# Theoretical systems neuroscience

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Baylor College of Medicine

- Big goal: understand relation between neural activity and behavior in quantitative terms
- Representation and computation
- Focus on perception

# Class schedule

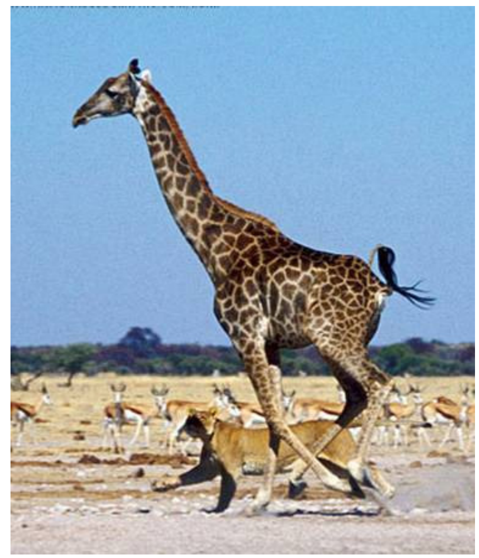
| | |
|---|---|
| Tue March 17 | Population encoding and decoding |
| Thu March 19 | Correlated activity in neural populations |
| Tue March 24 | Theories of perception |
| Thu March 26 | Cue combination |
| Tue March 31 | Bayesian models of perceptual tasks |
| ***Thu April 2*** | ***No class*** |
| Tue April 7 | Neural basis of Bayesian inference |
| Thu April 9 | Decision-making |
| Tue April 14 | Learning |
| Thu April 16 | Probabilistic models of cognition |

# Procedures

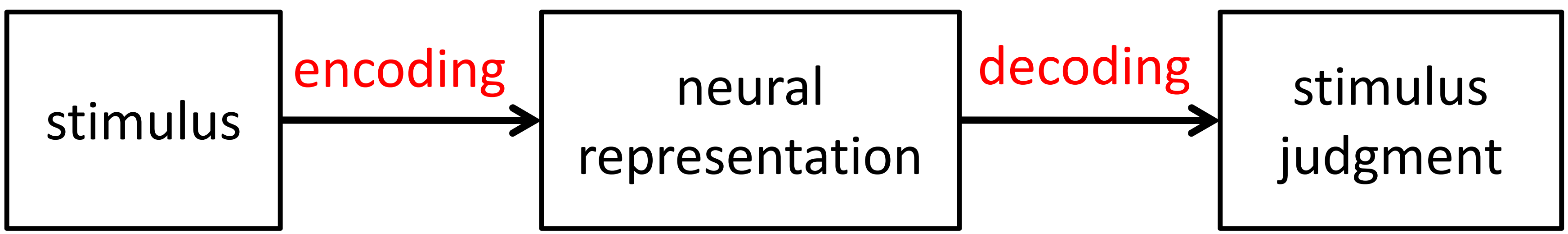
- Exercises
  - Some will be done in class, rest is homework
  - Will help a lot in understanding
  - Those marked “bonus” are optional
  - Due each Saturday - email to wjma@bcm.edu
  - Solutions will be discussed each Tuesday
  - Questions? Email or call at 713 798 8407
- Readings: for every Thursday lecture
- Comments very welcome!

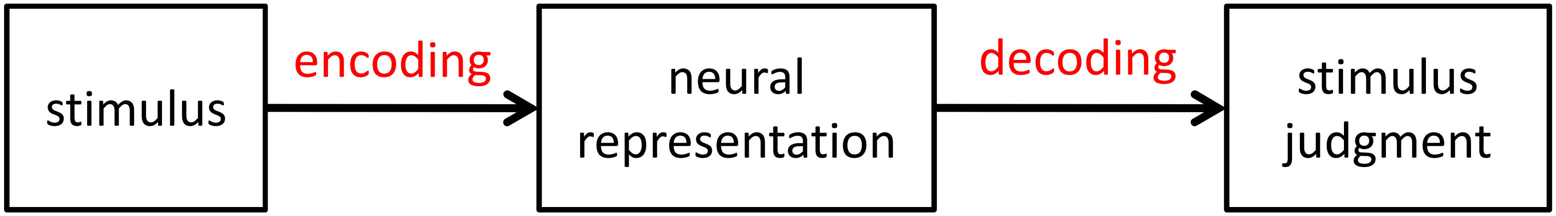
# Lecture 1:
# Population encoding and decoding

