Finite size effects are critical for self-organized synchrony in feedforward networks

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An “unfolding” of a feedforward path from a seemingly undirected population of neurons. We neglect inter-population coupling and feedback from higher populations back to the lower ones (dashed connections).

Question: how does the network activity in population 1 get propagated along the network “chain”.

Unfolding neural connectivity
In vitro network

Why does the synchrony come back?

Let’s model the system. Try firing rate equations. Let the time dependent firing activity of population $m$ be $\nu_m(t)$. The full network dynamics evolve according to:

$$\frac{d\nu_m(t)}{dt} = -\nu_m(t) + f(\nu_{m-1}(t))$$

$f$ is a standard transfer function (eg. $f=\tanh(\nu)$ or your favorite $f$-I relation). Let $\nu_0(t)=\nu_0 \Theta(t)$.

\[\begin{align*}
\nu_3 &= f(\nu_2) \\
\nu_2 &= f(\nu_1) \\
\nu_1 &= f(\nu_0) \\
\nu_0(t) &\text{ No synchrony.}
\end{align*}\]
Reasons for discrepancy between experiments and rate models.

- Stochastic input is important. Rate equations do not model the true stochastic nature of the input/response.

- Spike dynamics are important. Rate equations do not model the nonlinearities inherent in spiking.

- Alex is wrong. If he just ran his experiment longer he would eventually see stable asynchronous behaviour. It is all just transients.

Check 1-3 by building up a network model of spiking elements.
Consider the simplest possible spiking system – the Perfect (non-leaky) Integrate and Fire neuron model.

\[ \frac{dV_{im}}{dt} = I_{im}(t) - \beta \]

Important output:

\[ \sum_j \delta(t - t_j) \]

Consider $M$ populations of $N$ neurons each. Let the synaptic input to neuron $i$ in population $m$ be

$$I_{im}(t) = I_{im}^{ex}(t) + I_{im}^{in}(t) + I_{noise,im}(t)$$

$$I_{im}^{ex}(t) + g^{ex} \sum_j \rho_{ij(m-1)}^{ex} \sum_k \delta \left( t - t_{jk(m-1)} \right)$$

$$I_{im}^{in}(t) + g^{in} \sum_j \rho_{ij(m-1)}^{in} \sum_k \delta \left( t - t_{jk(m-1)} \right)$$

$$I_{im,noise}(t) = \sigma_{noise} \zeta_{im}(t)$$

$$\langle \zeta_{im}(t) \rangle = 0$$

$$\langle \zeta_{im}(t) \zeta_{im}(t') \rangle = \delta \left( t - t' \right)$$

$\rho_{ij(m-1)}^{ex}$ is 1 if there is an excitatory connection from neuron $j$ in population $m-1$ to neuron $i$ in population $m$; otherwise it is 0. Similarly for inhibition given by $\rho_{ij(m-1)}^{in}$. We only consider sparse connections.
IF network

Time (s)

10
9
8
7
6
5
4
3
2
1

Synchrony is still present long after the transient.
Synchronous discharge similar to Alex’s experiments is observable in network models of simple spiking neurons.

Goal: Explain the synchrony observed long after the transient by using a mean field theory for spiking networks (note: may not be possible).
Mean field basics

First define a mean statistic over the network. Since we are interested in spiking behaviour a natural statistic is the instantaneous firing probability for population $m$.

$$\nu_m(t) = \lim_{N \to \infty} \lim_{\Delta t \to 0} \frac{n_{\text{spikes}}(t; t + \Delta t)}{N} = \frac{1}{N} \sum_{jk} \delta(t - t_{jk})$$

Next derive a evolution equation for the ensemble density of membrane potentials in population $m$, $P_m(V,t)$. This will require a simple representation of $I_{im}(t)$.

Finally we need to relate the evolution equation and $\nu_m(t)$ to one another. In this way $P_m(V,t)$ and $\nu_m(t)$ will need to be determined self-consistently.

Feedorward specific: Note that $\nu_{m-1}(t)$ will determine $P_m(t)$ but not vice versa!
Diffusion approximation

Consider the scenario where the pulse inputs to neuron $i,m$ are all small in amplitude and there is a large sparse presynaptic population. We then replace the sum of random Poisson trains by a continuous time stochastic process.

$$I_{im}(t) = I_{im}^{ex}(t) + I_{im}^{in}(t) + I_{im}^{noise}(t)$$

$$\approx \mu_m(t) + \sigma_m(t)\xi_{im}(t)$$

$$\langle \xi_{im}(t) \rangle = 0$$

$$\langle \xi_{im}(t)\xi_{jn}(t') \rangle = \delta_{ij}\delta_{mn}\delta(t-t')$$

where

$$\mu_m(t) = \left( g^{ex} \varepsilon^{ex} N + g^{in} \varepsilon^{in} N \right) \nu_{m-1}(t)$$

$$\sigma_m^2(t) = \left( \left( g^{ex} \right)^2 \varepsilon^{ex} N + \left( g^{in} \right)^2 \varepsilon^{in} N \right) R_{st,m-1}^2 \nu_{m-1}(t) + \sigma_{noise,m}^2$$

Rescale the amplitude of the white noise by the coefficient of variance. Works for PIF only!
Density evolution: Fokker-Planck equations.

