶ Serve important functions (G. Buzaki, W. Singer)
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Three Phenomena of interest

Decorrelation

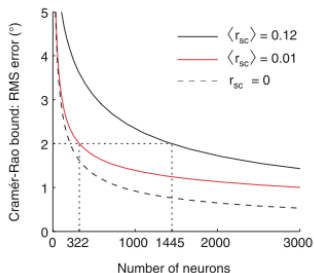
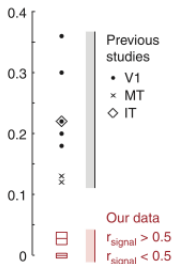
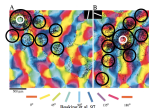
- ▶ Strongly connected neurons sharing a large amount of input show a **low correlation level**
- ▶ which **strongly improves coding efficiency**



Three Phenomena of interest

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The model

Setting of the problem:

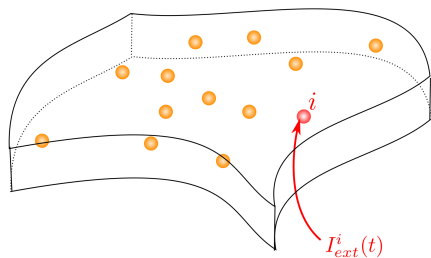
Each neuron has

- ▶ A spatial location $r \in \Gamma \subset \mathbb{R}^d$
- ▶ Its voltage has a stochastic dynamics (**external noise**)

$$dV_t = f(r, t, V_t) dt + g(r, t, V_t) dW_t$$

- ▶ is driven by external currents and its interactions with other neurons

Coupling between neurons and plasticity

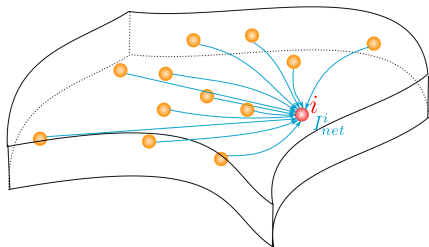


Neuron i receives at time t the input:

$$I_e^i(t) = I_{ext}^i(t) + I_{net}^i(t)$$

- ▶ $I_{ext}^i(t)$ are extra-network input
- ▶ $I_{net}^i(t)$ intra-network input

Coupling between neurons and plasticity

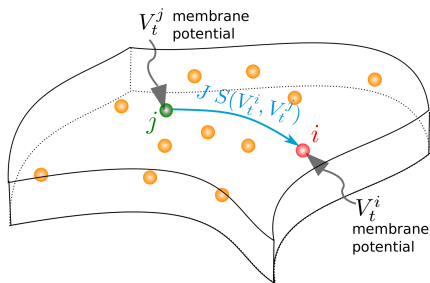


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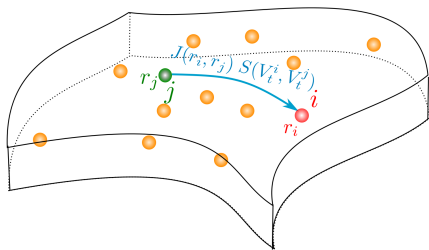
Coupling between neurons and plasticity



Neuron i receives at time t the input:

$$I_e^i(t) = I_{\text{ext}}^i(t) + \sum_{j=1}^N J S(V_t^i, V_t^j)$$

Coupling between neurons and plasticity



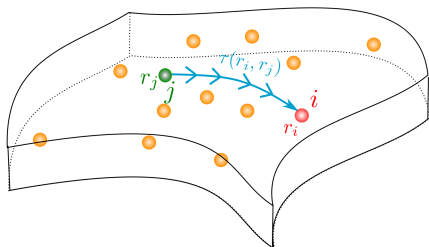
Neuron i receives at time t the input:

$$I_e^i(t) = I_{ext}^i(t) + \sum_{j=1}^N J_{ij} S(V_t^i, V_t^j)$$

To model heterogeneities, weights are considered equal to:

- ▶ Stochastic synaptic noise: J_{ij} are independent stochastic processes, e.g.: $J(r_i, r_j) + \sigma(r_i, r_j)\xi_t$
- ▶ Quenched heterogeneity: J_{ij} are independent random variables $\sim \mathcal{N}(J(r_i, r_j), \sigma(r_i, r_j))$

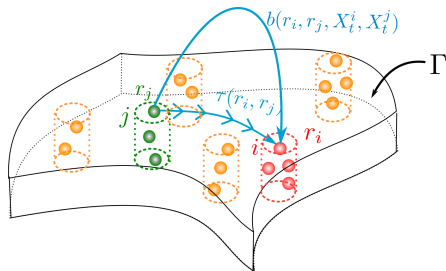
Coupling between neurons and plasticity



Neuron i receives at time t the input:

$$I_e^i(t) = I_{\text{ext}}^i(t) + \sum_{j=1}^N J_{ij} S(V_t^i, V_{t-\tau(r_i, r_j)}^j)$$

Mesoscopic, spatially extended scale



The model:

- ▶ $P(N)$ columns at positions $r_\alpha \in \Gamma$ ($\Omega', \mathcal{F}', \mathbb{P}'$) r.v. iid $\sim \lambda(\cdot) / \text{lambda}(\Gamma)$
- ▶ N_γ neurons in each population
- ▶ delays
- ▶ Noisy input driven by $(\Omega, \mathcal{F}, \mathbb{P})$ Brownian motions.

The neuronal network equations:

Finite network equations: neuron i in population α at r_α

$$\left\{ \begin{aligned} dV_t^i &= \left(f(r_\alpha, t, V_t^i) + I(r_\alpha, t) \right) dt + g(r_\alpha, V_t^i, t) dW_t^i \\ &+ \frac{1}{P(N)} \sum_{\beta=1}^P \sum_{j=1}^{N_\beta} \frac{J(r_\alpha, r_\beta)}{N_\beta} b(V_t^i, V_{t-\tau(r_\alpha, r_\beta)}^j) dt \\ &+ \frac{1}{P} \sum_{\beta=1}^{P(N)} \sum_{j=1}^{N_\beta} \frac{\sigma(r_\alpha, r_\beta)}{N_\beta} \tilde{b}(V_t^i, V_{t-\tau(r_\alpha, r_\beta)}^j) dB_t^{i\beta} \end{aligned} \right.$$

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How to analyze collective macroscopic behaviors, and their relationship with noise levels?

