Biological Modeling of Neural Networks:

10.1 Cortical Populations
- columns and receptive fields

10.2 Connectivity
- cortical connectivity
- model connectivity schemes

10.3 Mean-field argument
- asynchronous state

10.4 Random Networks
- Balanced state

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Biological Modeling of Neural Networks – Review from week 1

- 10,000 neurons
- 3 km wire
- Motor cortex
- Frontal cortex
- To motor output
population of neurons with similar properties

Brain

stim

neuron 1

neuron 2

Neuron K
population activity - rate defined by population average

\[ A(t) = \frac{n(t; t + \Delta t)}{N\Delta t} \]
Week 10-part 1: Population activity

population of neurons with similar properties
Week 10-part 1: Population activity

population of neurons with similar properties

population activity

A(t)

Are there such populations?

Brain
Week 10-part 1: Scales of neuronal processes

Population of neurons with similar properties
Week 10 – part 1b: Cortical Populations – columns and receptive fields

Biological Modeling of Neural Networks:

Week 10 – Neuronal Populations

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Week 10-part 1b: Receptive fields

[Diagram of brain with labeled visual cortex and electrode]
Week 10-part 1b: Receptive fields
Neighboring cells in visual cortex have similar preferred center of receptive field.
Week 10-part 1b: Orientation tuning of receptive fields

Receptive fields:
Retina, LGN

Receptive fields:
visual cortex V1

Orientation selective
Week 10-part 1b: Orientation tuning of receptive fields

Receptive fields:
**visual cortex V1**

Orientation selective
Week 10-part 1b: Orientation tuning of receptive fields

Receptive fields: visual cortex V1

Orientation selective

Stimulus orientation

rate

preferred orientation

Week 10-part 1b: Orientation tuning of receptive fields

Receptive fields: visual cortex V1

Orientation selective

Stimulus orientation

rate

preferred orientation
Receptive fields: visual cortex V1

Neighboring neurons have similar properties

Orientation selective

Week 10-part 1b: Orientation columns/orientation maps
Neighboring cells in visual cortex
Have similar preferred orientation:

**cortical orientation map**
Week 10-part 1b: Orientation columns/orientation maps

Population of neighboring neurons: different orientations

Week 10-part 1b: Interaction between populations / columns

\( I(t) \) 

\( A_n(t) \)
Week 10-part 1b: Do populations / columns really exist?
Week 10-part 1b: Do populations / columns really exist?

Course coding

Many cells (from different columns) respond to a single stimulus with different rate.
The receptive field of a visual neuron refers to
[ ] The localized region of space to which it is sensitive
[ ] The orientation of a light bar to which it is sensitive
[ ] The set of all stimulus features to which it is sensitive

The receptive field of an auditory neuron refers to
[ ] The set of all stimulus features to which it is sensitive
[ ] The range of frequencies to which it is sensitive

The receptive field of a somatosensory neuron refers to
[ ] The set of all stimulus features to which it is sensitive
[ ] The region of body surface to which it is sensitive
Biological Modeling of Neural Networks:

Week 10 – part 2: Connectivity

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Week 10-part 2: Connectivity schemes (models)

1 population = What?
Week 10-part 2: model population

population = group of neurons
with
- similar neuronal properties
- similar input
- similar receptive field
- similar connectivity

make this more precise
Week 10-part 2: local cortical connectivity across layers

Here:
Excitatory neurons

1 population = all neurons of given type in one layer of same column (e.g. excitatory in layer 3)

Lefort et al. NEURON, 2009
Week 10-part 2: Connectivity schemes (models)

- Full connectivity
- Random: prob $p$ fixed
- Random: number $K$ of inputs fixed

random: probability $p=0.1$, fixed

Fig. 12.7: Simulation of a model network with a fixed connection probability $p = 0.1$. A. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen neurons.
Can we mathematically predict the population activity?

given
- connection probability $p$
- properties of individual neurons
- large population

asynchronous activity
Biological Modeling of Neural Networks:

Week 10 – Neuronal Populations

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10.4 Balanced state
Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

Random firing in a populations of neurons

Neuron # 32374
50

A [Hz]

Neuron #
32440
32340
100

time [ms]

u [mV]
0

input  \{ low rate, high rate \}
Week 10-part 3: asynchronous firing

Blackboard:
- Definition of $A(t)$
- filtered $A(t)$
- $\langle A(t) \rangle$

Asynchronous state
$\langle A(t) \rangle = A_0 = \text{constant}$

Week 10-part 3: counter-example: $A(t)$ not constant

population of neurons with similar properties

Systematic oscillation $\rightarrow$ not ‘asynchronous’
Populations of spiking neurons

population activity?

