Theory of correlation transfer and correlation structure in recurrent networks

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Part I: a Pair of Neurons

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200ms



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200ms







Shadlen and Newsome, 1998

Fano factor, $F = Var(N) / \langle N \rangle \sim 1.2$



Fano factor, $F = Var(N) / \langle N \rangle \sim 1.2$

Correlated activity



monkey behavior

peaks in CCFs: temporal coincidences

This is why you should care

• variability and correlations set fundamental limits of how much information can be extracted from the neuronal responses

Zohary et al, Nature, 1994

• how the observed variability and correlations arise from the underlying neuronal dynamics is largely unknown

Ginzburg and Sompolinsky, *Phys. Review E*, 1994 Moreno-Bote and Parga, *Phys. Review Letters*, 2006 de la Rocha et al, *Nature*, 2007 Kriener et al, *N. Computation*, 2008 Kumar et al, *N. Computation*, 2008 Renart et al, *Science*, 2010 Hertz, *N. Computation*, 2010

This is why you should care

• correlations open the door to estimate functional connectivity between neurons

Aertsen et al, *J. Neurophys*, 1989 Schneidman et al, *Nature*, 2006 Pillow et al, *Nature*, 2008 Cocco et al, *PNAS*, 2009

• variability and correlations might indicate the type of neuronal computations carried out by neuronal circuits

Abeles, Book: Corticonics, 1991 Softky, *Current Opi. Neurobiology*, 1995 Shadlen and Newsome, *J. of Neurosci.*, 1998 Diesmann et al, *Nature*, 1999

- Information limits set by neuronal correlations (an example)
- Firing rate and variability in LIF neurons with fast and slow synapses (FPE formalism and solutions)
- Correlation transfer in LIF neurons with fast and slow synapses (FPE and approximate solutions)
- Review of literature & main results about correlation transfer:
 - Neurons are sensitive to input correlations (strength and correlation time; Salinas and Sejnowski, *J. of Neurosci.*, 2000; Moreno-Bote et al, *Phys. Review Letters*, 2002)
 - 2. Output correlation is lower than input correlation in spiking neurons (Moreno-Bote and Parga, *Phys. Review Letters*, 2006)
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- Open questions

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Signal/Noise limits induced by correlations



• In homogenous neuronal populations, correlations are deleterious

• Whether it is possible to decorrelate while keeping firing rate and variability constant is under investigation

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A Golden Problem: Input-Output relationship



The problem can be faced in the statistical sense: average quantities



A Golden Problem: Input-Output relationship



Firing rate for a leaky integrate & fire (LIF) neuron with instantaneous synapses

$$\frac{dV(t)}{dt} = -\frac{V(t)}{\tau_m} + I(t),$$

$$I(t) = \sum_{j=1}^{C_E} J_{E_j} s_j(t) - \sum_{k=1}^{C_I} J_{I_k} s_k(t)$$

$$v^{-1} = \tau_{\text{ref}} + \tau_m \sqrt{\pi} \int_{\frac{V_{\text{th}} - \mu_V}{\sigma_V \sqrt{2}}}^{\frac{V_{\text{th}} - \mu_V}{\sigma_V \sqrt{2}}} dx \ e^{x^2} [1 + \text{erf}(x)]$$
$$CV^2 = 2\pi v^2 \int_{\frac{V_{\text{th}} - \mu_V}{\sigma_V \sqrt{2}}}^{\frac{V_{\text{th}} - \mu_V}{\sigma_V \sqrt{2}}} dx \ e^{x^2} \int_{-\infty}^{x} dy \ e^{y^2} [1 + \text{erf}(y)]^2$$
$$\mu_V = \tau_m \mu; \quad \sigma_V^2 = \frac{1}{2} \tau_m \sigma^2$$



Figure 2: Mean firing rate ν (left), CV (middle), and product ν CV² (right) of the LIF neuron as a function of the mean and standard deviation of the depolarization. Parameters: $V_{\text{th}} = 20 \text{ mV}$, $V_{\text{res}} = 10 \text{ mV}$, $\tau_m = 10 \text{ ms}$, and $\tau_{\text{ref}} = 2 \text{ ms}$.