Three Main Topics:

- ▶ Noise induced collective oscillations
- ▶ Noise-induced pattern formation and spatially extended limits
- ▶ Heterogeneous networks

Collective Dynamics: The propagation of chaos and the Mean-Field Equations

The simplest case:

The network is composed of P populations, homogeneous recurrent connectivities and no delay:

$$dV_t^i = \left(f_\alpha(V_t^i) + I_\alpha(t) \right) dt + \lambda_\alpha dW_t^i \\ + \frac{1}{P} \sum_{\beta=1}^P \sum_{j=1}^{N_\beta} \frac{J(r_\alpha, r_\beta)}{N_\beta} b(V_t^i, V_t^j) dt \quad (1)$$

Theorem

Under relatively weak assumptions on the parameters, we can show that in the limit $N \rightarrow \infty$, all neurons are independent and have the same probability distribution solution solution of a mean-field equation. The convergence is in $O(1/\sqrt{N})$.

Proof : coupling method, close to usual proofs of propagation of chaos, now extended to the infinite-dimensional space $\mathcal{C}([-\tau, 0], E)$.

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The simplest case:

The network is composed of P populations, homogeneous recurrent connectivities and no delay:

$$d\bar{V}_t^\alpha = \left(f_\alpha(\bar{V}_t^\alpha) + I_\alpha(t) \right) dt + \lambda_\alpha dW_t^i \\ + \frac{1}{P} \sum_{\beta=1}^P J(r_\alpha, r_\beta) \mathbb{E}_Z[b(\bar{V}_t^\alpha, \bar{Z}_t^\beta)] dt \quad (1)$$

Theorem

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The stochastic limit theorem: a simple principle

The coupling method (Dobrushin 70, Sznitman 89):

Simplified Model:

$$V_t^i = V_0^i + \int_0^t \frac{1}{N} \sum_j S(V_s^j) ds + \sigma W_t^i$$

converges almost surely towards

$$\bar{V}_t^i = V_0^i + \int_0^t \mathbb{E}[S(\bar{V}_s^i)] ds + \sigma W_t^i.$$

Take the difference:

$$V_t^i - \bar{V}_t^i = \int_0^t \frac{1}{N} \sum_j S(V_s^j) - S(\bar{V}_s^j) ds + \int_0^t \frac{1}{N} \sum S(\bar{V}_s^j) - \mathbb{E}[S(\bar{V}_s)] ds$$

and using independence of \bar{V}^j :

$$\mathbb{E}\left[\frac{1}{N} \sum S(\bar{V}_s^j) - \mathbb{E}[S(\bar{V}_s)]\right] \leq \mathbb{E}\left[\left|\frac{1}{N} \sum S(\bar{V}_s^j) - \mathbb{E}[S(\bar{V}_s)]\right|^2\right]^{1/2} \leq \frac{K}{\sqrt{N}}$$

yielding $\mathbb{E}[\sup_{0 \leq t \leq T} |V_t^i - \bar{V}_t^i|] \leq \frac{K'}{\sqrt{N}}$

The basic result

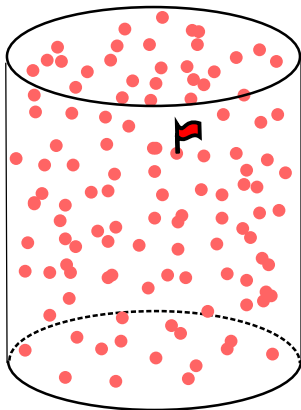
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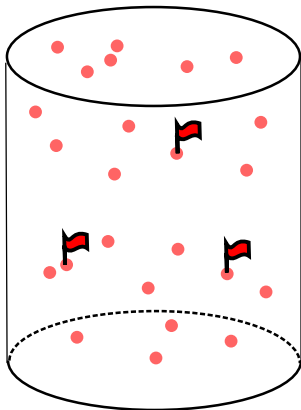
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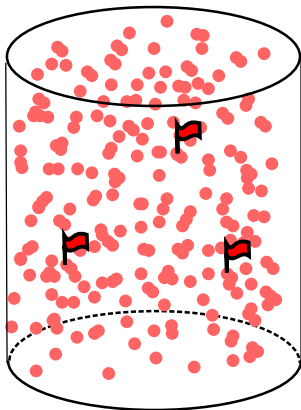
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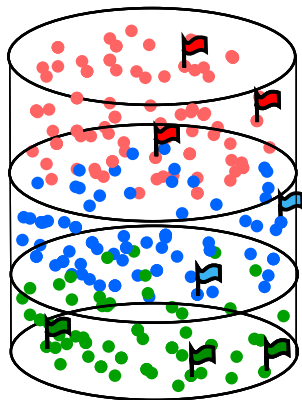
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The basic result



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$$f(X) = -X, \quad b(x, y) = S(y).$$

$$dV_t^i = \left(-V_t^i + I^\alpha(t) + \sum_{\beta=1}^P \frac{J(r_\alpha, r_\beta)}{N_\beta} \sum_{j=1}^{N_\beta} S(V_t^j) \right) dt + \lambda_\alpha dW_t^i$$

converges, when all $N_\alpha \rightarrow \infty$, towards:

Firing-rate networks

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converges, when all $N_\alpha \rightarrow \infty$, towards:

$$dV_t^\alpha = \left(-\frac{1}{\tau_\alpha} V_t^\alpha + \sum_{\beta=1}^P J_{\alpha\beta} \mathbb{E}[S(V_t^\beta)] \right) dt + \lambda_\alpha dW_t^\alpha$$

- ▶ We have a **uniform** propagation of chaos property towards the unique solution of the MFE
- ▶ The unique solution of the MFE is a Gaussian process
- ▶ The mean and standard deviation of the solution satisfy a set of coupled ordinary differential equations

