Part 2.1

Neural Decoding

How neural activities relate to an animal's behavior
Derivatives and Integration:

\[ f(x) = \frac{d}{dx} F(x) \quad \Rightarrow \quad \int_a^b dx \ f(x) = F(b) - F(a) \]
Probability Theory

Apples and Oranges
Probability Theory

Joint Probability

\[ p(X = x_i, Y = y_j) = \frac{n_{ij}}{N} \]

Marginal Probability

\[ p(X = x_i) = \frac{c_i}{N}. \]

Conditional Probability

\[ p(Y = y_j | X = x_i) = \frac{n_{ij}}{c_i} \]
Probability Theory

**Sum Rule**

\[
p(X = x_i) = \frac{c_i}{N} = \frac{1}{N} \sum_{j=1}^{L} n_{ij}
\]

\[
= \sum_{j=1}^{L} p(X = x_i, Y = y_j)
\]

**Product Rule**

\[
p(X = x_i, Y = y_j) = \frac{n_{ij}}{N} = \frac{n_{ij}}{c_i} \cdot \frac{c_i}{N}
\]

\[
= p(Y = y_j | X = x_i) p(X = x_i)
\]
The Rules of Probability

- Sum Rule
  \[ p(X) = \sum_{Y} p(X, Y) \]

- Product Rule
  \[ p(X, Y) = p(Y|X)p(X) \]
Bayes’ Theorem

\[ p(Y|X) = \frac{p(X|Y)p(Y)}{p(X)} \]

\[ p(X) = \sum_Y p(X|Y)p(Y) \]

posterior \( \propto \) likelihood \( \times \) prior
probability:  
**discrete variable**  
\[ x \in A = \{a_1, a_2, a_3, \ldots\} \]
probability to obtain the value \( x \):
\[ p(x) \]
Math reminder: probabilities

probability:
discrete variable

\[ x \in A = \{a_1, a_2, a_3, \ldots\} \]

probability to obtain the value \( x \):

\[ p(x) \]

probability to obtain a value within \( x \in \Omega \subset A \):

\[ \sum_{x \in \Omega} p(x) \]
Math reminder: probabilities

probability:

discrete variable

\[ x \in A = \{a_1, a_2, a_3, \ldots\} \]

probability to obtain the value \( x \):

\[ p(x) \]

probability to obtain a value within \( x \in \Omega \subset A \):

\[ \sum_{x \in \Omega} p(x) \]

probability to obtain a value within \( x \in A \):

\[ \sum_{x \in A} p(x) = 1 \]
Math reminder: probabilities

probability: discrete variable
\[ x \in A = \{a_1, a_2, a_3, \ldots\} \]

probability to obtain the value \( x \):
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probability to obtain a value within \( x \in \Omega \subset A \):
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probability to obtain a value within \( x \in A \):
\[ \sum_{x \in A} p(x) = 1 \]

probability density: continuous variable
\[ x \in [a, b] \subset \mathbb{R} \]
Math reminder: probabilities

**probability:**
- **discrete variable**
  \[ x \in A = \{a_1, a_2, a_3, \ldots\} \]
  probability to obtain the value \( x \):
  \[ p(x) \]

**probability to obtain a value within** \( x \in \Omega \subset A \):
\[
\sum_{x \in \Omega} p(x)
\]

**probability to obtain a value within** \( x \in A \):
\[
\sum_{x \in A} p(x) = 1
\]

**probability density:**
- **continuous variable**
  \[ x \in [a, b] \subset \mathbb{R} \]
  probability to obtain a value within \( [x, x + dx] \):
  \[ p(x) \, dx \]
  probability to obtain a value with \( c < x < d \):
  \[
  \int_{c}^{d} dx \, p(x)
  \]
Math reminder: probabilities

probability: discrete variable
\[ x \in A = \{a_1, a_2, a_3, \ldots\} \]
probability to obtain the value \( x \):
\[ p(x) \]
probability to obtain a value within \( x \in \Omega \subset A \):
\[ \sum_{x \in \Omega} p(x) \]
probability to obtain a value within \( x \in A \):
\[ \sum_{x \in A} p(x) = 1 \]

probability density: continuous variable
\[ x \in [a, b] \subset R \]
probability to obtain a value within \([x, x + dx] \):
\[ p(x)dx \]
probability to obtain a value with \( c < x < d \):
\[ \int_{c}^{d} dx \, p(x) \]
probability to obtain a value with \( a < x < b \):
\[ \int_{a}^{b} dx \, p(x) = 1 \]
Example: Gaussian distribution

