Correlations (part I)
1. Mechanistic/biophysical plane:

- What is the impact of correlations on the output rate, CV, ...
  

- How are correlations generated? Timescale?
  
  Shadlen & Newsome ’98, Brody ’99, Svirkis & Rinzel ’00, Tiensinga et al ’04, Moreno & Parga, ...

2. Systems level:

- do correlations participate in the encoding of information?
  
  Shadlen & Newsome ’98, Singer & Gray ’95, Dan et al ’98, Panzeri et al ’00, DeCharms & Merzenich ’95, Meister et al, Neimberg & Latham ‘00

- linked to behavior?
  
  Vaadia et al, ’95, Fries et al ’01, Steinmetz et al ’00, …
Type of correlations:

1.- Noise correlations:

\[ p(r_1, r_2, \ldots, r_n | s) \neq \prod_{i=1}^{n} p(r_i | s) \]

2.- Signal correlations:

\[ p(r_1, r_2, \ldots, r_n) \neq \prod_{i=1}^{n} p(r_i) \]
Quantifying spike correlations

\[ S_{i}^{r}(t) = \sum_{k} \delta(t - t_{k}^{i,r}) \]

\[ \left\langle S_{i}^{r}(t) \right\rangle_{r,t} = \nu_{i} \]

\[ C_{ij}(t, t') = C_{ij}(t' - t) = \left\langle S_{i}^{r}(t) S_{j}^{r}(t') \right\rangle_{r,t} - \nu_{i} \nu_{j} \]

\[ \text{Cov}(X, Y) = \left\langle (X - \langle X \rangle) (Y - \langle Y \rangle) \right\rangle \]
Quantifying spike correlations

\[ \langle S^r_i(t) \rangle_r = \nu_i(t) \]

\[ C_{ij}(t, t') = \langle S^r_i(t) S^r_j(t') \rangle_r - \nu_i(t)\nu_j(t') \]

\[ C_{ij}(\tau) = \langle C_{ij}(t, t+\tau) \rangle_t = \]

\[ = \langle S^r_i(t) S^r_j(t+\tau) \rangle_{r,t} - \langle \nu_i(t)\nu_j(t+\tau) \rangle_t \]
Quantifying spike correlations

\[ \rho_{XY} = \frac{\text{Cov}(X, Y)}{\sigma_X \sigma_Y} \]

\[ \rho_{ij} = \frac{\int C_{ij}(\tau) d\tau}{\sqrt{\int A_{ii}(\tau) d\tau \int A_{jj}(\tau) d\tau}} \]

\[ N_i^r(T) = \int_0^T S_i^r(t) \, dt \]

\[ \rho_{ij} = \frac{\text{Cov}(N_i(T), N_j(T))}{\sigma_{N_i(T)} \sigma_{N_j(T)}} \]
How to generate artificial correlations?

1. Thinning a “mother” train.

“mother” train (rate R)

deletion

rate = p * R
How to generate artificial input correlations?
2. Thinning a “mother” train (with different probs.)

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  deletion

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“mother” train (rate R)

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  rate = p * R
  rate = q * R
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How to generate artificial input correlations?

3. Thinning & jittering a “mother” train

“mother” train (rate R)

deletion + jitter

random delay: \( \exp(-t/\tau_c) / \tau_c \)

rate = \( p \times R \)
How to generate artificial input correlations?

4. Adding a “common” train

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summation
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“common” train (rate R)

rate = r + R
How to generate artificial input correlations?:

5. Gaussian input

\[
C_m \frac{dV(t)}{dt} = -g_L(V(t) - E_L) - g_{ampa}(t)(V(t) - E_{ampa}) - g_{gaba}(t)(V(t) - E_{gaba}) \quad \text{if } V < \theta
\]

\[
\frac{dg_{\alpha}(t)}{dt} = -\frac{g_{\alpha}(t)}{\tau_{\alpha}} + \sum_{i, l} J_i \delta(t - t_i^l - D)
\]

\[
\frac{dg(t)}{dt} = -\frac{(g(t) - \mu(t))}{\tau} + \sqrt{D(t)}\xi(t)
\]

\[\mu(t), D(t) \rightarrow 1\]
How to generate artificial input correlations?:

5. Gaussian input

White input:

\[
\frac{d g_i(t)}{dt} = -\frac{g_i(t)}{\tau} + I_i(t) = -\frac{(g_i(t) - \mu)}{\tau} + \sqrt{D}\xi_i(t) + \sqrt{\rho}\eta(t) \quad (i = 1, 2)
\]

\[
\langle I_1(t)I_2(t') \rangle - \langle I_1(t) \rangle \langle I_2(t') \rangle = \rho \delta(t' - t)
\]
Impact of correlations

A. Uncorrelated stimulus

B. Synchronous stimulus

C. Auto-correlated stimulus

D. Phase-locked periodic stimulus
Impact of correlations on the input current of a single cell:

\[ \mu = N_E \nu_E J_E - N_I \nu_I J_I \]

\[ \sigma^2 = N_E \nu_E J_E^2 \left(1 + (N_E - 1) \rho_{EE} \right) + N_I \nu_I J_I^2 \left(1 + (N_I - 1) \rho_{II} \right) - 2N_E N_I \sqrt{\nu_E \nu_I} J_E J_I \rho_{EI} \]
Impact of correlations on the output rate:

Balance state

Unbalance state

**a**

**b**

**c**

**d**

Time shift (ms)

200 ms

Input rate (spikes s⁻¹)

Output rate (spikes s⁻¹)
The development of correlations: a minimal model.

1. Morphological common inputs.
The development of correlations: a minimal model.

2. Afferent correlations
The development of correlations: a minimal model.

3. Connectivity
Development of correlations: common inputs

Shadlen & Newsome ‘98
Development of correlations: common inputs & synaptic failures

• Independent: \( R_p(1-x) + R_p x(1-p) = R_p(1-xp) = R_{\text{eff}} (1-x_{\text{eff}}) \)

• Common: \( R_p^2 x = R_{\text{eff}} x_{\text{eff}} \)

where we have defined:

• Effective rate: \( R_{\text{eff}} = R p \)

• Effective overlap: \( x_{\text{eff}} = x p \)
Development of correlations: common inputs & synaptic failures
Development of correlations: common inputs.
Experimental data.
Development of correlations: correlated inputs.
Development of correlations: correlated inputs.
Development of correlations: correlated inputs.

![Graph showing development of correlations with correlated inputs.](image-url)
Development of correlations: correlated inputs.

- \( \tau_c = 0 \)
- \( \tau_c = 4 \)
- \( \tau_c = 8 \)
Biophysical constraints of how fast neurons can synchronize their spiking activity

Rubén Moreno Bote

Nestor Parga, Jaime de la Rocha and Hide Cateau
I. Introduction.

II. Rapid responses to changes in the input variance.

III. How fast correlations can be transmitted? Biophysical constrains.

Goals:

1. To show that simple neuron models predict responses of real neurons.

2. To stress the fact that “qualitative”, non-trivial predictions can be made using mathematical models without solving them.
I. Introduction. Temporal changes in correlation

Vaadia et al., 1995

deCharms and Merzenich, 1996
I. Temporal modulations of the input.

\[ I(t) = J_E \sum_{i=1}^{N_E} \sum_{k} \delta(t - t_i^k) - J_I \sum_{j=1}^{N_I} \sum_{l} \delta(t - t_j^l) \]

\[ \mu(t) = N_E J_E \nu_E(t) - N_I J_I \nu_I(t) \]

\[ \sigma^2(t) = N_E J_E^2 F_E(t) \nu_E(t) + (\text{Inh. term}) + \]
\[ + f_{EE} N_E f_{EE} (N_E - 1) F_E(t) \rho_E(t) \nu_E(t) \]
\[ + (\text{Inh. term}) + \ldots \]

Diffusion approximation:

\[ I(t) = \mu(t) + \sigma(t) \eta(t) \]

white noise process with mean zero and unit variance
I. Temporal modulations of the input.