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Exact Reduction to ODEs

The mean and standard deviation of the Gaussian solution satisfy the set of ordinary differential equations:

$$\begin{cases} \dot{\mu}_\alpha(t) = -\frac{1}{\tau_\alpha} \mu_\alpha(t) + \sum_{\beta=1}^P J_{\alpha\beta} f(\mu_\beta, v_\beta) + I_\alpha(t) \\ \dot{v}_\alpha = -\frac{2}{\tau_\alpha} v_\alpha + \lambda_\alpha^2(t) \end{cases} \quad (2)$$

where $f(\mu, v) = \mathbb{E}(S(G))$ where G is a Gaussian process with mean μ and standard deviation v . For instance, if $S_\alpha(x) = \text{erf}(g_\alpha x + \gamma_\alpha)$, we have:

$$f_\alpha(\mu, v) = \text{erf} \left(\frac{g_\alpha \mu + \gamma_\alpha}{\sqrt{1 + g_\alpha^2 v}} \right).$$

Noise-induced phenomena

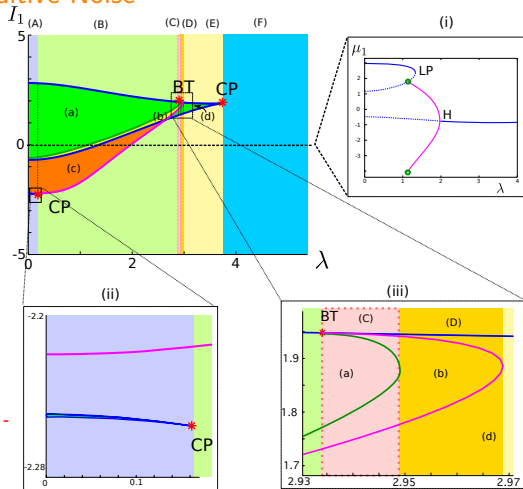
The stochastic dynamics of the cells in the macroscopic limit is governed by ODEs where noise appears as a parameter! Bifurcation theory as a function of λ_α allows to uncover noise-induced transitions!

Noise-induced synchronization

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Role of the additive Noise

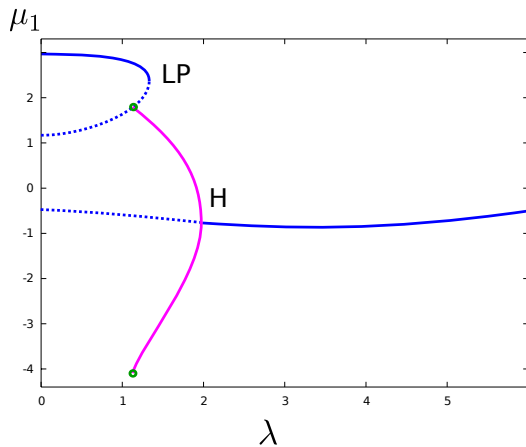


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Generation of oscillations



Network Dynamics

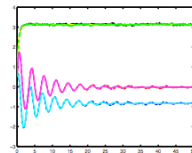
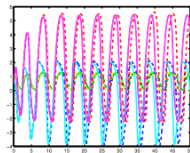
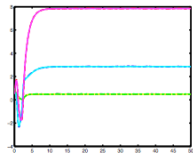
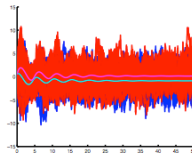
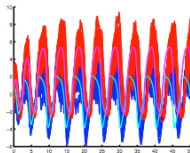
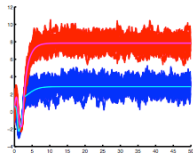
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Towards a Dynamical Systems analysis of MFE?

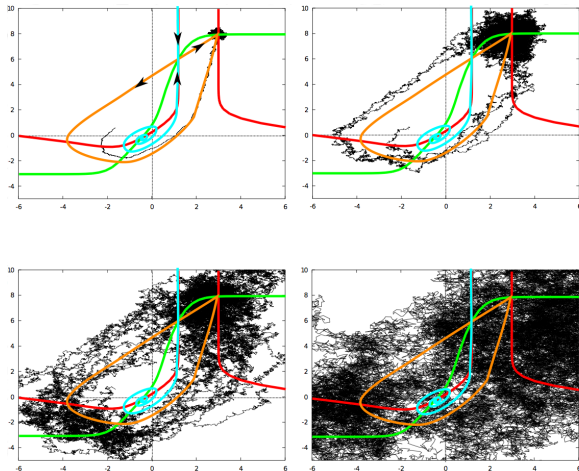
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- ▶ Neurons act as a statistical sampler: each neuron provide an independent realization of the same process
- ▶ The dynamics is reduced to a small set of equations, but with a more complicated dynamics
- ▶ Accounts for our biological phenomena of interest: reliability, decorrelation
- ▶ Noise induces oscillations in finite-populations systems!

But the brain is more complex

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- ▶ In macroscopic limits (finite populations networks), heterogeneities need to be taken into account in the connectivity map and delays
- ▶ Can we obtain mesoscopic limits at intermediate scales resolving spatial finer structures of the brain?

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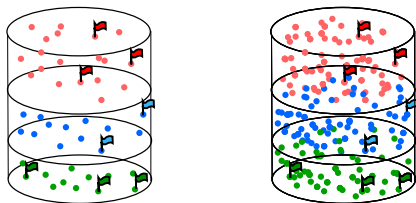
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Mesoscopic Models

How about spatially extended systems?



- ▶ Any approximation of a continuous neural field has the property of propagation of chaos and convergence towards an equation of McKean-Vlasov type.
- ▶ However, noise is independent population per population
...

Continuous Neural Field

The possible continuous neural field equation will involve a singular Brownian motion. The solutions will not be measurable with respect to $(\Gamma, \mathcal{B}(\Gamma))$. Do the same result hold in a continuum limit?