\[
x \sim N(\mu, \sigma^2)
\]

\[
p(x) = \frac{1}{\sigma \sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}
\]

\[
\int_{-\infty}^{\infty} dx \ p(x) = 1
\]

\[
\sigma \quad \text{standard deviation}
\]

\[
\sigma^2 \quad \text{variance}
\]

\[
\mu \quad \text{mean}
\]
Probability Densities

\[ p(x) \geq 0 \quad \int_{-\infty}^{\infty} p(x) \, dx = 1 \]

\[ p(x \in (a, b)) = \int_{a}^{b} p(x) \, dx \]

\[ P(z) = \int_{-\infty}^{z} p(x) \, dx \]
What we had so far

Sensory Stimuli
(including rewards)

Organism

Behavioral Response
(decisions, actions, etc)
What we had so far

Sensory Stimuli
(including rewards)

Organism

Behavioral Responses
(actions, decisions, etc)

Model:
- Rescorla-Wagner
- Reinforcement Learning
- Bayesian Models etc.

conditional probability!
What we want now

Sensory Stimuli
(including rewards)

Organism

Neural activities:

Behavioral Response
(decisions, actions, etc)

s → r → a

Cogmaster CO6 / Christian Machens
Activity in the brain
fMRI (non-invasive)

fMRI = functional Magnetic Resonance Imaging

+ record activity in the whole brain (!)
- activity = BOLD (Blood-oxygen-level dependent signal)
- averages over millions of neurons, slow time course
- signal is noisy

Cogmaster CO6 / Christian Machens
Microscope Imaging (invasive)

Calcium imaging

- single cell resolution of activity of hundreds of neurons
- no single spike resolution
- signal is noisy
- difficult to record in vivo

![Image of calcium imaging](image-url)
Microscope Imaging (invasive)

Voltage-sensitive dyes

- single cell resolution of hundreds of neurons (!)
- dyes affect tissue
- signal is noisy
- difficult to do in vivo recordings
Electrode Recordings (invasive)

One electrode / several electrodes (extracellular)

- can measure spike train activity of single cells
- only a few cells at a time, only indirect identification
- sampling bias towards active neurons

Cogmaster CO6 / Christian Machens
Electrode Recordings (invasive)

One electrode (intracellular)

- can measure intracellular activity of single cells
- only one cell at a time
- sampling bias towards large cells
- very difficult in vivo
Electrode Recordings (invasive)

Tetrodes (extracellular)

- can measure spike train activity of 10-100 cells
- only indirect cell identification
- elaborate spike sorting required

Cogmaster CO6 / Christian Machens
Electrode Recordings (invasive)

Electrode arrays (extracellular)

+ can measure spike train activity of 100s of cells
- only indirect cell identification
- can only record at the brain surface
Example: Classical Conditioning

Training:
- Sound → Food → Salivation

Neural activities:
- Activity of single neurons in the dopaminergic system
TD-learning: prediction error

before training:

stimulus $u(t)$
reward $r(t)$
prediction error

$\delta(t) \approx r(t) + \nu(t+1) - \nu(t)$

after training:

unpredictable timing

stimulus $u(t)$
reward $r(t)$
prediction error $\delta(t)$

unpredictable timing
Activity of dopamine neurons

Behavior:
Classical Conditioning

Schultz, Dayan, Montague, Science 1997
Sensory processing

Sensory Stimuli (including rewards)

Organism

Neural activities:

\( S \rightarrow r \)
Neural Encoding

Encoding: given a stimulus, what will the neural response be?

Sensory Stimuli $S$

Neural System

$p(r|s)$

Neural Responses
Neural Encoding

Encoding: given a stimulus, what will be the neural response be?

\[ p(r|s) \]

Sensory Stimuli \( S \)

Neural Responses

soon to come ...
Neural Decoding

Decoding: given a neural response, what was the stimulus?

\[ p(s | r) \]

Sensory Stimuli \( p(s | r) \)

Neural Responses \( r \)
Detecting weak flashes of light
Detecting weak flashes of light
Detecting weak flashes of light
Psychophysical threshold curve

Hecht et al (1942)
Psychophysical threshold curve

Hecht et al (1942)
Psychophysical threshold curve

Flashes seen - percent

Logarithm of average number of photons per flash

S.H.

n=6

Hecht et al (1942)
Psychophysical threshold curve

What are the neural processes underlying the perception of the light flashes?