Rate with non-instantaneous synapses Fast neuronal dynamics



In the long synaptic time scale limit $\tau_s \geq \tau_m$ we treat $\epsilon = \sqrt{\tau_m/\tau_s}$ as a small parameter

This limit is useful in the high conductance regime (Destexhe et al.,Nat.Rev.Neurosc. 2003) or when slow filters (NMDA, GABA_B, etc) are important

firing rate
$$v = \int_{\hat{\Theta}/\epsilon}^{\infty} \frac{dz}{\sqrt{2\pi}} e^{-z^2/2} v_0(z)$$

 $v_0^{-1}(z) = \tau_m \ln\left(\frac{\hat{H} - \epsilon z}{\hat{\Theta} - \epsilon z}\right)$
 $\hat{\Theta} = \sqrt{2}(\Theta - \mu \tau_m)/\sigma \sqrt{\tau_m} \text{ and } \hat{H} = \sqrt{2}(H - \mu \tau_m)/\sigma \sqrt{\tau_m}$

Moreno-Bote and Parga, Phys Rev. Lett, 2004 Moreno-Bote and Parga, Neural Computation, 2010

Rate with non-instantaneous synapses



The only approx. is $\tau_s \ge \tau_m$

Rate with non-instantaneous synapses



here
$$\tau_s = \tau_m = 10ms$$

This is surprising because here z is not constant during an ISI of typical duration T = 100-200 ms.



Rate with non-instantaneous synapses



Why not
$$T = \int dz P(z) T(z)$$
?
It does not do a very good job ISI for fixed z

Rate with non-instantaneous synapses Fast synapses

In the short synaptic time scale limit $\tau_s \leq \tau_m$ we treat the inverse of $\epsilon = \sqrt{\tau_m/\tau_s}$ as a small parameter

This limit is useful when AMPA receptors are abundant

firing rate

1

$$\frac{1}{\nu} = \tau_m \sqrt{\pi} \int_{\frac{V_r - \mu}{\sigma} + \frac{\alpha}{2} \sqrt{\frac{\tau_s}{\tau_m}}} \Psi(s) \, ds$$
$$\Psi(s) = e^{s^2} (1 + \operatorname{erf}(s))$$
$$\alpha = \sqrt{2} \left| \zeta\left(\frac{1}{2}\right) \right| \simeq \sqrt{2} \ 1.46$$

 $c \frac{\theta - \mu}{2} + \frac{\alpha}{2} \sqrt{\frac{\tau_s}{\tau_s}}$



Brunel and Sergi, J theor Biol, 1998 Fourcaud and Brunel, Neural Comput., 2002 Moreno-Bote and Parga, Phys Rev Lett, 2004

Interpolating the fast and slow synaptic time scale limits

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- Open questions

Correlations with non-instantaneous synapses



$$\tau_m \dot{V}_1 = -V_1 + \tau_m (I_1(t) + I_c(t)),$$

$$\tau_m \dot{V}_2 = -V_2 + \tau_m (I_2(t) + I_c(t)).$$

$$\tau_s \dot{I}_i(t) = -I_i(t) + \mu_{ind} + \sigma_{ind} \eta_i(t),$$

$$\tau_s \dot{I}_c(t) = -I_c(t) + \mu_c + \sigma_c \eta_c(t),$$



$$C(t, t') \simeq \int dI_1 \, dI'_2 \, dI_c \, dI'_c \, P(I_c, t; I'_c, t') \, P(I_1) \, P(I'_2)$$

 $\times v_1(I_1 + I_c) \, v_2(I'_2 + I'_c).$

Moreno-Bote and Parga, Phys Rew Lett, 2006 Moreno-Bote and Parga, Neural Comput, 2010

Correlations with non-instantaneous synapses



d. The linear approximation of the cross-correlation function for two LIF neurons given in **c** is

$$C(\Delta) = \tilde{\nu}(\mu_c)^2 + \tilde{\nu}'(\mu_c)^2 C_{I,c}(\Delta), \qquad (2.62)$$

where $\tilde{\nu}(I_c) = \int dI P(I)\nu(I + I_c)$ with $\nu^{-1}(I) = \tau_m \ln(\frac{\tau_m I - H}{\tau_m I - \Theta})$, $\tilde{\nu}'(\mu_c)$ is the derivative of $\tilde{\nu}(I_c)$ evaluated at μ_c , and

$$C_{I,c}(\Delta) = \frac{\sigma_c^2}{2\tau_s} e^{-|\Delta|/\tau_s}.$$
(2.63)