\[ \sigma_c^2(t) = N_{E,c} J_{E,c}^2 F_{E,c}(t) \nu_E(t) + (Inh.\ term) + \\
+ f_{EE,a} N_{E,a} f_{EE,b} N_{E,b} F_{E,ab}(t) \rho_{E,ab}(t) \nu_{E,ab}(t) \\
+ (Inh.\ term) + \ldots \]
I. Problems

Problem 1: How fast a change in $\mu$ and $\sigma$ can be transmitted?

$$\frac{dV}{dt} = -\frac{V}{\tau_m} + \mu(t) + \sigma(t) \eta(t)$$

Leaky Integrate-and-Fire (LIF) neuron

Problem 2: How fast two neurons can synchronize each other?

$$\frac{dV_1}{dt} = -\frac{V_1}{\tau_m} + \mu_1(t) + \sigma_1(t) \eta_1(t) + \sigma_c(t) \eta_c(t)$$
$$\frac{dV_2}{dt} = -\frac{V_2}{\tau_m} + \mu_2(t) + \sigma_2(t) \eta_2(t) + \sigma_c(t) \eta_c(t)$$

common source of noise
II. Probability density function and the FPE

\[ \frac{dV}{dt} = - \frac{V}{\tau_m} + \mu(t) + \sigma(t) \eta(t) \]

Description of the density \( P(V,t) \) with the FPE

Firing rate:

\[ \nu = - \frac{1}{2} \sigma^2 \frac{\partial}{\partial V} P(V)\bigg|_{V=\Theta} \]
II. Non-stationary response. 
Fast responses predicted by the FPE

\[ \frac{dV}{dt} = - \frac{V}{\tau_m} + \mu(t) + \sigma(t) \eta(t) \]

1. \( \mu \uparrow \) 
   Mean input current
   Firing rate response
   time

2. \( \sigma \uparrow \) 
   Variance of the current
   Firing rate response
   time

Described by the equation

\[ \nu(t) = -\frac{1}{2} \sigma^2(t) \frac{\partial}{\partial V} P(V, t) \bigg|_{V=\Theta} \]
II. Rapid response to instantaneous changes of $\sigma$ (validity for more general inputs)

Silberberg et al, 2004

II. Stationary rate as a function of $\tau_c$

III. Correlation between a pair of neurons

Cross-correlation function $= P(t_1, t_2)$

Moreno-Bote and Parga, submitted
The join probability density of having spikes at $t_1$ and $t_2$ for IF neurons 1 and 2 receiving independent and common sources of white noise is:

$$C(t_1, t_2) = \frac{1}{4} \left( \sigma_1^2(t_1)+\sigma_c^2(t_1) \right) \left( \sigma_2^2(t_2)+\sigma_c^2(t_2) \right) \frac{\partial^2}{\partial V_1 \partial V_2} P(V_1, t_1, V_2, t_2)|_{V_1, V_2=\Theta}$$

Total input variances at indicated times for neurons 1 and 2.

Joint probability density of the potentials of neurons 1 and 2 at indicated times.
III. Predictions

1. Increasing any input variance produces an “instantaneous” increase of the synchronization in the firing of the two neurons.

2. If the common variance increases and the independent variances decrease in such a way that the total variance remains constant, the neurons slowly synchronize.

3. If the independent variances increase, there is a sudden increase in the synchronization, and then it reduces to a lower level.

\[ C(t_1, t_2) = \frac{1}{4} \left( \sigma_1^2(t_1) + \sigma_c^2(t_1) \right) \left( \sigma_2^2(t_2) + \sigma_c^2(t_2) \right) \frac{\partial^2}{\partial V_1 \partial V_2} P(V_1, t_1, V_2, t_2) \big|_{V_1, V_2 = \Theta} \]

... biophysical constraints that any neuron should obey!!
III. Slow synchronization when the total variances does not change.
III. Fast synchronization to an increase of common variance.
III. Fast synchronization to an increase of independent variance, and its slow reduction.