Hecht et al (1942)
Cat retinal ganglion cell

Barlow et al (1971)
Cat retinal ganglion cell

Assumption: transmission of the flash of light by a single ganglion cell

Barlow et al (1971)
Cat retinal ganglion cell

Barlow et al (1971)
Based on the output of this cell, what would an ideal observer decide?

Barlow et al (1971)
Cat retinal ganglion cell

Based on the output of this cell, what would an ideal observer decide?

Barlow et al (1971)
The neuron’s response

$p(r|\neg)$

no flash

$p(r|\neg)$

flash

probability

firing rate (Hz)
The neuron’s response

Note! These are probability densities with

\[ \int_0^\infty dr \, p(r|+) = 1 \]

\[ \int_0^\infty dr \, p(r|-) = 1 \]
“Did you see a flash?”

<table>
<thead>
<tr>
<th>Did You See A Flash?</th>
<th>Answer “Yes”</th>
<th>Answer “No”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flash</td>
<td>Correct (“Hit”)</td>
<td>False (“Miss”)</td>
</tr>
<tr>
<td>No Flash</td>
<td>False (“False Alarm”)</td>
<td>Correct</td>
</tr>
</tbody>
</table>
The ideal observer

\[ z = 50 \text{ Hz} \]

\[ p(r|-) \quad \text{no flash} \quad p(r|+) \quad \text{flash} \]

\[ z = 50 \text{ Hz} \]
The ideal observer: “Hits”

\[ z = 50 \text{ Hz} \]

\[ \beta(z) = P(r \geq z | +) = \int_{z}^{\infty} dr' p(r' | +) \]

- \[ p(r | -) \]
- \[ p(r | +) \]

Hit rate \( \beta \)

- Probability
  - Y-axis: 0 to 0.05
  - X-axis: 0 to 100
- Firing rate (Hz)

False alarm rate \( \alpha \)

- Y-axis: 0 to 1
- X-axis: 0 to 1
The ideal observer: “False alarms”

\[ \alpha(z) = P(r \geq z | -) = \int_{z}^{\infty} dr' \, p(r' | -) \]

\( z = 50 \text{ Hz} \)

false alarm rate \( \alpha \)
"Did you see a flash?"

<table>
<thead>
<tr>
<th>&quot;Did you?&quot;</th>
<th>Answer &quot;Yes&quot;</th>
<th>Answer &quot;No&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flash</td>
<td>Correct/ Hit $\beta(z)$</td>
<td>False/ Miss $1 - \beta(z)$</td>
</tr>
<tr>
<td>No Flash</td>
<td>False/ False Alarm $\alpha(z)$</td>
<td>Correct $1 - \alpha(z)$</td>
</tr>
</tbody>
</table>
Discrimination threshold

\[ z = 50 \text{ Hz} \]

- **Probability**
  - X-axis: Firing rate (Hz)
  - Y-axis: Probability

- **Hit rate \( \beta \)**
  - X-axis: False alarm rate \( \alpha \)
  - Y-axis: Hit rate \( \beta \)
What if a “miss” is more expensive?

(Example: you missed the tiger...)

<table>
<thead>
<tr>
<th>“Tiger?”</th>
<th>Answer “Yes”</th>
<th>Answer “No”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiger</td>
<td>Hit: Rescued!</td>
<td>Miss: Pay with your life.</td>
</tr>
<tr>
<td>No Tiger</td>
<td>False Alarm: Be laughed at.</td>
<td>Correct.</td>
</tr>
</tbody>
</table>
Moving the discrimination threshold
(don’t want to miss the flash!)

$z = 40 \text{ Hz}$

- Probability distribution of firing rate (Hz)
- Hit rate $\beta$ vs. false alarm rate $\alpha$
What if a “false alarm” is more expensive?

(Example: early start on the 100m race...)

<table>
<thead>
<tr>
<th>“Start?”</th>
<th>Answer “Yes”</th>
<th>Answer “No”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start Signal</td>
<td>Hit: Off you go!</td>
<td>Miss: Too slow!</td>
</tr>
<tr>
<td>No Start Signal</td>
<td>False Alarm: Disqualified!</td>
<td>Correct: Keep waiting.</td>
</tr>
</tbody>
</table>
Moving the discrimination threshold
(don’t want to produce a false alarm!)

\[ z = 64 \text{ Hz} \]

![Graph showing probability distributions and hit rates](image)
Moving the discrimination threshold
“Receiver-operating characteristics”

(ROC curve)
"Receiver-operating characteristics"

(ROC curve)

![Graph showing probability vs. firing rate (Hz) and hit rate vs. false alarm rate (α).]
"Receiver-operating characteristics"

(ROC curve)

How different are the distributions?
ROC curve and distribution overlap
ROC curve and distribution overlap

- Probability vs. firing rate (Hz)
- Hit rate $\beta$ vs. false alarm rate $\alpha$
ROC curve and distribution overlap

- **Probability vs. Firing Rate (Hz)**
  - Two overlapped distributions.
  - Red and blue lines.