Moreno-Bote and Parga, Phys Rew Lett, 2006 Moreno-Bote and Parga, Neural Comput, 2010

Correlations with instantaneous synapses



$$\tau_{\rm m} \frac{\mathrm{d}V_i}{\mathrm{d}t} = -V_i + \mu + \sigma \sqrt{\tau_{\rm m}} \left(\sqrt{1 - c} \xi_i(t) + \sqrt{c} \xi_c(t) \right)$$
$$I_i = \mu_i + \sigma_i \left(\sqrt{1 - c} \xi_i(t) + \sqrt{c} \xi_c(t) \right)$$

$$\rho \approx S(\mu, \sigma) c = \frac{\sigma^2 \left(\frac{\mathrm{d}v}{\mathrm{d}\mu}\right)^2}{\mathrm{CV}^2 v} c$$

de la Rocha et al, Nature, 2007

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- Open questions

I. Correlated activity in primary auditory cortex



deCharms and Merzenich, 1996

I. Model. The total presynaptic current



$$\dot{V}(t) = -\frac{V(t)}{\tau_m} + I(t)$$

Leaky Integrate-and-Fire neuron

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

I. Model. Temporal Correlations



Auto-correlations:

$$C_{p}(t,t') \equiv \left\langle \left(\sum_{k} \delta(t-t_{i}^{k}) - \nu_{p}\right) \left(\sum_{k'} \delta(t'-t_{i}^{k'}) - \nu_{p}\right) \right\rangle$$

$$\mathbf{p}=\mathbf{E},\mathbf{I} = \underbrace{\nu_{p}} \delta(t-t') + \nu_{p} \underbrace{\left(\frac{F_{p}}{1} - 1\right)}_{\mathbf{rate}} e^{-\frac{\mathbf{r}-\mathbf{r}'}{\tau_{c}}} e^{-\frac{\mathbf{r}-\mathbf{r}'}{\tau_{c}}}$$

$$\mathbf{rate} \quad \mathbf{Fano factor}$$

$$Cross-correlations:$$

$$C_{pq}(t,t') \equiv \left\langle \left(\sum_{k_{p}} \delta(t-t_{i}^{k_{p}}) - \nu_{p}\right) \left(\sum_{k_{q}} \delta(t'-t_{j}^{k_{p}}) - \nu_{q}\right) \right\rangle \right\rangle$$

$$= \sqrt{\nu_{p}\nu_{q}} \underbrace{\left(\frac{\rho_{pq}\sqrt{F_{p}F_{q}}}{2\tau_{c}}\right)} e^{-\frac{|\mathbf{r}-\mathbf{r}'|}{\tau_{c}}}$$

correlation coefficient

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I. Model. Spatial Correlations



I. Results. Properties of the syn. current



$$\begin{split} C_{current}(t,t') &= \sigma_w^2 \left[\delta(t-t') + \underbrace{\alpha}_{2\tau_c} e^{-\frac{|t-t'|}{\tau_c}} \right] \\ \text{correlation magnitude} \\ \end{split}$$

$$\begin{aligned}
\sigma_w^2 &= J_E^2 N_E \nu_E + J_I^2 N_I \nu_I \\
\alpha \,\sigma_w^2 &= J_E^2 N_E \nu_E [(F_E - 1) + f_{EE} (f_{EE} N_E - 1) F_E \,\rho_{EE}] \\
&+ J_I^2 N_I \nu_I [(F_I - 1) + f_{II} (f_{II} N_I - 1) F_I \,\rho_{II}] \\
&- 2 \, J_E J_I \, f_{EI} f_{IE} N_E N_I \, \sqrt{\nu_E \nu_I} \, \sqrt{F_E \, F_I} \rho_{EI} \,.
\end{aligned}$$

I. How to generate such a current?

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

$$\mu = J_E N_E \nu_E - J_I N_I \nu_I \qquad C_{current}(t, t') = \sigma_w^2 \left[\delta(t - t') + \frac{\alpha}{2\tau_c} e^{-\frac{|t - t'|}{\tau_c}} \right]$$

Why a simple representation of the current is required?