# Why do we have a brain?



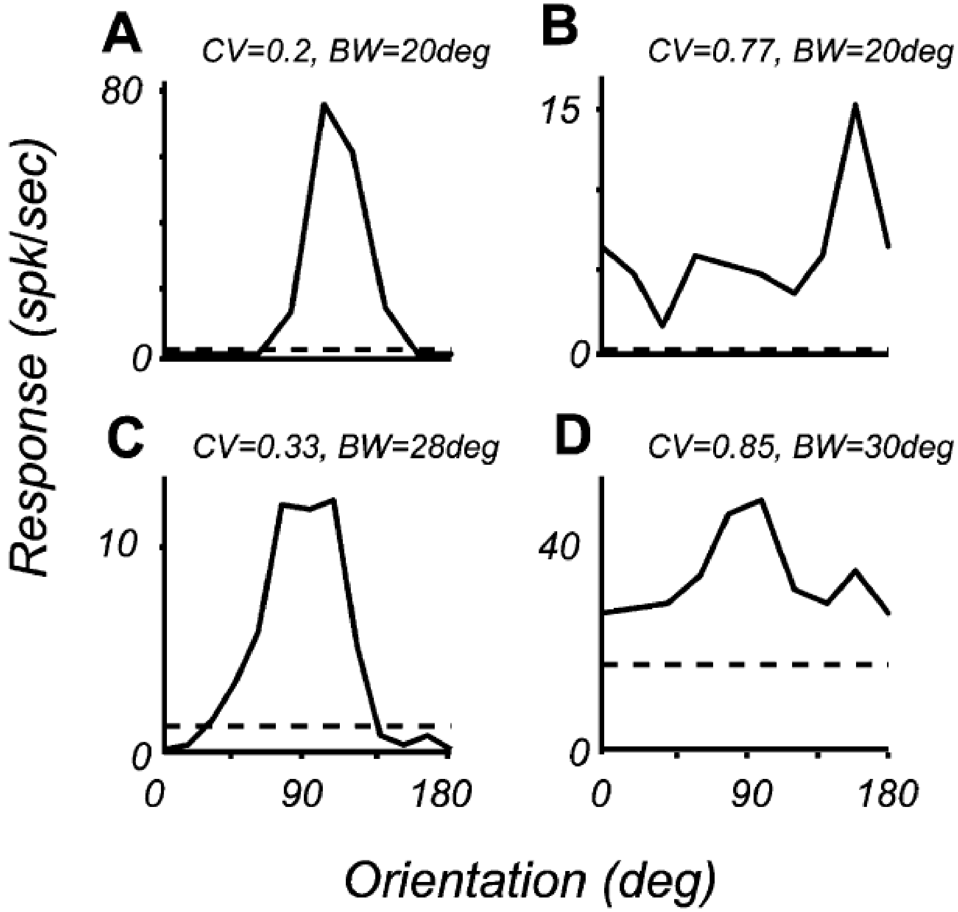
Essential function: using sensory information to guide motor actions


stimulus
encoding
neural representation
decoding
stimulus judgment



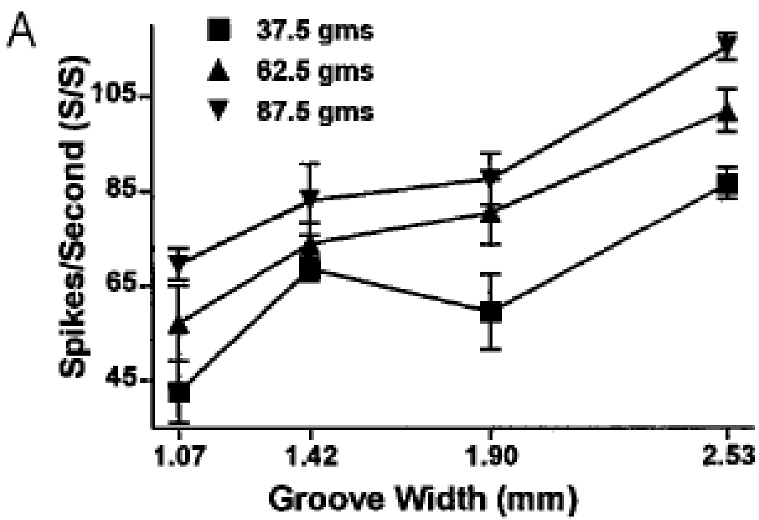

- Stimulus: physical feature of the world (often 1D)
  - Orientation of a contour
  - Direction of self-motion
  - Number of students in class
  - Whether object A is bigger than object B
  - ….
- Neural representation: spike activity of neurons in response to stimulus (population code)
- Stimulus judgment: often motor response
- Not in this framework: computation