Infinite number of populations:

Neuron i in population α at r_α

$$\begin{cases} dV_t^i = \left(f(r_\alpha, t, V_t^i) + I(r_\alpha, t) \right) dt + g(r_\alpha, V_t^i, t) dW_t(r_\alpha) \\ + \frac{1}{P(N)} \sum_{\beta=1}^{P(N)} \sum_{j=1}^{N_\beta} \frac{J(r_\alpha, r_\beta)}{N_\beta} b(V_t^i, V_{t-\tau(r_\alpha, r_\beta)}^j) dt \end{cases}$$

Theorem

Under the assumption that:

$$\varepsilon(N) := \frac{1}{P(N)} \sum_{\gamma=1}^{P(N)} \frac{1}{N_\gamma} \rightarrow 0,$$

we have propagation of chaos, and convergence towards a non-local mean-field equation.

Infinite number of populations:

Neuron i in population α at r_α

$$\begin{cases} dV_t^i = \left(f(r_\alpha, t, V_t^i) + I(r_\alpha, t) \right) dt + g(r_\alpha, V_t^i, t) dW_t(r_\alpha) \\ + \frac{1}{P(N)} \sum_{\beta=1}^{P(N)} \sum_{j=1}^{N_\beta} \frac{J(r_\alpha, r_\beta)}{N_\beta} b(V_t^i, V_{t-\tau(r_\alpha, r_\beta)}^j) dt \end{cases}$$

Theorem

Under the assumption that:

$$\varepsilon(N) := \frac{1}{P(N)} \sum_{\gamma=1}^{P(N)} \frac{1}{N_\gamma} \rightarrow 0,$$

we have propagation of chaos, and convergence towards a non-local mean-field equation.

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The BM $W_t(r)$ and $B_t(r, r')$ are termed *chaotic* Brownian motions:

- ▶ $W_t(r)$ and $W_t(r')$ are independent Brownian motions for $r \neq r'$
- ▶ $B_t(r_1, r_2)$ and $B_t(r'_1, r'_2)$ are independent Brownian motions for $r_i \neq r'_i$
- ▶ These are **not** measurable functions of $(\Gamma, \mathcal{B}(\Gamma))$

The mesoscopic equation

$$\begin{cases} dV_t(r) = \left(f(r, t, V_t(r)) + I(r, t) \right) dt + g(r, V_t(r), t) dW_t(r) \\ \quad + \int_{\Gamma} J(r, r') \mathbb{E}_Z [b(V_t(r), Z_{t-\tau(r, r')}(r'))] d\lambda(r') dt \end{cases}$$

How do we make sense of this equation?

- ▶ The process is not measurable wrt $(\Gamma, \mathcal{B}(\Gamma))$
- ▶ However, the law of the process $dp(t, r, x)$ will be measurable
- ▶ This allows computing the expectation term as

$$\int_{\Gamma} J(r, r') \left\{ \int_E b(V_t(r), y) dp(t - \tau(r, r'), r', y) \right\} d\lambda(r')$$

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Theorem

For any $(\zeta_t^0(r), t \in [-\tau, 0], r \in \Gamma) \in \mathcal{M}^2(C([-\tau, 0], \mathbb{L}^2(\Omega')))$ a square-integrable process, the mean-field equation with initial condition ζ^0 has a unique strong solution on $[0, T]$ for any $T > 0$.

Second Step of the proof: The propagation of chaos and convergence to the MFE

Coupling method:

Problem: We need to couple a finite-dimensional process V_t^i solution of the N -neurons network and an infinite-dimensional chaotic process solution of the MFE.

Solution: (\tilde{W}_t^i) governing neuron i in the network and $\zeta^i \in \mathcal{M}(\mathcal{C}_\tau)$ the IC.

Coupling in the dynamics: Let $(W_t(r)) \in \mathcal{M}(C[0, T], \mathbb{L}^2(\Gamma, \mathbb{R}^{m \times d}))$ chaotic BM independent of the processes (\tilde{W}_t^j) and define the process

$$\begin{cases} (W_t^i(r)) = (W_t(r)) & r \neq r_\alpha \\ (W_t^i(r_\alpha)) = (\tilde{W}_t^i) \end{cases}$$

Second Step of the proof: The propagation of chaos and convergence to the MFE

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Solution: (\tilde{W}_t^i) governing neuron i in the network and $\zeta^i \in \mathcal{M}(\mathcal{C}_\tau)$ the IC.

Coupling of the IC: Define a process $(\tilde{\zeta}_t^0(r)) \in \mathcal{M}^2([- \tau, 0], \mathbb{L}^2(\Omega'))$ equal in law to $(\zeta_t^0(r))$ and independent of ζ_t^i , and

$$\begin{cases} \zeta_t^{i,0}(r) = \tilde{\zeta}_t^0(r) & r \neq r_\alpha \\ \zeta_t^{i,0}(r_\alpha) = \zeta_t^i \end{cases}$$

Theorem

Let $i \in \mathbb{N}$ a fixed neuron in population α . For almost all realizations of the population locations $(r_\alpha, \alpha \in \mathbb{N})$, the process $(V_t^{i,N}, t \leq T)$ solution of the network equations converges in law towards the process $(\bar{X}_t(r_\alpha), t \leq T)$ solution of the MFE with IC $(\zeta_t^0(r))$. Moreover, if f and g are globally Lipschitz-continuous we have, for any $T > 0$:

$$\max_i \mathbb{E} \left[\sup_{-\tau \leq s \leq T} |X_s^{i,N} - \bar{X}_s^i(r_\alpha)|^2 \right] = O \left(\varepsilon(N) + \frac{1}{P(N)} \right) \quad (3)$$

JT, Annals of Applied Probability, 2013

$$f(r, t, X) = 1/\theta(r)X + I(r, t), \quad g(r, t, X) = \Lambda.$$

$$dV_t^i = \left(-\frac{1}{\theta(r_\alpha)} V_t^i + I(r_\alpha, t) + \sum_{\beta=1}^{P(N)} \frac{J(r_\alpha, r_\beta)}{N_\beta} \sum_{j=1}^{N_\beta} S(V_t^j) \right) dt + \Lambda dW_t^i$$

Reduction to a system of integro-differential equations:

Theorem

The solution of the MFE is Gaussian $\mathcal{N}(\mu(r, t), v(r, t))$ with:

$$\begin{cases} \frac{\partial \mu}{\partial t}(r, t) = -\frac{1}{\theta(r)}\mu(r, t) + \int_{\Gamma} \lambda(r') dr' J(r, r') \\ \quad f(r, \mu(r', t - \tau(r, r')), v(r', t - \tau(r, r'))) + I(r, t) \\ \frac{\partial v}{\partial t}(r, t) = -\frac{2}{\theta(r)} v(r, t) + \Lambda^2(r, t) \end{cases} \quad (4)$$

The spatially homogeneous state

$$\begin{cases} \dot{\mu}_\alpha(t) = -\frac{1}{\tau_\alpha} \mu_\alpha(t) + \sum_{\beta=1}^P J_{\alpha\beta} f(\mu_\beta, v_\beta) + I_\alpha(t) \\ \dot{v}_\alpha = -\frac{2}{\tau_\alpha} v_\alpha + \sum_{\beta=1}^P \sigma_{\alpha\beta}^2 f(\mu_\beta, v_\beta)^2 + \lambda_\alpha^2(t) \end{cases} \quad (5)$$

Effect of Noise: Dynamic Turing Patterns

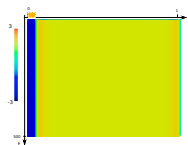
Mean Field
Dynamics

Jonathan
Touboul

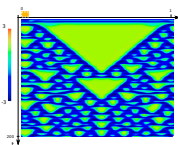
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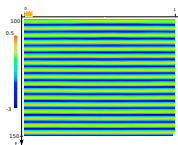
Conclusion



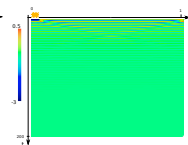
(a) $\Lambda = 1$



(b) $\Lambda = 1.6$



(c) $\Lambda = 2.3$



(d) $\Lambda = 2.5$

Macroscopic Models with spatial heterogeneities

Problem

Large-scale model may gather the activity of cells that are anatomically remote. In that case, the homogeneity of delays and recurrent connectivity no more hold:

- ▶ Cells tend to preferentially connect to anatomically close ones
- ▶ Delays are proportional to the distance

Here, we shall consider a distribution of neurons in a space $\Gamma \subset \mathbb{R}^d$ and assume that the connectivity and delays are function of the distance between neurons: e.g. for neuron i located at r_i and j at r_j :

- ▶ $J_{ij} = \begin{cases} J & \beta(r_i - r_j) \\ 0 & 1 - \beta(r_i - r_j) \end{cases}$
- ▶ $\tau_{ij} = \tau_s + \frac{|r_i - r_j|}{c}$

Question

Does the heterogeneity play a role in the qualitative dynamics?
To answer this question, we prove the following result for randomly connected networks with random delays

Theorem

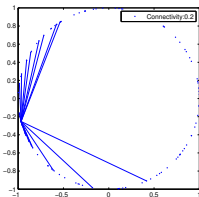
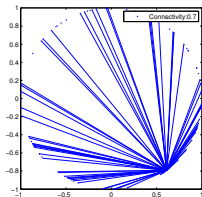
Assuming $(J_{ij}, \tau_{ij})_j$ iid with law $\Lambda_{\alpha\beta}$, we have **quenched** (for a.a. realization of the τ_{ij}) propagation of chaos and convergence towards a distributed delayed McKean-Vlasov equation. The limit equation involves the effective interaction term:

$$\sum_{\gamma=1}^P \int_{\mathbb{R}} \int_{-\infty}^0 j \mathbb{E}[b(X_{t-s}^{\beta})] d\Lambda(j, s)$$

Networks in a box

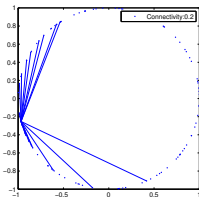
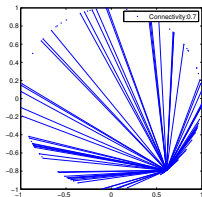
We now consider the following simple example:

- ▶ Assume that neurons are uniformly distributed on \mathbb{S}_a the periodic interval $[0, a]$
- ▶ The distribution of the distance can be computed in closed form and depends on a
- ▶ the law of $\tau_{ij} = |r_j - r_i|/c + \tau_s$ is known in closed form
- ▶ Small-world type of connectivity: connection with probability $\beta(r) = e^{-r/r_0}$



We now consider the following simple example:

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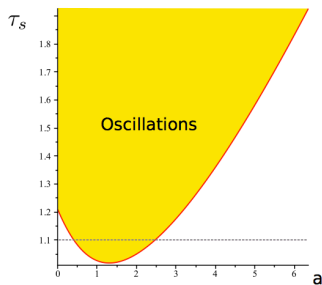
- ▶ Firing-rate model (hence, Gaussian solutions etc. . .)
- ▶ Assuming $S(0) = 0, I = 0, \mu = 0$ is a solution, whose stability is governed by the real part of the characteristic roots ξ

$$\xi = -\frac{1}{\theta} + \frac{Jg}{\sqrt{2\pi(1 + g^2\lambda^2/2)}} \int_{-\tau}^0 e^{\xi s} d\eta(s).$$

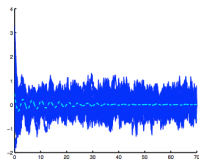
- ▶ Hopf bifurcations when $\exists \xi = i\omega$, yielding for $\Omega = \omega$ a the parametric Hopf bifurcation curve:

$$\begin{cases} a^2 = \frac{\Omega^2}{-\frac{1}{\theta^2} + |Z(\Omega)|^2} \\ \tau_s = \left(-\frac{\pi}{2} + \text{Arg}(Z(\Omega))\right) - \tan\left(\frac{\Omega\theta}{a}\right) + 2k\pi \frac{a}{\Omega}. \end{cases}$$

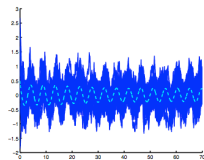
Size-induced transitions



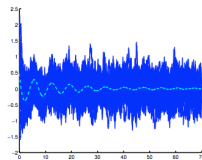
(e) Bifurcation diagram



(f) $a = 0.1$



(g) $a = 1.5$



(h) $a = 3.5$

Conclusion

Conclusion

- ▶ Noise is not only perturbing the solution, it induces qualitative changes in the dynamics
- ▶ Similar phenomena occur in disordered networks.

