Recapitulation TN1

Electrical properties of neurons
Single-Compartment model
Voltage-Dependent Conductances
Hodgkin-Huxley Model
Integrate-and-fire neuron
Spatially extended neuron and synapse
Rate networks
Information theory and elements of neural coding
Hodgkin-Huxley Model

\[ c_m \frac{dV}{dt} = -i_m + \frac{I_e}{A} \]

\[ i_m = \sum_i g_i (V - E_i) \]

gating variables

Hodgkin-Huxley model:

\[ i_m = g_L (V - E_L) + g_K n^4 (V - E_K) + g_{Na} m^3 h (V - E_{Na}) \]

leak current  
delayed rectifier K⁺  
fast Na⁺

\[ \tau_n (V) \frac{dn}{dt} = n_\infty (V) - n \]

(similar equations for m and h)
Connor Stevens Model

• adds A-type potassium current to HH model:

\[ i_m = \bar{g}_L(V - E_L) + \bar{g}_K n^4 (V - E_K) + \bar{g}_Na m^3 h(V - E_{Na}) + \bar{g}_A a^3 b(V - E_A) \]

• A-type potassium current is:
  • transient
  • hyperpolarizing: \( E_A = -75 \text{mV} \)

• Effects:
  • tends to lower firing rates
  • can lead to slower spiking onset after step input
  • one mechanism to go from type II to type I behavior
  • involved in intrinsic plasticity
type I

\( \bar{g}_A \neq 0 \)

\( \bar{g}_A = 0 \)

constant current injection

current switching sign

_type II_ (as HH)
Integrate-and-fire neuron

\[
c_{m} \frac{dV}{dt} = -\overline{g}_L (V - E_L) + \frac{I_e}{A},
\]

\[
\tau_m \frac{dV}{dt} = E_L - V + R_m I_e.
\]

- Spike, whenever \( V \) crosses threshold \( V_0 \)
- Reset voltage to \( V_r \)
- Include refractory period
Irregularity of firing
### Classes of Neuron Models

<table>
<thead>
<tr>
<th>a: compartmental vs. point model</th>
<th>b: cont. activation vs. spiking</th>
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**a:**
- **Compartmental Models**
  - More realistic
  - More difficult to simulate

**b:**
- **Point Models**
  - Least realistic
  - Easiest to simulate

**Examples:**
- **a:** Neuron tree structure
- **b:** Simple linear activation curve
• so far: single compartment

• but: spatially extended neuron with different membrane potential at different locations: $V(x,t)$; cable theory

• A: delay and attenuation of action potential propagating from soma to dendrites
• B: delay and attenuation of EPSP
Linear Cable Theory

\[
\frac{\partial V}{\partial t} = \frac{1}{2ar_L} \frac{\partial}{\partial x} \left( a^2 \frac{\partial V}{\partial x} \right) - i_m + i_e
\]

Three simplifications: 1) ignore synaptic currents; 2) treat membrane current as linear function of membrane potential; 3) set radius \( a \) to be constant

\[
\tau_m \frac{\partial v}{\partial t} = \lambda^2 \frac{\partial^2 v}{\partial x^2} - v + r_m i_e
\]

\[
v = V - V_{\text{rest}}
\]

\[
i_m = (V - V_{\text{rest}})/r_m
\]

\[
\lambda = \sqrt{\frac{ar_m}{2r_L}} \quad R_\lambda = \frac{r_L \lambda}{\pi a^2}
\]

electrotonic length
Idealized cable equation with infinite cable:
A) constant current injection
B) injection of brief current pulse

A) \[ v(x) = \frac{I_e R_\lambda}{2} \exp \left( -\frac{|x|}{\lambda} \right) \]

B) \[ v(x, t) = \frac{I_e R_\lambda}{\sqrt{4\pi t/\tau_m}} \exp \left( -\frac{\tau_m x^2}{4\lambda^2 t} \right) \exp \left( -\frac{t}{\tau_m} \right) \]
• Idea: every compartment has its own membrane potential and gating variables, etc.:

\[ c_m \frac{dV_\mu}{dt} = -i^\mu_m + \frac{I_e^\mu}{A_\mu} + g_{\mu,\mu+1}(V_{\mu+1} - V_\mu) + g_{\mu,\mu-1}(V_{\mu-1} - V_\mu) \]
Example: action potential propagation along unmyelinated axon.

![Diagram of action potential propagation along an unmyelinated axon.](image)

Speed proportional to $\lambda / \tau_m = (a/(2c_m^2r_Lr_m))^{1/2}$.