Homogeneous network:
- each neuron receives input from $k$ neurons in network
- each neuron receives the same (mean) external input

$A(t) = \frac{n(t; t + \Delta t)}{N\Delta t}$
Week 10-part 3: mean-field arguments

Blackboard: Input to neuron i
Full connectivity
Week 10-part 3: mean-field arguments

Fully connected network

\[ w_{ij} = w_0 \]

Synaptic coupling

\[ I(t) = I^{ext}(t) + I^{net}(t) \]

\[ I^{net}(t) = \sum_j \sum_f w_{ij} \alpha(t - t^f_j) \]

All spikes, all neurons
Week 10-part 3: mean-field arguments

All neurons receive the same total input current (‘mean field’)

\[ I_i(t) = J_0 \int \alpha(s) A(t-s) ds + I_{ext}(t) \]

Index \( i \) disappears

\[ w_{ij} = \frac{J_0}{N} \]

All spikes, all neurons

\[ I^{net}(t) = \sum_j \sum_f w_{ij} \alpha(t-t_j^f) + I_{ext} \]
Week 10 - part 3: stationary state/asynchronous activity

\[ I_0 = [J_0 q A_0 + I_0^{ext}] \]

Homogeneous network
All neurons are identical, Single neuron rate = population rate \[ \nu = g(I_0) = A_0 \]

blackboard

frequency (single neuron) \[ \nu = \frac{1}{s} \int_0^\infty s P_I \hat{t} + s | \hat{t} \, ds \] = \( g(h_0) \)
Stationary solution

\[ \nu = g(I_0) \]
\[ \nu = A_0 \]

\[ I_0 = \left[ J_0 \eta A_0 + I_0^{\text{ext}} \right] \]

Homogeneous network, stationary,
All neurons are identical,
Single neuron rate = population rate

\[ \nu = g(I_0) = A_0 \]
Exercise 1: homogeneous stationary solution

Homogeneous network
All neurons are identical,
Single neuron rate = population rate

\[ v = g(h_0) \]

fully connected

N \gg 1

Next lecture: 11h15
Single Population
- population activity, definition
- full connectivity
- stationary state/asynchronous state

Single neuron rate = population rate

\[ \nu = g(I_0) = A_0 \]

What is this function \( g \)?

Examples:
- leaky integrate-and-fire with diffusive noise
- Spike Response Model with escape noise
- Hodgkin-Huxley model (see week 2)
Week 10-part 3: mean-field, leaky integrate-and-fire

\[ I_0 = J_0 q A_0 + I_0^{\text{ext}} \]

\[ [I_0 - I_0^{\text{ext}}] / J_0 q = A_0 \]

\[ \nu = g_\sigma(I_0) \]

Different noise levels

Function \( g \) can be calculated
**Review: Spike Response Model with Escape Noise**

Spike reception: EPSP

\[ \varepsilon(t - t^f_j) = \exp\left[-\frac{t - t^f_j}{\tau}\right] \]

Spike emission: AP

\[ \eta(t - \hat{\tau}) \]

Last spike of i

\[ u_i(t) = \eta(t - \hat{\tau}_i) + \sum_{j} \sum_{f} w_{ij} \varepsilon(t - t^f_j) \]

All spikes, all neurons

Firing intensity

\[ \rho(t \mid u) = f(u - \mathcal{G}) \]
Review: Spike Response Model with Escape Noise

Spike emission: AP

Response to current pulse

\[ u_i(t | \hat{t}_i) = \eta(t - \hat{t}_i) + \int \kappa(s) I(t - s) ds \]

Blackboard - Renewal model - Interval distrib.

\[ \rho(t) = f(h(t)) = \rho_0 \exp\left(\frac{h(t) - \theta}{\Delta}\right) \]
Week 10-part 3: Example - Asynchronous state in SRM₀

\[ h₀ = RI₀ = R \left[ J₀q A₀ + I₀^{ext} \right] \]

Homogeneous network
All neurons are identical,
Single neuron rate = population rate

\[ \nu = g(I₀) = A₀ \]

frequency (single neuron)

\[ \nu = \langle s \rangle^{-1} = \left[ \int_0^∞ s P_t \, \hat{t} + s | \hat{t} \, ds \right]^{-1} = g(I₀) \]
Week 10-part 3: Example - Asynchronous state in SRM₀

\[ u(t \mid \hat{t}) = \eta(t - \hat{t}) + h₀ \]

\[ h₀ = RI₀ = R \left[ J₀qA₀ + I₀^{ext} \right] \]

\[ A₀ = \frac{1}{J₀qR} \left[ h₀ - RI₀^{ext} \right] \]

\[ A(t) = \text{const} \]

\[ \int \alpha(s) ds = q \]

Typical mean field (Curie Weiss)

Homogeneous network
All neurons are identical,

Frequency (single neuron)

\[ \nu = \langle s \rangle^{-1} = \left[ \int₀^{\infty} s Pₜ \hat{t} + s \mid \hat{t} ds \right]^{-1} = \tilde{g}(h₀) \]
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Week 10-part 4: mean-field arguments – random connectivity

random connectivity

- full connectivity
- random: prob p fixed
- random: number K of inputs fixed
Week 10-part 4: mean-field arguments – random connectivity

I&F with diffusive noise (stochastic spike arrival)

For any arbitrary neuron in the population

$$\tau \frac{d}{dt} I_i = -I_i + \sum_{k,f} w_{ik} q_e \delta(t - t_k^f) - \sum_{k',f'} w_{ik'} q_i \delta(t - t_{k'}^{f'})$$

Blackboard: excit. – inhib.

