Dynamics of networks of binary neurons
Networks of binary neurons

- $N$ neurons;
- Neurons described by binary variables $S_i(t) = 0, 1$;
- Depend on inputs $h_i(t)$ (‘local fields’)
  \[ h_i(t) = I_iX + \sum_{j \neq i} J_{ij} S_j(t) \]
- Update rules: specify how $S_i$s are computed from $h_i$s
  - Synchronous updates: define a time step $dt$, and a threshold $T$
    * Deterministic case:
      \[ S_i(t + dt) = \Theta(h_i(t) - T) = \begin{cases} 
          1 & h_i(t) \geq T \\
          0 & h_i(t) < T 
        \end{cases} \]
Stochastic case:

\[ S_i(t + dt) = \begin{cases} 
1 & \text{with probability } \phi(h_i(t)) \\
0 & \text{with probability } 1 - \phi(h_i(t)) 
\end{cases} \]

- Asynchronous updates: can happen at any time, with transition rates

\[ w(S_i(t) = 0 \rightarrow S_i(t) = 1) = \frac{\phi(h_i(t))}{\tau} \]
\[ w(S_i(t) = 1 \rightarrow S_i(t) = 0) = \frac{1 - \phi(h_i(t))}{\tau} \]

- \( \phi \) sigmoidal function (monotonically increasing from 0 to 1)

\[ \phi(x) = \frac{1}{1 + \exp(-\beta(x - T))} \]

where \( \beta \) is analogous to an inverse temperature
Synchronous updates

• Dynamics:

\[ S_i(t + dt) = \Theta \left( I_{iX} + \sum_{j \neq i} J_{ij} S_j(t) - T \right) \]

• Toy model: \( J_{ij} = J/N \) for all \( J \), \( I_{iX} = I_X \) for all \( i \) (infinite-range Ising model with constant external field)

• In the large \( N \) limit, all neurons receive the same input at any time,

\[ h_i(t) = J r(t) \]

where \( r(t) \) is the average activity of the whole population,

\[ r(t) = \frac{1}{N} \sum_i S_i(t) \]

• Dynamics of \( r(t) \) given by discrete-time map

\[ r(t + dt) = \Theta(I + J r(t) - T) \]
Asynchronous updates: Master equation

- Transition rates

\[ w(S_i(t) = 0 \rightarrow S_i(t) = 1) = \frac{\phi(h_i(t))}{\tau} \]

\[ w(S_i(t) = 1 \rightarrow S_i(t) = 0) = \frac{1 - \phi(h_i(t))}{\tau} \]

- Master equation

\[
\frac{d}{dt} P(S_1, \ldots, S_N, t) = - \sum_{i=1}^{N} w(S_i \rightarrow 1 - S_i) P(S_1, \ldots, S_N, t)
+ \sum_{i=1}^{N} w(1 - S_i \rightarrow S_i) P(S_1, \ldots, 1 - S_i, \ldots, S_N, t)
\]

- From master equation, we can compute averages over any function of the neuronal variables

\[
\langle f(S_1, \ldots, S_N, t) \rangle = \sum_{S_1, \ldots, S_N} P(S_1, \ldots, S_N, t) f(S_1, \ldots, S_N, t)
\]
Equations for mean rates and correlations

• Mean rates

\[ r_i(t) = \langle S_i(t) \rangle \]

obey

\[ \tau \frac{dr_i}{dt} = -r_i(t) + \langle \phi(h_i(t)) \rangle \]

• Correlations

\[ C_{ij}(t, t + \tau) = \langle (S_i(t) - \langle S_i(t) \rangle) (S_j(t + \tau) - \langle S_j(t + \tau) \rangle) \rangle \]

obey

\[ \tau \frac{dC_{ij}(t, t + \tau)}{d\tau} - 2C_{ij}(t, t) + \langle \delta S_i(t) \delta \phi(h_j(t)) \rangle + \langle \delta S_j(t) \delta \phi(h_i(t)) \rangle \]

\[ \tau \frac{dC_{ij}(t, t + \tau)}{d\tau} = -C_{ij}(t, t + \tau) + \langle \delta S_i(t) \delta \phi(h_j(t + \tau)) \rangle \]
Weak coupling $J \sim 1/N$, homogeneous populations

- $n = O(1)$ homogeneous populations of $N_a = N/n$ neurons each;
- Synaptic couplings $J_{ij} = J_{ab}/N_b$
- Equations for mean rates become:

$$
\tau \frac{dr_a}{dt} = -r_a(t) + \phi \left( I_{aX} + \sum_b J_{ab} \tilde{r}_b(t) \right)
$$

with fixed points

$$
\tilde{r}_a = \phi \left( I_{aX} + \sum_b J_{ab} \tilde{r}_b \right)
$$

- Same equations as in rate models!
- Cross-correlations $\sim O(1/N)$ can be computed in terms of eigenvalues and eigenvectors of Jacobian matrix
Randomly diluted network

- One population, randomly connected (connection probability $p$), $J \sim 1/N$;
- Mean rate obeys standard rate equation;
- Cross-correlations are the sum of two terms:
  - Average cross-correlations, due to collective dynamics (governed by global connectivity);
  - Cross-correlations due to direct interactions
E-I network

Excitatory Population

Inhibitory Population

$J_{EE}$

$J_{EI}$

$J_{II}$

$J_{IE}$
E-I network - averaged CCs

- Shape of CCs depend on whether eigenvalues of Jacobian matrix are real or complex;
- Close to Hopf bifurcation, strong damped oscillations in CCs;
- Montonically decaying CCs close to saddle node bifurcation
E-I network - individual CCs between E neurons

- Relative strengths of collective term and individual connection term depend on distance from bifurcation.
Symmetric networks

- Symmetric network $J_{ij} = J_{ji}$ for all $i \neq j$ with no self-coupling (autapses) $J_{ii} = 0$ for all $i$;

- One can define an ‘energy function’ (or Lyapunov function)

$$E(S_1, \ldots, S_N) = -\frac{1}{2} \sum_{j \neq i} J_{ij} S_i S_j - \sum_i (I_i X - T) S_i$$

- At zero temperature ($\beta \to \infty$), starting from any initial condition, $E$ decreases monotonically towards a local minimum.

