Covariability in Coupled Neural Systems

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Outline

• Background: variability and covariability
  • What is it? Why is it important?
• The effect of coupling on covariability
  • A simple model of coupled units, explaining some curious somatosensory data
  • A first glance at a fully coupled, realistic model
    • Efficient implementation and analysis of these models
Neural responses are variable

Nevertheless, it is well known that neural responses are quite variable across trials meaning that single neuron response within any given trial may differ significantly from the trial averaged response. To illustrate this important observation, I review some recent data from Carandinni. Figure 0.1 shows intracellular recordings from cortical neurons in the primary visual cortex obtained during presentation of a drifting grating stimulus at the optimal orientation. The mean neural response is a quasi-sinusoidal membrane trajectory and a mean firing rate that resembles a rectified copy of the mean membrane dynamic. However, significant trial-to-trial membrane variability is very apparent and for comparison purposes, I show three trials. As Carandinni remark, the trial-to-trial variability of the firing rate is in a relative sense much larger than the membrane variability. The source of the membrane variability is likely a combination of random synaptic bombardment and intrinsic channel variability, with synaptic inputs being the dominate culprits. However, spike train mechanisms exhibit very low variability giving question to.

Firing rate is to be interpreted as $N(t)/\delta t$ where $N(t)$ is the number of spikes in a time window of length $\delta t$ centered at $t$. Carrandini, 2004
The effect of variability on coding

Motivated by Stein (1967) and Knight (1972). Figure from Doiron (2009).
Using variability for coding

Fig. 0.4. Mean versus noise coded signals

A. Sample current trace used to drive an neocortical pyramidal cell in vitro. Following Eqn 8, the mean current changes abruptly at $t = y$ ms. The spike rasters for $w$ trials and the population instantaneous firing rate $\nu$ computed from 4 sequential trials.

B. The same as A except the current used in each trial is given by Eqn 9. Experimental details are given in Silberberg et al., 2004. I thank Matthias Bethge for the donation of the figure.

To understand why the response speed is dramatically enhanced for noise coded signals as compared to mean coded signals it is useful to write down the evolution equation for the membrane density $P_n$, for an ensemble of LIF neurons described by Eqn 4:

$$\frac{\partial P_n}{\partial t} = \frac{\partial}{\partial V} \left( V - \mu_n \sigma^2_n \nu_n \delta(V - V_R) \right).$$

$P_n$ also satisfies a continuity relation with an effective probability current $S_n$.
Neural co-variability is important

Pre-synaptic populations

Post-synaptic population

FIG. 2a

Neuron 1 (spikes)
Neuron 2 (spikes)

Neuron 2 (spikes)
Neuron 1 (spikes)

Neuron 2 (spikes)
Neuron 1 (spikes)

ΔI_{shuffled} < 0

ΔI_{shuffled} > 0

ΔI_{shuffled} = 0

Averbeck et al, 2006
Calculating Spike Count Correlation

![Graph showing spike count correlation](image)

- Time scale: 100 ms
Calculating Spike Count Correlation
Calculating Spike Count Correlation
Calculating Spike Count Correlation
Calculating Spike Count Correlation
Calculating Spike Count Correlation

\[ n_1 = \ldots \ 2, \ 2, \ 3, \ 2, \ \ldots \]

\[ n_2 = \ldots \ 3, \ 2, \ 2, \ 2, \ \ldots \]
Calculating Spike Count Correlation

\[ Cov_{12,T} = E_T(n_1 n_2) - E_T(n_1)E_T(n_2) \]

\[ \rho_T = \frac{Cov_{12,T}}{\sqrt{Var_{1,T} Var_{2,T}}} \]

\[ \rho = \lim_{T \to \infty} \rho_T \]

Correlation coefficient

\[ \rho = -1 \quad - \text{completely anti-correlated} \]

\[ \rho = 0 \quad - \text{uncorrelated} \]

\[ \rho = 1 \quad - \text{completely correlated} \]
Predicting Output Correlation Given Input Statistics

A correlation rate relationship?

de la Rocha, Doiron, et al, 2007
Why?

\( \mu = 1.3 \)
\( \mu = 0.95 \)
\( \mu = 0.6 \)

\( l_2 \)
\( l_1 \)
\( n_1 \)

\( f \)

oval → circle → point

de la Rocha, Doiron, et al, 2007
Predicting Output Correlation Given Input Statistics

A correlation rate relationship?

E-I correlations

Because 10 Hz whisker stimulation reduced whisker-evoked spikes for RS units (Chung et al., 2002; Khatri et al., 2004) (Figures 1B and 1C), the increased jitter could merely reflect weaker excitatory input to RS units or increased contamination of weak whisker-evoked responses by spontaneous spikes. To address this possibility, we tested whether spike jitter was correlated with spike probability across RS units. No correlation existed (r = 0.04) (Figure 1D).

In addition, an identical increase in jitter occurred when long recovery times were used between 10 Hz trains, a protocol that leads to less adaptation and more spikes (Figure 1D). Thus, the increase in spike jitter during trains was not due to reduced excitation of RS neurons or the small number of whisker-evoked spikes.