Proportional to square root of axon radius. Thus, thick cable necessary for high propagation speed.
Synapses of integrate-and-fire neurons

\[ \tau_m \frac{dV}{dt} = E_L - V - r_m \bar{g} S (V - E_s) + R_m I_e \]
### Classes of Neuron Models

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**Diagram:**
- a: Neurons with detailed structure vs. simplified models
- b: Continuous activation vs. spiking patterns
Firing-Rate Models

\[ \tau_r \frac{dv}{dt} = -v + F(w \cdot u) \]
Now we're ready to look at some simple network topologies and the corresponding equations for the firing rates:

\[
\tau_r \frac{dv_a}{dt} = -v_a + F\left(\sum_{b=1}^{N_u} W_{ab} u_b\right) \\
\tau_r \frac{dv}{dt} = -v + F(Wu + Mv)
\]
• In the previous formulation, we have not imposed any restrictions on the values of the weights.
• We can express excitatory synaptic connections with positive weight values and inhibitory synaptic connections with negative weights.
• But biology tells us in the form of Dale’s law that a neuron will either excite or inhibit all of its targets.
• This leads to excitatory-inhibitory networks, where we distinguish separate populations of excitatory and inhibitory cells:

\[ \tau_E \frac{dv_E}{dt} = -v_E + F_E(W_E u + M_{EE} v_E + M_{EI} v_I) \]

\[ \tau_I \frac{dv_I}{dt} = -v_I + F_I(W_I u + M_{IE} v_E + M_{II} v_I) \]
Linear recurrent networks

- Simpler, much more amenable to analytic treatment
- E.g. by choosing
  \[ F(h + M \cdot r) = h + M \cdot r \]
- ‘Firing rates’ can be negative
- Approximates dynamics around fixed point
- Approximation often reasonable in presence of weak background activity
- In this case, firing rate is relative to baseline rate
- Rough, but often useful approximation: calculate dynamics of linear network, apply nonlinearity to solution
Solution for symmetric $\mathbf{M}$ and time-independent input $\mathbf{h}$:

Idea: Express firing rate $\mathbf{v}$ in terms of eigenvectors of $\mathbf{M}$ and solve for time-dependent coefficients $c_\mu$

\[ \mathbf{v}(t) = \sum_{\mu=1}^{N_\nu} c_\mu(t) \mathbf{e}_\mu \]

For a real symmetric matrix this is always possible. The eigenvectors satisfy

\[ \mathbf{M} \cdot \mathbf{e}_\mu = \lambda_\mu \mathbf{e}_\mu \]

They are orthogonal and can be normalized to unit length

\[ \mathbf{e}_\mu \cdot \mathbf{e}_\nu = \delta_{\mu\nu} \]

The eigenvalues $\lambda_\nu$ are real for real symmetric matrices.
Substituting

\[ \mathbf{v}(t) = \sum_{\mu=1}^{N_v} c_\mu(t) \mathbf{e}_\mu \]

into the network equation yields

\[ \tau_r \sum_{\mu=1}^{N_v} \frac{d c_\mu}{dt} \mathbf{e}_\mu = - \sum_{\mu=1}^{N_v} (1 - \lambda_\mu) c_\mu(t) \mathbf{e}_\mu + \mathbf{h} \]

Taking the dot product of each side with \( \mathbf{e}_v \) yields:

\[ \tau_r \frac{d c_v}{dt} = -(1 - \lambda_v) c_v(t) + \mathbf{e}_v \cdot \mathbf{h} \]

This involves only one coefficient \( c_\mu \), i.e. the different components are decoupled
The solution of

\[ \tau_r \frac{dc_v}{dt} = -(1 - \lambda_v)c_v(t) + e_v \cdot h \]

for time-independent input \( h \) is

\[ c_v(t) = \frac{e_v \cdot h}{1 - \lambda_v} \left( 1 - \exp \left( - \frac{t(1 - \lambda_v)}{\tau_r} \right) \right) + c_v(0) \exp \left( - \frac{t(1 - \lambda_v)}{\tau_r} \right) \]

with initial condition \( c_v(0) = e_v \cdot v(0) \)

The full solution is then obtained by \( v(t) = \sum_{\mu=1}^{N_v} c_\mu(t)e_\mu \)

The above equation for \( c_\mu(t) \) has a number of important characteristics to be discussed in the following!
\[ c_v(t) = \frac{e_v \cdot h}{1 - \lambda_v} \left( 1 - \exp \left( -\frac{t(1 - \lambda_v)}{\tau_r} \right) \right) + c_v(0) \exp \left( -\frac{t(1 - \lambda_v)}{\tau_r} \right) \]

**Discussion**

- If \( \lambda_v > 1 \), the exponential functions grow without bound, reflecting a fundamental instability
- If \( \lambda_v < 1 \), \( c_v \) approaches the steady-state value \( \frac{e_v \cdot h}{1 - \lambda_v} \) exponentially
- The time constant is \( \tau_r / (1 - \lambda_v) \)

Thus, strictly speaking, the system has no memory, i.e. the effect of the initial condition decays to zero exponentially

However, the time constant of decay can be very large, much larger than the time constant \( \tau_r \) of an individual neuron.
\[ c_v(t) = \frac{e_v \cdot h}{1 - \lambda_v} \left( 1 - \exp \left( -\frac{t(1 - \lambda_v)}{\tau_r} \right) \right) + c_v(0) \exp \left( -\frac{t(1 - \lambda_v)}{\tau_r} \right) \]

- The steady state value is proportional to \( e_v \cdot h \), the projection of the input vector onto the relevant eigenvector.

- The steady state value of the firing rate is

\[ v_\infty = \sum_{v=1}^{N_v} \frac{(e_v \cdot h)}{1 - \lambda_v} e_v \]

- Selective amplification: If one eigenvalue is close to one and all others are significantly different from one:

\[ v_\infty \approx \frac{(e_1 \cdot h)e_1}{1 - \lambda_1} \]

- More general: Projection onto \( k \)-dimensional subspace, in case of \( k \) degenerate eigenvalues close to one.