- The equilibrium probability of any state $(S_1, \ldots, S_N)$ is given by the Boltzmann (or Gibbs) distribution

$$P(S_1, \ldots, S_N) = \frac{1}{Z} \exp (-\beta E(S_1, \ldots, S_N))$$

where $Z = \sum_{S_1, \ldots, S_N} \exp (-\beta E(S_1, \ldots, S_N))$ is the partition function.
Network of binary neurons with $O(1/N)$ couplings

- In the large $N$ limit, inputs to neurons become deterministic (fluctuations around the mean are of order $1/\sqrt{N}$)
- Stochastic single neuron behavior entirely due to stochastic update rule
- Is this consistent with single neuron recordings *in vitro* and *in vivo*?
Response of neurons to constant currents *in vitro*
Large fluctuations in inputs to neurons *in vivo*

- Large fluctuations in inputs;
- Irregularity due to these fluctuations, not to spike generation process;
- Inconsistent with dynamics of the network with $O(1/N)$ couplings

Haider et al 2013
Strong coupling scenario (balanced network)

- $N_E$ E neurons, $N_I$ I neurons;
- Random sparse connectivity matrix:
  each neuron receives in average
  - $K$ external E inputs;
  - $K \ll N_E$ E recurrent inputs,
  - $K \ll N_I$ I inputs
- Strong coupling: Coupling strengths $J_{ab} \sim 1/\sqrt{K}$
- Deterministic updates:
  $$S_i(t) = \Theta(h_i(t) - T)$$
  with random, or fixed, sequence updatings (each neuron updated every $1/\tau$)
Synaptic inputs: means and fluctuating terms

- Inputs to neuron $i \in E$:

$$h_i(t) = J_{EX} \sqrt{K} r_X + \frac{J_{EE}}{\sqrt{K}} \sum_{j \in E} c_{ij} S_j(t) - \frac{J_{EI}}{\sqrt{K}} \sum_{j \in I} c_{ij} S_j(t)$$

$$= \mu_E + Q_i + \eta_i(t)$$

where

- $\mu = \text{mean inputs}$

$$\mu_E = \sqrt{K} (J_{EX} r_X + J_{EE} r_E - J_{EI} r_I)$$

- $Q_i = \text{quenched fluctuations (spatial variability) with variance}$

$$Q^2 = J_{EE}^2 (r_E^2 + \Delta r_E^2) + J_{EI}^2 (r_I^2 + \Delta r_I^2)$$

- $\eta_i = \text{temporal fluctuations (temporal variability)}$

$$\langle \eta_i(t)^2 \rangle = J_{EE}^2 (r_E - r_E^2 - \Delta r_E^2) + J_{EI}^2 (r_I - r_I^2 - \Delta r_I^2)$$
Balance condition

- To obtain finite rates, leading order term in $\sqrt{K}$ should vanish:

  \[ J_{EX}r_X + J_{EE}r_E - J_{EI}r_I = 0 \]
  \[ J_{IX}r_X + J_{IE}r_E - J_{II}r_I = 0 \]

- Rates depend linearly on external inputs!

- Balanced state stable provided inhibition is strong enough.
Highly irregular activity in balanced state
Irregularity and variability of single neurons in vivo

Maimon and Assad 2009

Haider et al 2013 et al 1999
Wide distribution of rates

- Quenched fluctuations lead to wide distributions of firing rates (due to variability in numbers of connections from neuron to neuron)
Distributions of spontaneous firing rates in vivo

Cat visual cortex
Griffith and Horn 1966

Monkey parietal cortex
Koch and Fuster 1989

Rat auditory cortex
Hromadka et al 2008
Chaotic nature of the dynamics

- Small perturbations in the network state grow initially exponentially
Fast tracking of external inputs

- Strong inhibitory feedback leads to fast response to external inputs
Correlations in balanced networks

A. Diagram of balanced network with excitatory (E) and inhibitory (I) populations.

B. Graph showing input currents with time (ms) ranging from -20 to 1500, and network size N ranging from 100 to 10,000.

C. Graph showing correlation with network size N, with correlation values ranging from 0.0001 to 0.01.

D. Population activity with a time scale of τ = 10 ms, showing data for N = 1024 and N = 8192.

E. Current correlation graph with lag (ms) ranging from -10 to 10 and current correlation ranging from -0.4 to 0.4, showing data for N = 1024 and N = 8192.

F. Diagram illustrating asynchronous firing with τ ~ 1/N, weakly asynchronous total currents c, width ~ 1/√N, and synchronous current components c_{EE}, c_{II}, c_{EI}, c_{XX}.

G. Firing correlation graph with firing correlation r ranging from -0.03 to 0.03 and σ_f ~ 1/√N.
Distributions of correlations in vivo
Conclusions

• Balanced network: simplest model accounting for ubiquitous features of background activity in vivo:
  – highly irregular firing,
  – wide distributions of rates,
  – weak correlations
References

• Amit 1989
• Hertz, Krogh and Palmer 1991
• Ginzburg and Sompolinsky 1994
• van Vreeswijk and Sompolinsky 1996, 1998
• Renart et al 2010