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- ▶ Similar phenomena occur in disordered networks.

Increasing disorder effects: Topological and Dynamical Complexity at the Edge of Chaos

Chaos in Random Neural Networks

H. Sompolinsky^(a) and A. Crisanti

*AT&T Bell Laboratories, Murray Hill, New Jersey 07974, and
Racah Institute of Physics, The Hebrew University, 91904 Jerusalem, Israel^(b)*

and

H. J. Sommers^(a)

Fachbereich Physik, Universität-Gesamthochschule Essen, D-4300 Essen, Federal Republic of Germany

(Received 30 March 1988)

A continuous-time dynamic model of a network of N nonlinear elements interacting via random asymmetric couplings is studied. A self-consistent mean-field theory, exact in the $N \rightarrow \infty$ limit, predicts a transition from a stationary phase to a chaotic phase occurring at a critical value of the gain parameter. The autocorrelations of the chaotic flow as well as the maximal Lyapunov exponent are calculated.

PACS numbers: 05.45.+b, 05.20.-y, 47.20.Tg, 87.10.+e

Theoretical investigations of the onset and the nature of chaotic flows in deterministic dynamical systems have focused, in recent years, mainly on systems with few degrees of freedom.¹ Quite often chaos is achieved in these systems by the variation of a parameter through a sequence of bifurcation points, which represent increasing complexity of the motion. It is still an open question whether these scenarios are realized in large systems which cannot be described by a small number of collective modes. In this Letter we study the nature of chaotic

linearity of the neural response. The dynamics of the network is given by N coupled first-order differential equations ("circuit" equations)^{3,4}

$$\dot{h}_i = -h_i + \sum_{j=1}^N J_{ij} S_j = -h_i + \sum_{j=1}^N J_{ij} \phi(h_j). \quad (2)$$

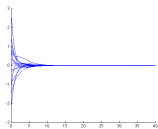
Here J_{ij} is the synaptic efficacy which couples the output of the (presynaptic) j th neuron to the input of the (postsynaptic) i th neuron, and $J_{ii} = 0$. In electrical terms Eqs. (2) are Kirchhoff equations in which the left-hand side

Sompolinsky-Crisanti-Sommers

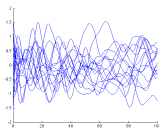
The model: 1 population, Centered sigmoids, centered coefficients $J_{ij} \sim \mathcal{N}(0, \sigma^2/N)$, no input and no noise:

$$\dot{x}_t^i = -x_t^i + \sum_j J_{ij} S(x_t^j)$$

- Dynamical mean-field theory: $\dot{x}_t = -x_t + U_t^x$ with U_t^x centered Gaussian process with covariance $\mathbb{E}[U_t^x U_s^x] = \sigma^2 \mathbb{E}[S(x_t) S(x_s)]$
- Phase transition at $\sigma = 1$ between a regime with unique attractive fixed point (0) and a chaotic behavior for $\sigma > 1$, characterized by a Lyapunov exponent equivalent to $(\sigma - 1)^2/2$ for σ close to 1.



(e) $\sigma = 0.7$

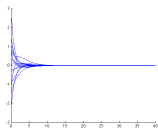


Sompolinsky-Crisanti-Sommers

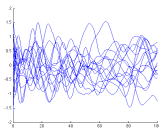
The model: 1 population, Centered sigmoids, centered coefficients $J_{ij} \sim \mathcal{N}(0, \sigma^2/N)$, no input and no noise:

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- ▶ Dynamical mean-field theory: $\dot{x}_t = -x_t + U_t^x$ with U_t^x centered Gaussian process with covariance $\mathbb{E}[U_t^x U_s^x] = \sigma^2 \mathbb{E}[S(x_t) S(x_s)]$
- ▶ **Phase transition** at $\sigma = 1$ between a regime with unique attractive fixed point (0) and a chaotic behavior for $\sigma > 1$, characterized by a Lyapunov exponent equivalent to $(\sigma - 1)^2/2$ for σ close to 1.



(g) $\sigma = 0.7$



(h) $\sigma = 1.3$

Quenched Synaptic Heterogeneity

$$dV_t^i = \left(f(V_t^i) + \sum_{j=1}^N J_{ij} S(V_{t-\tau_{\alpha\beta}}^j) + I_e(t) \right) dt + \lambda dW_t^i$$

- ▶ J_{ij} are random, Gaussian, independent, with statistics only depending on the pre- and postsynaptic **populations**

$$J_{ij} \sim \mathcal{N} \left(\frac{\bar{J}_{\alpha\beta}}{N_\beta}, \frac{\sigma_{\alpha\beta}}{\sqrt{N_\beta}} \right).$$

- ▶ $I_e(t)$ are deterministic inputs only depending on the population of the neuron
- ▶ λ is the variance of the Brownian inputs.

The Mean-Field Equation

We can show that the empirical measure

$$\hat{\mu}_n = \sum_{j=1}^N \delta_{V_j}$$

satisfies a large deviation principle and converges towards the solution of the *Mean-Field Equation*:

$$dV_t = \left(f(V_t) + U^V(t) + I_e(t) \right) dt + \lambda dW_t$$

- ▶ $V \in \mathbb{R}^P$ is a process having the law of any vector $(V_{i_1}, \dots, V_{i_P})$ for i_k neuron of population k .
- ▶ $U^V(t)$ is the effective interaction process, a Gaussian process of parameters

$$\left\{ \begin{array}{l} \mathbb{E} [U_\alpha^V(t)] = \sum_{\beta} \bar{J}_{\alpha\beta} \mathbb{E}[S(V_{t-\tau_{\alpha\beta}}^\beta)]; \\ \text{Cov}(U_\alpha^V(t), U_\alpha^V(s)) = \sum_{\beta} \sigma_{\alpha\beta} \Delta_{\alpha\beta}^V(t, s) \text{ where} \\ \Delta_{\alpha\beta}^V(t, s) = \mathbb{E} [S(V_\beta(t - \tau_{\alpha\beta})) S(V_\beta(s - \tau_{\alpha\beta}))]; \end{array} \right.$$