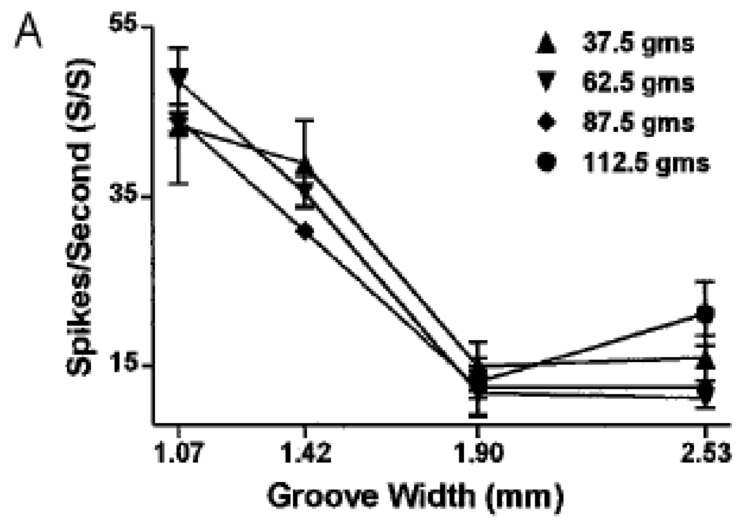
# Tuning curve of a single neuron




Macaque V1
Shapley et al., 2003

# Tuning curve of a single neuron

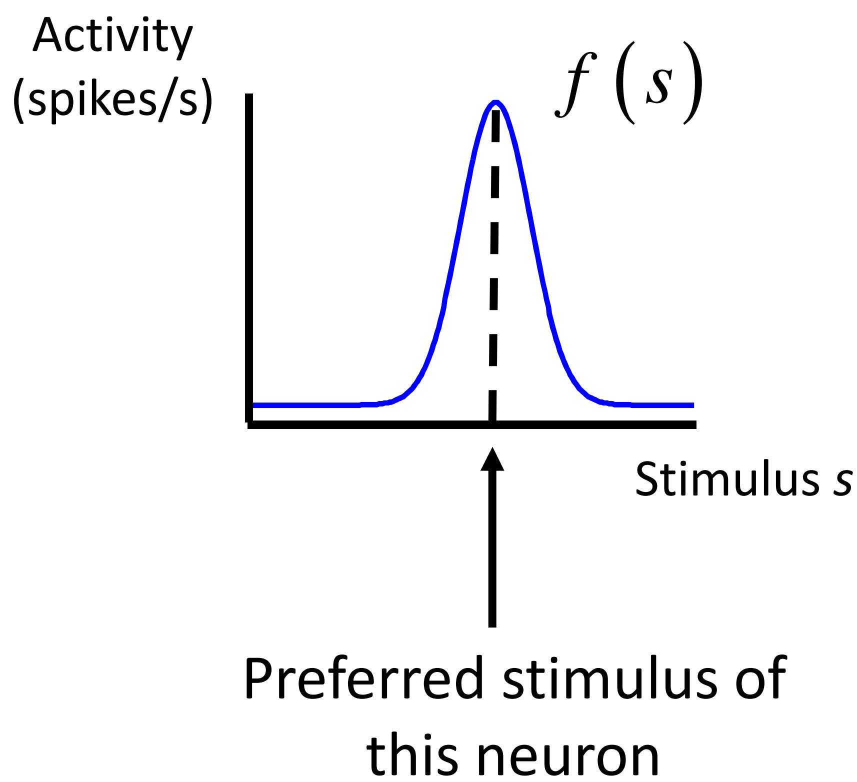


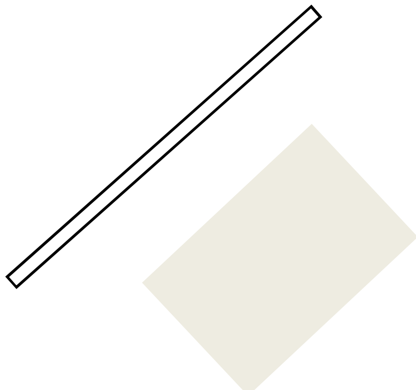

Macaque S2
Pruett et al., 2000

# Tuning curve of a single neuron

Mean response as a function of the stimulus

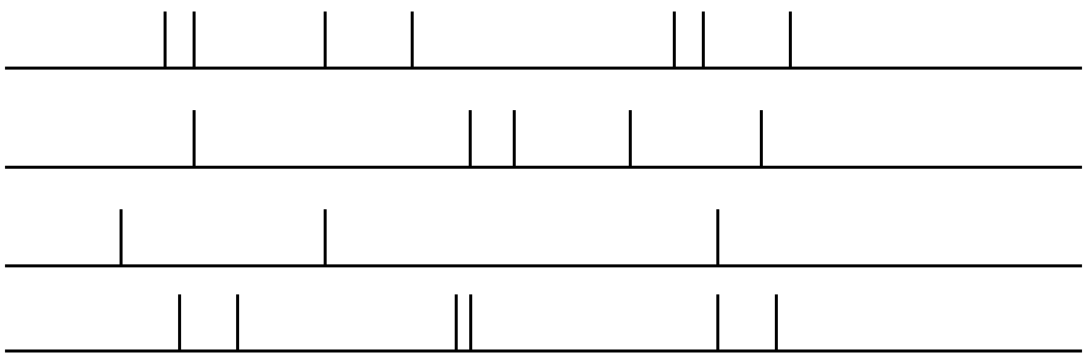


# Variability around the mean response



Response distribution: $p(r \mid s)$

Variability is <u>Poisson-like</u>*:* spike count variance proportional to mean



Trial 1: 7 spikes

Trial 2: 5 spikes

Trial 3: 3 spikes

Trial 4: 6 spikes