- 1. Generating the current in the way defined above is complex.
- 2. If the representation of the current is simple enough, it can allow us to find an analytical solution in some limits.
- 3. It can be used to simulate neurons receiving correlated inputs.
- 4. It can be used to stimulate real neurons with current waves mimicking correlated inputs.

I. Results. Generating I(t) using an auxiliar OUP



The FPE associated to the equation for V and the current is

$$[L_x + \frac{L_z}{k^2} + \frac{2}{k}\frac{\partial}{\partial x}(\frac{\partial}{\partial z} - \frac{\beta z}{2})]P_\beta(x,z) = -\tau_m\delta(x - \sqrt{2}\hat{H})J_\beta(z)$$

It can be solved in the long correlation time limit

$$\nu_{out} = \nu_0 + \frac{C}{\tau_c}$$

A similar FPE is solved in the **short correlation time limit**

$$\nu_{out} = \nu_{eff} - \alpha \sqrt{\tau_c \tau_m} \nu_0^2 R(\hat{\Theta})$$
Interpolation
$$\sigma_{eff}^2 = \sigma_w^2 (1 + \alpha)$$

$$\tau_c$$

I. Results. Stationary rate as a function of τ_c



I. Results. Non-stationary response. Fast responses predicted by the FPE

The instantaneous firing rate of the neuron is exactly

$$\begin{split} \nu_{out}(t) &= -\underbrace{\sigma_w^2(t)}_{2 \sqrt{\partial V}} \frac{\partial}{\partial V} \int_{-\infty}^{\infty} dw P(V,w,t)|_{V=\Theta} \\ & \quad \text{Changing} \ \ \sigma_w^2(t) \text{ will procude an instantaneous change in the rate} \end{split}$$

When the correlation time becomes zero, it can be expressed as

$$\begin{split} \nu_{out}(t) &= -\frac{\sigma_{eff}^2(t)}{2} \frac{\partial}{\partial V} \int dw P(V, w, t)|_{V=\Theta} \\ \sigma_{eff}^2 &= \sigma_w^2 (1 + \alpha) \end{split}$$

Changing it will procude an instantaneous change in the rate

For short enough correlation times, the response has also to be very fast!

I. Results. Rapid response to instantaneous changes of α



Silberberg et al, 2004

I.... in conclusion

- 1. We have described the statistical properties of a current that considers the acitivity of many correlated neurons.
- 2. This current has been generated using an auxiliary OU process.
- 3. The associated FPE to this current and to an IF neuron has been solved in the limits of short and long correlation times.
- 4. These solutions predict the modulation of neuronal resposes to variations of the parameters defining the correlated activity.
- 5. Changing the correlation magnitude of pre-synaptic populations produces a very fast increase of the output firng rate.

I. Weak effects of correlations on firing rate?

3880 J. Neurosci., May 15, 1998, 18(10):3870-3896

Shadlen and Newsome . Variable Discharge of Cortical Neurons





Figure 9. Effect of common input on response covariance. The correlation coefficient is plotted as a function of the fraction of shared excitatory and shared inhibitory input to a pair of model neurons. Each *point* was obtained from 20 sec of simulated spike discharge using a variety of model parameters (input spike rate, number of inputs, and barrier height). In each simulation, the output spike rate was approximately the same as the average of any one input (within a factor of ± 0.25). The best fitting plane through the origin is shown. A substantial degree of shared input is required to achieve even modest correlation.

of shared excitatory and shared inhibitory connections affect the correlation coefficient. Shared excitation has a greater impact, because it can lead directly to a spike from both neurons.

