neural networks

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Hierarchy of the nervous system

1m  behaviour  CNS
10 cm  systems
1 cm  maps
1 mm  networks
100 μm  neurons
1 μm  synapses
10 nm  molecules
example II - Churchland et al. 2010
neural dynamics underlying motor control
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neural dynamics underlying motor control

large trial-to-trial variability

internally generated activity with rich temporal structure!
networks - overview

the dynamics of the network defines the computation

many different dynamics - huge variety of computation
how to model neural networks?

**bottom-up approach:** include every detail
- where to stop? dendrites? stochastic channels? molecular dynamics?
- are we going to understand the model? - analysis is difficult!
- simulations are computationally expensive!
- how to fit the model’s 1000s of parameters?

**top-down approach:** analyse simple networks
- input is so strong that the detailed dynamics of individual neurons can be less important than the network level interaction between neurons
- what are the important features we want to reproduce? how to choose our simplified model? binary? firing rate? IF?
from spikes to rates

neurons: implementing a mapping from input spike trains to a single output spike train:

\[
\begin{align*}
\rho_1(t) & \quad \Rightarrow \quad \rho^*(t) \\
\rho_2(t) & \quad \Rightarrow \quad \rho^*(t) \\
\rho_n(t) & \quad \Rightarrow \quad \rho^*(t)
\end{align*}
\]

\[
\rho^*(t) = F\left(\sum_{i=1}^{N} \rho_i(t)\right)
\]

averaging argument:

\[
\left< \sum_{i=1}^{N} \rho_i(t) \right> = \sum_{i=1}^{N} \left< \rho_i(t) \right> = \sum_{i=1}^{N} r_i(t) \propto N
\]

\[
\text{Std}\left[ \sum_{i=1}^{N} \rho_i(t) \right] \propto \sqrt{N}
\]

what if inputs can have different sign?

averaging over many independent neurons

averaging over time would lead to the same result

std is small compared to the mean
firing rate dynamics: \[ \tau_r \frac{dr}{dt} = -r + F(h + Wr) \]

\( W \): synaptic weight matrix
- symmetric
- (no self-connections)

**non-linear** recurrent networks:
- complex dynamics
- can perform difficult computations
- difficult to analyse

**linear** recurrent networks:
- simple dynamics
- only trivial computations
- easy to analyse
- not realistic (e.g., negative rates)
- first step towards nonlinear…
linear recurrent network models

firing rate dynamics:
\[ \tau_r \frac{dr}{dt} = -r + h + Wr \]

\( W \): synaptic weight matrix
  • symmetric
  • no self-connections

solution: eigenvalue decomposition
\[ We_\mu = \lambda_\mu e_\mu \]

\[ e^T_\mu e_\nu = \delta_{\mu\nu} = \begin{cases} 
1 & \text{if } \mu = \nu \\
0 & \text{otherwise} 
\end{cases} \]

\[ r(t) = \sum_{\mu=1}^{N} c_\mu(t) e_\mu \]

\[ \tau_r \frac{dc_\mu}{dt} = -(1 - \lambda_\mu)c_\mu + e^T_\mu h \]

\[ c_\mu(t) = \frac{e^T_\mu h}{1 - \lambda_\mu} + \left(c_\mu(0) - \frac{e^T_\mu h}{1 - \lambda_\mu}\right)e^{-t/(\tau_r/(1-\lambda_\mu))} \]

for normal matrices (loosely when \( W \) is symmetric),
eigenvectors are orthogonal.
linear recurrent network models

firing rate dynamics: \( \tau_r \frac{dr}{dt} = -r + \mathbf{h} + \mathbf{Wr} \)

**\( \mathbf{W} \): synaptic weight matrix**
- symmetric
- no self-connections

\[ \tau_\mu = \frac{\tau_r}{1 - \lambda_\mu} = \begin{cases} 
\lambda_\mu < 0 & \tau_\mu < \tau_r \rightarrow \text{fast dynamics} \\
0 < \lambda_\mu < 1 & \tau_\mu > \tau_r \rightarrow \text{slow dynamics} \\
1 < \lambda_\mu & \tau_\mu < 0 \rightarrow \text{unstable dynamics}
\end{cases} \]