Firing rate equations

In the case of firing rate neurons

- ▶ solutions are **Gaussian**
- ▶ The dynamics of the moments is **not** a dynamical system:

$$\begin{cases} \dot{\mu}_\alpha(t) &= -\frac{1}{\tau_\alpha} \mu_\alpha(t) + \sum_{\beta=1}^P J_{\alpha\beta} f_\beta(\mu_\beta, v_\beta) + I_\alpha(t) \\ C_\alpha(t, s) &= e^{-(t+s)/\tau_\alpha} \left[e^{2t_0/\tau_\alpha} C_\alpha(t_0, t_0) + \right. \\ &\quad \left. \sigma^2 \sum_{\beta=1}^P \int_{t_0}^t \int_{t_0}^s e^{(u+v)/\tau_\alpha} \mathbb{E} \left[S(V_u^\beta) S(V_v^\beta) \right] dudv \right] \end{cases}$$

However

- ▶ $\sigma \mapsto v_\alpha(t) = C_\alpha(t, t)$ is non-decreasing
- ▶ The mean equation is identical to the synaptic noise case
- ▶ Increasing σ hence yields transitions to synchronized oscillatory activity

Beyond Sompolinsky model: Excitatory and Inhibitory networks

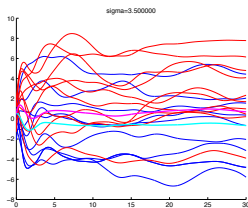
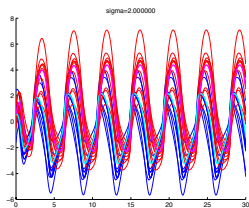
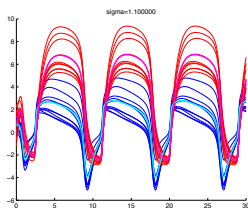
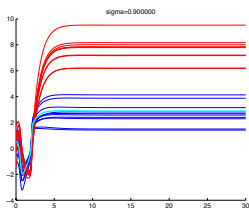
Mean Field
Dynamics

Jonathan
Touboul

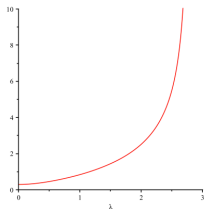
Brain & Neurons
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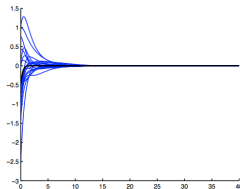
Conclusion



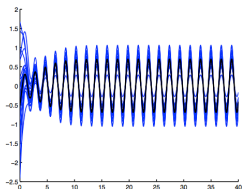
Beyond Sompolinsky model: effect of delays



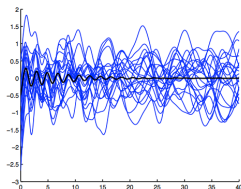
(a) Turing-Hopf bifurcation curve



(b) $\tau = 0.1, \sigma = 0.5$



(c) $\tau = 0.5, \sigma = 0.5$



(d) $\tau = 0.5, \sigma = 1$

T. Cabana, JT, J. Stat. Phys. (in revision, 2013)

What happens at the phase transition?

Let us start by characterizing **fixed points** (or singular points) of the dynamics:

$$\mathbf{x} = \mathbf{J}.S(\mathbf{x})$$

A longstanding problem in physics and spin glasses

Mean Field
Dynamics

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Brain & Neurons
Basics

Collective
Dynamics

Conclusion

[Disclaimer: Please don't ask me more detail!]

Singular (metastable points) of the potential seem to have a determinant impact on the behavior of the system at the phase transition.

Recently, mathematicians looked at the problem using random matrices theory and probability analysis provide estimates of the number of critical points

Fyodorov, Auffinger & Ben-Arous

The supercritical case $\sigma > 1$

Result

We have an exponentially large number of fixed points. The exponent (topological complexity) behaves as the Lyapunov exponent at the edge of chaos.

Proof: Inspired by Fyodorov and Ben-Arous, we use the **Kac-Rice formula**, that gives the number of a solutions of random algebraic equations.

The supercritical case $\sigma > 1$

We denote by $A_n(\sigma)$ the number of fixed points of the system.

$$\mathbb{E}[A_n(\sigma)] = \int_{\mathbb{R}^n} d\mathbf{x} \mathbb{E} \left[|\det(-\mathbf{I} + \mathbf{J} \cdot \Delta(S'(\mathbf{x})))| \times \delta_0(-\mathbf{x} + \mathbf{J} \cdot S(\mathbf{x})) \right].$$

Now what?

- (i) there is no underlying energy landscape, the system is not Hamiltonian and
- (ii) symmetry properties are relatively weak and do not enable the same drastic simplifications obtained in Fyodorov or Ben-Arous works.
- (iii) The determinant of the matrix is unknown...

The supercritical case at the edge of chaos

Near criticality $\sigma = 1 + \varepsilon$ with $0 < \varepsilon \ll 1$, we can obtain a first order estimate of the number of equilibria.

- (i) Show that equilibria remain in a small neighborhood $\mathcal{B}_\rho(\varepsilon)$ of 0 with arbitrarily high probability $1 - \xi(\varepsilon)$ [tricky...]
- (ii) This implies that:

$$\mathbb{E}[A_n(\sigma)] = \mathbb{E}[|\det(-\mathbf{I} + \mathbf{J})|] + O(\rho(\varepsilon) + \xi(\varepsilon))$$

- (iii) To evaluate this formula, we first compute the logarithm of the determinant:

$$\frac{1}{n} \log |\det(-\mathbf{I} + \mathbf{J})| =$$

- (iv) $c(\sigma) = \log(\sigma) + \frac{1}{2} \left(\frac{1}{\sigma^2} - 1 \right) \sim_{1+} (\sigma - 1)^2$

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$$\frac{1}{n} \log |\det(-\mathbf{I} + \mathbf{J})| = \frac{1}{n} \sum_{\lambda \in \text{sp}(\mathbf{J})} \log |\lambda - 1| = c(\sigma) + R(n)$$

with $c(\sigma) = \int_{\mathbb{C}} \log |z - 1| \mu_\sigma(dz)$ with $R(n) \rightarrow 0$.