EPSC

IPSC

excitatory input spikes
Exercises

2. Fully connected network. Assume a fully connected network of $N$ Poisson neurons with firing rate $\nu(t) = g(I(t)) > 0$. Each neuron sends its output spikes to all other neurons as well as back to itself. When a spike arrives at the synapse from a presynaptic neuron $j$ to a postsynaptic neuron $i$ is, it generates a postsynaptic current

$$I^{\text{syn}}_i = w_{ij} \exp[-(t - t^{(f)}_j)/\tau_s] \quad \text{for} \quad t > t^{(f)}_j,$$

where $t^{(f)}_j$ is the moment when the presynaptic neuron $j$ fired a spike and $\tau_s$ is the synaptic time constant.

   a) Assume that each neuron in the network fires at the same rate $\nu$. Calculate the mean and the variance of the input current to neuron $i$.

   Hint: Use the methods of Chapter 8

   b) Assume that all weights of equal weight $w_{ij} = J_0/N$. Show that the mean input to neuron $i$ is independent of $N$ and that the variance decreases with $N$.

   c) Evaluate mean and variance and the assumption that the neuron receives 4,000 inputs at a rate of 5Hz. The synaptic time constant is 5ms and $J_0 = 1\mu A$.

2. Stochastically connected network. Consider a network analogous to that discussed in the previous exercise, but with a synaptic coupling current

$$I^{\text{syn}}_i = w_{ij} \left\{ \left( \frac{1}{\tau_1} \right) \exp[-(t - t^{(f)}_j)/\tau_1] - \left( \frac{1}{\tau_2} \right) \exp[-(t - t^{(f)}_j)/\tau_2] \right\} \quad \text{for} \quad t > t^{(f)}_j,$$

which contains both an excitatory and an inhibitory component.

   a) Calculate the mean synaptic current and its variance assuming arbitrary coupling weights $w_{ij}$. How do mean and variance depend upon the number of neurons $N$?

   b) Assume that the weights have a value $J_0/\sqrt{N}$. How do the mean and variance of the synaptic input current scale as a function of $N$?
Week 10-part 4: Random Connectivity: fixed $p$

random: probability $p=0.1$, fixed

$w_{ik} \sim \frac{J}{pN}$

**Fig. 12.7:** Simulation of a model network with a fixed connection probability $p = 0.1$. A. Top: Population activity $A(t)$ averaged over all neurons in a network of 4,000 excitatory and 1,000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen fluctuations of $A$ decrease

fluctuations of $I$ decrease

**Week 10-part 4: Random connectivity – fixed number of inputs**

random: number of inputs $K=500$, fixed $W_{ik} \sim \frac{J}{K}$

Network $N=5\,000$


Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A.** Top: Population activity $A(t)$ averaged over all neurons in a network of 4,000 excitatory and 1,000 inhibitory neurons with $K=500$. **B.** Bottom: Close-up of input fluctuations $I(t)$ for the same network. Fluctuations of $A$ decrease, but fluctuations of $I$ remain constant.
Week 10-part 4: Connectivity schemes – fixed p, but balanced

\[ \tau \frac{d}{dt} u_i = -u_i + R(\sum_{k,f} w_{ik} q_e \delta(t - t_{k,k}^f) - \sum_{k',f'} w_{ik} q_i \delta(t - t_{k',f'}^{'f})) + I_{\text{ext}} \]

- Make network bigger, but
- Keep mean input close to zero
  \[ p N_e J_e = -p N_i J_i \]
- Keep variance of input

\[
\begin{align*}
  w_{ik} &\sim \frac{J_e}{\sqrt{pN_e}} & J_e &= \text{'random'} \\
  w_{ik} &\sim \frac{J_i}{\sqrt{pN_i}} & J_i &= \text{'random'}
\end{align*}
\]
Week 10-part 4: Connectivity schemes - balanced

Fig. 12.9: Simulation of a model network with balanced excitation and inhibition and fixed connectivity $p = 0.1$. A. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen neurons. B. Same as A, but for a network with 8 000 excitatory and 2 000 inhibitory neurons. The synaptic weights have been rescaled by a factor $1/\sqrt{2}$ and the common constant input has been adjusted. All neurons are leaky integrate-and-fire units with identical parameters coupled interacting by short current pulses.

fluctuations of $A$ decrease
fluctuations of $I$ decrease, but ‘smooth’
**Week 10-part 4: leaky integrate-and-fire, balanced random network**

Network with balanced excitation-inhibition
- 10 000 neurons
- 20 percent inhibitory
- randomly connected


**Fig. 12.18:** Pairwise correlation of neurons in the Vogels-Ambott network. 
A. Excess
Fig. 12.19: Interspike interval distributions in the Vogels-Abbott network. **A.** Interspike interval distribution of a randomly chosen neuron. Note the long tail of the distribution. The width of the distribution can be characterized by a coefficient of variation of $CV = 1.9$. **B.** Distribution of the CV index across all 10 000 neurons of the network. Bin width of
Week 10 – Introduction to Neuronal Populations

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The END

Course evaluations