- **Hit Rate $\beta$ vs. False Alarm Rate $\alpha$**
  - Green curve.
  - Y-axis from 0 to 1.
  - X-axis from 0 to 1.
ROC curve and distribution overlap
ROC curve and distribution overlap

- **Left graph**: Distribution of firing rate (Hz) with probability on the y-axis.
- **Right graph**: Hit rate $\beta$ against false alarm rate $\alpha$. The curve approaches 1 as $\alpha$ increases.
Measure of the difference of two distributions: Area under ROC curve

\[
AUC = \int_{0}^{1} d\alpha \beta(\alpha)
\]
Motion discrimination task
Motion discrimination task

0% coherence

50% coherence

100% coherence
Psychophysical threshold curve

fraction correct vs coherence (%)
Motion-sensitive neurons in MT

Macaque

FP

Screen
Motion-sensitive neurons in MT

Macaque

Electrode

Receptive Field

Screen

V1 (striate cortex)

V2

V3

V3A

V4

V5 (MT)

V5A

FP
Motion-sensitive neurons in MT

- Preferred Motion Direction (Cell fires)
- Receptive Field
- FP
- Screen
- Electrode
Motion-sensitive neurons in MT
Responses of a single neuron

![Diagram of a brain with labeled areas and an electrode](image)

**B**

- **Opposite Direction**
  - Coherence = 12.8%

- **Preferred Direction**
  - Coherence = 3.2%
  - Coherence = 0.8%

![Graphs showing firing rate distribution](image)
Decoding motion direction

"Did the dots move to the right?"

$p(r|-)$  $p(r|+)$

Firing rate distribution:
- Red curve: Distribution of firing rates if stimulus moved leftward.
- Blue curve: Distribution of firing rates if stimulus moved rightward.
ROC analysis for single neuron

"hit" vs. "false alarm" graph with motion coherence indicated.
Decoding with two neurons

Instead of using a fixed threshold, the monkey could also compare two neurons with opposite tuning.

Discrimination strategy: Decide for rightward movement if

\[ r_1 > r_2 \]
Decoding with two neurons

In this case, the probability of being correct equals the area under the ROC curve!

\[ p(\text{correct}) = \text{AUC} = \int_{0}^{1} d\alpha \beta(\alpha) \]
Psychophysical threshold curve
“Ideal observer”

Result:
A single neuron performs almost as well as the monkey!!!
Neurons can be "better" than monkey!
Neurons can be “better” than monkey!

Ok, but do these neurons really carry any information about the actual choice?
Neural Decoding

Decoding: given a neural response, what was the stimulus?

\[ p(s | r) \]

conditional probability!

Sensory Stimuli

neural system

Neural Responses
From stimulus to response

Sensory Stimuli (including rewards) \[ s \rightarrow \text{Organism} \rightarrow \text{Behavioral Response} \rightarrow a \]

Neural activities: hemodynamics
activity of 100s of neurons at the same time
From neural activity to behavior

Organism

Neural activities:

r

hemodynamics
activity of 100s of neurons at the same time

Behavioral Response
(decisions, actions, etc)

→ a
Decision-making / “Motor” processing

Neural Responses $r$ → neural system → Behavioral Response $a$
Neural Decoding

Neural Responses \( r \) → neural system → Behavioral Response \( p(a|r) \)
Neural Encoding

Neural Responses: $p(r|a)$

Behavioral Response: $a$
Neural activities as function of decision

- **0% coherence**
  - decision = preferred direction
  - decision = opposite direction

**Proportion of trials**

**Response (impulses/sec)**

Britten et al (1996)
Can an ideal observer predict the monkey’s choice?

\[ p(\text{correct}) = \text{AUC} = \int_{0}^{1} d\alpha \beta(\alpha) \]
Choice probability

= probability that the monkey decides
“motion direction = cell’s preferred direction”

Britten et al (1996)