- (iv) $c(\sigma) = \log(\sigma) + \frac{1}{2} \left(\frac{1}{\sigma^2} - 1 \right) \sim_{1+} (\sigma - 1)^2$

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The supercritical case at the edge of chaos

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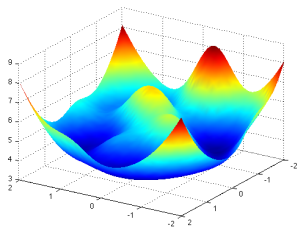
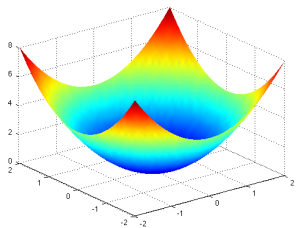
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$$\frac{1}{n} \log \mathbb{E}[A_n(\sigma)] \sim e^{n(\sigma-1)^2}$$

What happened to Sompolinsky's neurons?

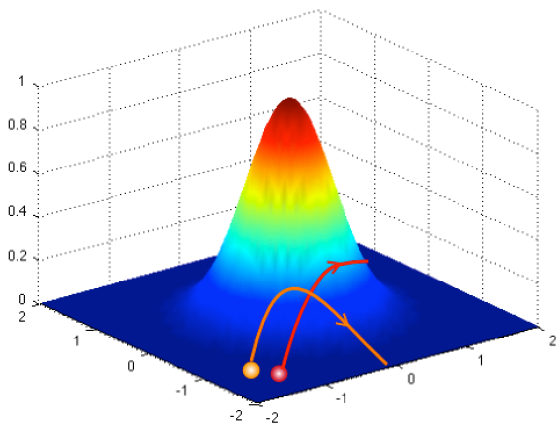


This explains the dynamical complexity...

- ▶ But how far?
- ▶ In particular, $\lambda(\sigma) \propto c(\sigma)$ at the edge of chaos...

Coincidence?

Coincidence?



If this is the case, simpler models have the same property...

Fakir's bed

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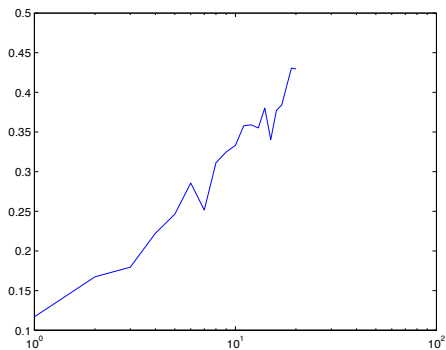
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Check out the movie.

Lyapunov vs Number of unstable singular points

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G. Wainrib, JT, Phys. Rev. Letters (2013, Editors' selection)

Conclusion

Consequences

In the finite-dimensional case, we recover our collective phenomena of interest:

- ▶ reliable response in law
- ▶ fluctuations are **uncorrelated** (they are even independent)
- ▶ Synchronization phenomena
- ▶ and transition to dynamical chaos

A limitation?

Beyond Firing-rate models:

The approach is very general, but unfortunately we were able to analyze them only in the **firing-rate mode**.

Appetizer: The Fitzhugh-Nagumo model with electrical synapses.

Excitable membranes: Stochastic Synapses

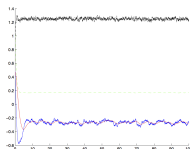
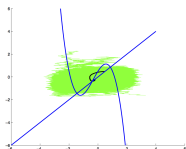
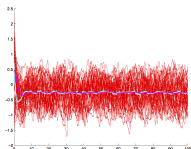
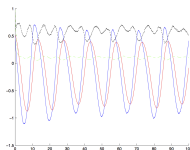
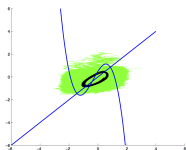
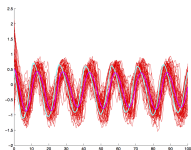
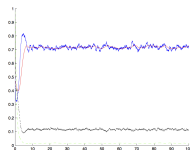
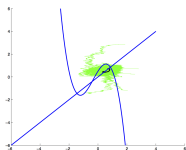
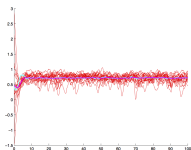
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Excitable membranes: Quenched Heterogeneity

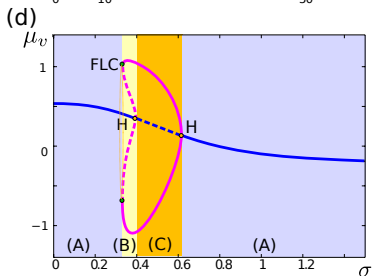
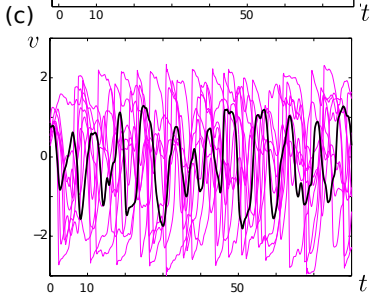
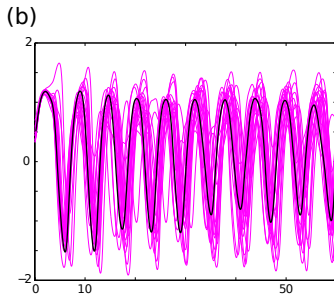
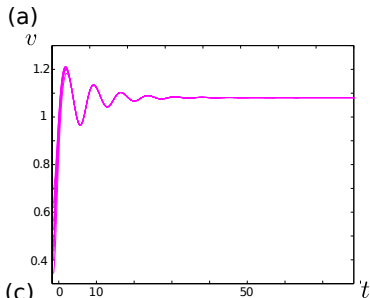
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The role of Noise, Disorder and Heterogeneity in macroscopic activity

Jonathan Touboul

Mathematical Neuroscience Team, Collège de France &
Inria, Mycenae Team

Between Theory and Applications: Mathematics in Action
- Bedlewo - May 2015