I. Strong effects correlations on rate and CV

Salinas and Sejnowski • Impact of Correlated Synaptic Input

J. Neurosci., August 15, 2000, 20(16):6193-6209 6201





Figure 5. Effect of input correlations generated by common drive on the firing rate and variability of the same balanced ($\beta = 1$) model neuron used in Figure 4. For each data point, the output spike train was recorded for 30-90 sec of simulation time, and the mean rate and coefficient of variation were computed from this segment. *a*, Mean output firing rate r_{out} as a function of input rate r_E , for four conditions. The *continuous line* indicates uncorrelated inputs ($\phi_E = 0$, $\phi_I = 0$), filled circles indicate correlations between excitatory inputs only ($\phi_E = 0.1$, $\phi_I = 0.1$), and dots indicate all pairs equally correlated ($\phi_E = 0.1$, $\phi_I = 0.1$). *b*, CV_{ISI} of the output spike trains as a function of input rate, computed from the same simulations as in *a*; symbols have identical meaning. The dashed line marks a CV_{ISI} of 1, expected from a Poisson process. *c*, Mean output firing rate r_{out} as a function of correlation strength, for a fixed input rate $r_E = 400$.

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- Open questions





The correlation coefficient of the output of a pair of non-linear rate neurons receiving correlated Gaussian noise is bounded by the correlation in the input



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Output correlation increases with output firing rate

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Relationship Between Simulated Common Synaptic Input and Discharge Synchrony in Cat Spinal Motoneurons

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Influence of membrane properties on spike synchronization in neurons: theory and experiments

Gytis Svirskis^{1,2,3} and Jørn Hounsgaard³

3646 • The Journal of Neuroscience, April 5, 2006 • 26(14):3646 - 3655

Behavioral/Systems/Cognitive

Correlation-Induced Synchronization of Oscillations in Olfactory Bulb Neurons

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Higher-Order Statistics of Input Ensembles and the Response of Simple Model Neurons

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PHYSICAL REVIEW LETTERS

week ending 23 JULY 2004

Oscillatory Activity in Electrosensory Neurons Increases with the Spatial Correlation of the Stochastic Input Stimulus

Brent Doiron,1,2 Benjamin Lindner,1 André Longtin,1 Leonard Maler,2 and Joseph Bastian3

PRL 96, 058101 (2006)

PHYSICAL REVIEW LETTERS

week ending 10 FEBRUARY 2006

Relation between Single Neuron and Population Spiking Statistics and Effects on Network Activity

Hidevuki Câteau^{1,2} and Alex D. Reves¹

Dependence of Neuronal Correlations on Filter Characteristics and Marginal Spike Train Statistics

Tom Tetzlaff* et al

Neural Computation 20, 2133-2184 (2008)

Mechanisms that modulate the transfer of spiking correlations

Robert Rosenbaum¹ and Krešimir Josić²



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LETTER _____ Communicated by Anthony Burkitt

Stimulus-Dependent Correlations in Threshold-Crossing Spiking Neurons

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Neural Computation 21, 2269-2308 (2009)

PRL 104, 058102 (2010) PHYSICAL REVIEW LETTERS

week ending 5 FEBRUARY 2010

Correlations and Synchrony in Threshold Neuron Models

Tatjana Tchumatchenko,1,2 Aleksey Malyshev,3,4 Theo Geisel,1 Maxim Volgushev,3,4,5 and Fred Wolf1

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- Review of literature & main results about correlation transfer:
 - Neurons are sensitive to input correlations (strength and correlation time; Salinas and Sejnowski, *J. of Neurosci.*, 2000; Moreno-Bote et al, *Phys. Review Letters*, 2002)
 - 2. Output correlation is lower than input correlation in spiking neurons (Moreno-Bote and Parga, *Phys. Review Letters*, 2006)
 - 3. Firing rate and correlation coefficients are not independent (de la Rocha et al, *Nature*, 2007)
- Open questions

Open questions

- The Fokker-Planck equation (FPE) for a pair of correlated neurons remains unsolved exactly for all limits, except for one case (however, very good approximations are available in some limits, as described in this tutorial)
- How correlation transfer operates in more complex neuronal models (e.g., Hodgkin & Huxley) is not known
- How correlation transfer depends on reciprocal connections is largely unknown (but await to the 2nd part of the tutorial)
- The relationship between correlations and information in a pair of neurons remains unexplored