These data show that the temporal precision of cortical responses to somatosensory stimuli is dynamically regulated by a circuit downstream of the thalamus. To establish what controls this dynamic range, we determined the integration window (IW) of cortical units to thalamic inputs in vitro.

Gabernet, Jadhav, Feldman, Carandini, Scanziani, 2005
Measuring E-I correlation \textit{in vivo}

Middleton et al, in prep
Measuring E-I correlation *in vivo*

Figure 1: Correlation coefficient.

Figure 2: Power spectrum.

Figure 3: Spike probability.

Middleton et al, in prep
What's the problem?

correlated slow noise

layer IV whisker input
What's the problem?

correlated slow noise

layer IV whisker input
A Coupled Model

layer IV whisker input

correlated slow noise

\[ W_E(t) = \mu_E + A_E t^{-3/2} e^{-0.55/t} \]
\[ W_I(t) = \mu_I + A_I t^{-3/2} e^{-0.55/t} \]

\[
\begin{align*}
    r_I(t) & = \max\{0, W_I(t) + \eta_I(t)\} \\
    \tau_I \frac{d\eta_I}{dt} & = -\eta_I(t) + \sigma_I \xi_I(t) \\
    \tau_s \frac{dI}{dt} & = -I(t) + r_I(t) \\
    r_E(t) & = \max\{0, W_E(t) - gI(t) + \eta_E(t)\} \\
    \tau_E \frac{d\eta_E}{dt} & = -\eta_E(t) + \sigma_E \xi_E(t)
\end{align*}
\]

\[
\langle \xi_E(t) \rangle = \langle \xi_I(t) \rangle = 0 \\
\langle \xi_E^2(t) \rangle = \langle \xi_I^2(t) \rangle = 1 \\
\langle \xi_E(t)\xi_I(t) \rangle = c \in [0, 1]
\]
Fitting the model

Firing rate (Hz)

Time (ms)

Whisker

Mean firing rate (Hz)

Time (ms)

Stimulus onset
Fitting the model

Figure 3:

![Graph](image)

Figure 1:

![Graph](image)

Tuesday, September 1, 2009
The effect of feedforward inhibition

depicted schematic

decreasing coupling
Mechanism

uncoupled
coupled

time (ms)

E-I correlation coefficient $c$

decreasing coupling

stimulus onset
coupled
uncoupled

input distribution

transfer function:
- non linear
- linear

Tuesday, September 1, 2009
Summary so far

- Inhibitory coupling anti-correlates neural populations
- Non-linearities dilute this effect
- The evoked state moves you toward the linear part of the transfer function, unlocking the anti-correlating effect of inhibition
Issues with this model

• Missing full set of connections
• Not-quite-realistic non-linearities
• Externally-imposed noise with a fixed and fitted input correlation
A Spiking Model with Internally Generated Variability

\[
\tau \frac{dV}{dt} = (V_{\text{rest}} - V) + g_{\text{ex}}(E_{\text{ex}} - V) + g_{\text{inh}}(E_{\text{inh}} - V)
\]

\[
\tau_{\text{ex}} \frac{dg_{\text{ex}}}{dt} = -g_{\text{ex}} \quad g_{\text{ex}} \rightarrow g_{\text{ex}} + \Delta g_{\text{ex}}
\]

\[
\tau_{\text{inh}} \frac{dg_{\text{inh}}}{dt} = -g_{\text{inh}} \quad g_{\text{inh}} \rightarrow g_{\text{inh}} + \Delta g_{\text{inh}}
\]

(Vogels & Abbott, 2005)
Efficiently simulating and analyzing thousands of trials with a large spiking network

• 4000 neurons, 1000 trials

• 8 million pairwise correlations to calculate per bin, 50 bins

• Conventional code: 1.5 hours for simulations, 8 hours to calculate correlations
GPUs
(Graphics Processing Units)

- Massively parallel single precision floating point
- Have to program in SPMD (single program multiple data) style - thousands of threads all running the same code on different parts of memory
SpikeStream

- Python framework for simulation and spike train analysis
- Specify models and computations in Python (a very nice language!)
- Code generation techniques produce underlying CUDA code for the device
Example

• (show Python code and generated CUDA code)
SpikeStream

• Interesting performance characteristics:

• More complex models not much slower (rate-limiting step: spike propagation)
  
  • Large memory access latency, hundreds of accesses per spike

• Memory limits: 4GB per card, so millions of synapses (or thousands of repeats of a smaller sim), but not billions

• Multiple cards can be used for repeats, but not easy to extend one sim over multiple cards
A Spiking Model with Internally Generated Variability

(1.2 hours on CPU, 30 seconds on GPU = 130x speedup)
The system is acting linearly

(8 hours on CPU, 2 minutes on GPU = 240x speedup)
I-I Correlation Distribution For Each Bin
Questions

• Can we understand the peculiar shape of the correlation distribution in this network?

• Can we modify the network to behave like Jay’s data?
  • More realistic connectivity (sparse vs. dense)
  • More realistic coupling (strong feedforward inhibition)
  • Different non-linearities in the neurons
  • More realistic input
Summary

- Correlations in neural systems are affected by connectivity and non-linearities in complex ways. The details matter.

- GPU computing opens up new avenues for approaching this problem with larger-scale models with more realistic characteristics.
Thank You!