An differential equation driven by a Gaussian white noise forcing is called a *Langevin* equation. One can derive from simple Markovian assumptions the associated *Fokker-Planck* equation that governs the evolution of the probability density for the stochastic processes. For the simple PIF model we have:

\[
\frac{\partial P_m(V, t)}{\partial t} = L_m P_m(V, t) + \nu_m(t) \delta(V - V_R)
\]

\[
L_m = \frac{\partial}{\partial V} \left[ -\mu_m(t) + \frac{\sigma_m^2(t)}{2} \frac{\partial}{\partial V} \right]
\]

\[
\nu_m(t) = -\frac{\sigma_m^2(t)}{2} \left[ \frac{\partial P_m(V, t)}{\partial V} \right]_{V=V_T}
\]

Spiking behaviour and our mean statistic!
To solve for $P_m(V, t)$ we need to know the boundary conditions that accompany the operator $L_m$.

$$P_m(V = V_T, t) = 0$$  \hspace{1cm} \text{Spike threshold is an absorbing boundary}

$$\left[ \frac{\partial P_m(V, t)}{\partial V} \right]_{V = V_L} = 0$$  \hspace{1cm} \text{Voltage floor is a reflecting boundary}

$$\int_{V_L}^{V_T} P_m(V, t) dV = 1$$  \hspace{1cm} P_m(V, t) \text{ must be normalized.}

What about spike dynamics?
Spiking and resetting: the source term $\nu_m(t)\delta(V - V_R)$

$P_m(V)$

$V_L$ $V_R$ $V_T$

$\nu_m(t)$
Despite our success in getting the transient right, we still have no synchrony after the initial transient has decayed?

From simulations

From FP eqn
What’s left: Finite size effects (N < \( \mathcal{F} \))

\( \nu_m(t) \) is the expected firing probability of population \( m \). For a finite size population there is an inherent error in \( \nu_m(t) \) describing the true firing statistics of the population (weak law of large numbers). We can correct for this by fluctuating the mean field term \( \nu_m(t) \) to account for random errors.

\[
\frac{\partial P_m(V,t)}{\partial t} = L_m P_m(V,t) + \nu_m(t) \delta(V - V_R)
\]

\[
L_m = \frac{\partial}{\partial V} \left[ -\mu_m(t) + \frac{\sigma_m^2(t)}{2} \frac{\partial}{\partial V} \right]
\]

\[
\nu_m(t) = -\frac{\sigma_m^2(t)}{2} \left[ \frac{\partial P_m(V,t)}{\partial V} \right]_{V = V_R} + \sqrt{\frac{\nu_m(t)}{N}} \eta_m(t)
\]

\[
\langle \eta_m(t) \rangle = 0
\]

\[
\langle \eta_m(t) \eta_m(t') \rangle = \delta(t - t')
\]
Infinite size system has a well defined equilibrium where the flux of probability current is a constant.

In this treatment we see that a finite size system is constantly being perturbed from equilibrium by its own finite nature.

$\text{Finite size} = \text{nonequilibrium statistics}$
Does the finite size mean field system give the right population statistics? Rigorous check is needed. Compare the second order statistics of the population firing rate $\nu_m(t)$ computed from network simulations of the Langevin equations and the solutions to the finite size FP system.

$$A_m(\tau) = \frac{\langle \nu_m(t)\nu_m(t+\tau) \rangle_t}{\langle \nu_m(t) \rangle_m^2}$$

Normalized population autocorrelation
What do the solutions for $\nu_m(t)$ look like. Do they suggest synchrony in the populations?

Synchronous activity?

$\nu_{10}$

$\nu_{5}$

$\nu_{1}$

$P_{10}$

$P_{5}$

$P_{1}$

Skewed Gaussian

Time (s)  $\nu$ (Hz)
Intuitive explanation

\[ \nu_M(t) \]

\[ \nu_{M-1}(t) \]

\[ \nu_2(t) \]

\[ \nu_1(t) \]

Total effect of finite size is

\[ (M)^{\frac{1}{M}} \sqrt{\frac{\nu_m(t)}{N}} \]

Total effect of finite size is

\[ (M-1)^{\frac{1}{M-1}} \sqrt{\frac{\nu_m(t)}{N}} \]

Total effect of finite size is

\[ 2^{\frac{1}{M}} \sqrt{\frac{\nu_m(t)}{N}} \]

Total effect of finite size is

\[ \sqrt{\frac{\nu_m(t)}{N}} \]
Conclusions

• Neural populations synchronize in feedforward assemblies; for small networks sizes synchronous population events occur well beyond the stimulus onset.

• These effects can be treated in a mean field scenario with a modification to the diffusion limit as well as the addition of a stochastic term to the field equations.

• Asynchronous (equilibrium) activity is untenable in a finite size network when a) there is a directed feedforward path b) activity is at high firing rate.