**solution:** eigenvalue decomposition

\( \mathbf{W} \mathbf{e}_\mu = \lambda_\mu \mathbf{e}_\mu \)

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

\[ \tau_r \frac{dc_\mu}{dt} = -(1 - \lambda_\mu)c_\mu + \mathbf{e}_\mu^T \mathbf{h} \]

\[ c_\mu(t) = \frac{\mathbf{e}_\mu^T \mathbf{h}}{1 - \lambda_\mu} + \left( c_\mu(0) - \frac{\mathbf{e}_\mu^T \mathbf{h}}{1 - \lambda_\mu} \right) e^{-t/(\tau_r/(1-\lambda_\mu))} \]
the value of the eigenvalues determine the dynamics

\[
W = \begin{pmatrix}
W_{11} & W_{21} \\
W_{12} & W_{22}
\end{pmatrix} = \begin{pmatrix}
0.325 & -0.22 \\
-0.22 & 0.575
\end{pmatrix}
\]

\[
\begin{align*}
\lambda_1 &= 0.7 \\
\lambda_2 &= 0.2
\end{align*}
\]

\[
\tau_r \frac{dr}{dt} = -r + h + Wr
\]

\[
c_\mu(t) = c_\mu(0) e^{-t/\left(\tau_r/(1-\lambda_\mu)\right)}
\]

\[
\tau_\mu = \frac{\tau_r}{1-\lambda_\mu} = \begin{cases}
\lambda_\mu < 0 & \tau_\mu < \tau_r \rightarrow \text{fast dynamics} \\
0 < \lambda_\mu < 1 & \tau_\mu > \tau_r \rightarrow \text{slow dynamics} \\
1 < \lambda_\mu & \tau_\mu < 0 \rightarrow \text{unstable dynamics}
\end{cases}
\]

Connectivity causes slowing

- Connected
- Unconnected
the value of the eigenvalues determine the dynamics

\[ \tau_r \frac{dr}{dt} = -r + h + Wr \]

\[ W = \begin{pmatrix} W_{11} & W_{21} \\ W_{12} & W_{22} \end{pmatrix} = \begin{pmatrix} 0.325 & -0.22 \\ -0.22 & 0.575 \end{pmatrix} \]

\[ \lambda_1 = 0.7 \]
\[ \lambda_2 = 0.2 \]

\[ c_\mu(t) = \frac{e^\mu h}{1 - \lambda_\mu} + \left( c_\mu(0) - \frac{e^\mu h}{1 - \lambda_\mu} \right) e^{-t/(\tau_r/(1-\lambda_\mu))} \]
the value of the eigenvalues determine the dynamics

\[ \frac{dr}{dt} = -r + h + Wr \]

\[ W = \begin{pmatrix} W_{11} & W_{21} \\ W_{12} & W_{22} \end{pmatrix} = \begin{pmatrix} -1.25 & 0.43 \\ 0.43 & -1.75 \end{pmatrix} \]

\[ \lambda_1 = -1 \]

\[ \lambda_2 = -2 \]

\[ c_\mu(t) = \frac{e_\mu^T h}{1 - \lambda_\mu} + \left( c_\mu(0) - \frac{e_\mu^T h}{1 - \lambda_\mu} \right) e^{-t/(\tau_r/(1-\lambda_\mu))} \]
homework problem

\[ W = \begin{pmatrix} W_{11} & W_{21} \\ W_{12} & W_{22} \end{pmatrix} = \begin{pmatrix} 4/5 & \sqrt{3}/5 \\ \sqrt{3}/5 & 2/5 \end{pmatrix} \]

\[ \tau_r \frac{dr}{dt} = -r + h + Wr \]

- Milyen aktivitást mutat a hálózat bemenetek hiányában tetszőleges kezdeti feltétel esetén, és hogyan reagál a külső bemenetekre? (4p)
- Miként változik meg a hálózat dinamikája, hogyha a súlymátrix jobb alsó elemét megváltoztatom (pl. \( W_{22} = 1/5 \) vagy \( W_{22} = 3/5 \))? (2p)
- Hogyan értelmeznéd ezeket az eredményeket? Milyen számításokat végéznek az egyes a neuronhálózatok? Milyen biológiai vagy komputációs problémát vetnek fel a megfigyelt aktivitásmintázatok? (4p)
symmetric, linear nets

Data

connected
unconnected
excitatory - inhibitory (EI) networks

Previous assumption: symmetric $W$: $W_{ij} = W_{ji}$

Dale’s law: neurons are either excitatory or inhibitory

EI networks:
Eigenvectors of non-normal matrices are not orthogonal!

eigenmodes do not give an intuitive picture about the dynamics of the network
example of a non-normal network

\[ \tau_r \frac{dr}{dt} = -r + h + Wr \]

\[ W = \begin{pmatrix} W_{11} & W_{21} \\ W_{12} & W_{22} \end{pmatrix} = \begin{pmatrix} 4 & -4.4 \\ 4 & -4.4 \end{pmatrix} \]

\[ \lambda_1 = -1.4 \]

\[ \lambda_2 = -1 \]

large initial eigenmodes

eigenmodes decay exponentially as before

transient activity

connected

unconnected
structured El nets are able to generate rich transients
is the large variability of spikes consistent with the large number of synapses?

Consistency argument:

- incoming and outgoing rates should be matched

\[ N \sim 10,000 \text{ incoming synapses:} \]

\[
\begin{align*}
r^* &\approx \sum_{i=1}^{N} g r_i; \quad \mathbb{E}[r_i] = r; \quad \text{Var}[r_i] = \sigma^2 \\
\end{align*}
\]

\[ g \approx \frac{1}{N} \]

\[
\begin{align*}
\mathbb{E}[r^*] &= \frac{1}{N} \sum_{i=1}^{N} \mathbb{E}[r_i(t)] = r \\
\text{Var}[r^*] &= \frac{1}{N^2} \sum_{i=1}^{N} \text{Var}[r_i(t)] = \frac{1}{N} \sigma^2 \approx 0
\end{align*}
\]

gets the mean but misses the variance
is the large variability of spikes consistent with the large number of synapses?

Consistency argument:
• incoming and outgoing rates should be matched
N ∼ 10,000 incoming synapses:

\[ r^* \approx \sum_{i=1}^{N} g r_i; \quad E[r_i] = r; \quad \text{Var}[r_i] = \sigma^2 \]

\[ r^* \approx r \iff g \sum_{i=1}^{N} r_i(t) \approx O(1) \]

\[ g \approx \frac{1}{N} \]

\[ E[r^*] = \frac{1}{N} \sum_{i=1}^{N} E[r_i(t)] = r \]

\[ \text{Var}[r^*] = \frac{1}{N^2} \sum_{i=1}^{N} \text{Var}[r_i(t)] = \frac{1}{N} \sigma^2 \approx 0 \]

\[ g \approx \frac{1}{\sqrt{N}} \]

\[ E[r^*] = \frac{1}{\sqrt{N}} \sum_{i=1}^{N} E[r_i(t)] = \sqrt{N} r \]

\[ \text{Var}[r^*] = \frac{1}{N} \sum_{i=1}^{N} \text{Var}[r_i(t)] \approx \sigma^2 \]
excitatory - inhibitory (EI) networks

- Internally generated activity with rich temporal structure!
- Large trial-to-trial variability
- CV: std/mean, ~1 for a Poisson process
what we learned:

• activity dynamics in linear symmetric networks
• eigenvalues and eigenvectors
• rich transients in non-normal networks
• balance of excitation and inhibition is responsible for irregular firing

what we missed:

• computation
• nonlinear networks
• spiking networks

slides are based on
David Barrett's slides (University of Cambridge)
Dayan and Abbott: Theoretical Neuroscience (2001)
Guillaume Hennequin's (U Cam) tutorial and papers (Hennequin et al., 2009)
Murphy and Miller, 2009, Vogels et al., 2005