# Poisson variability

- Discrete distribution (spike counts)

$$p(r \mid s) = \frac{e^{-f(s)} f(s)^r}{r!}$$

- Variance = mean = $f(s)$.
- $r$ is an integer, $f(s)$ not necessarily
- Fano factor = Variance/mean = 1
  (Physiology: near Poisson, but Fano not 1)

# Gaussian Variability

- Continuous distribution

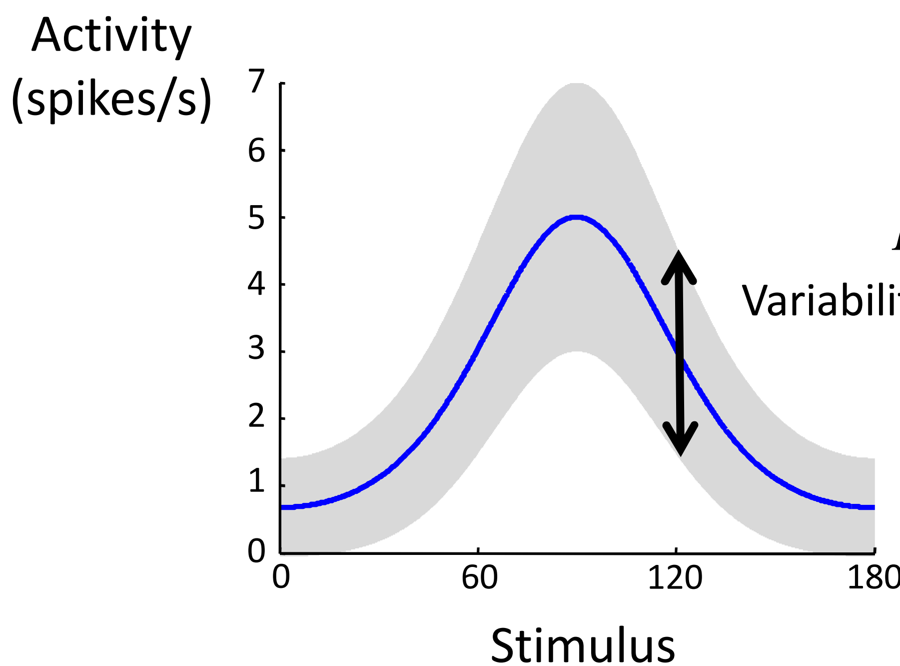
$$p(r \mid s) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(r-f(s))^2}{2\sigma^2}}$$

- Problem at small means
- Variance is not fixed →

$$p(r \mid s) = \frac{1}{\sqrt{2\pi\sigma(s)^2}} e^{-\frac{(r-f(s))^2}{2\sigma(s)^2}}$$

- Very similar to Poisson for large means

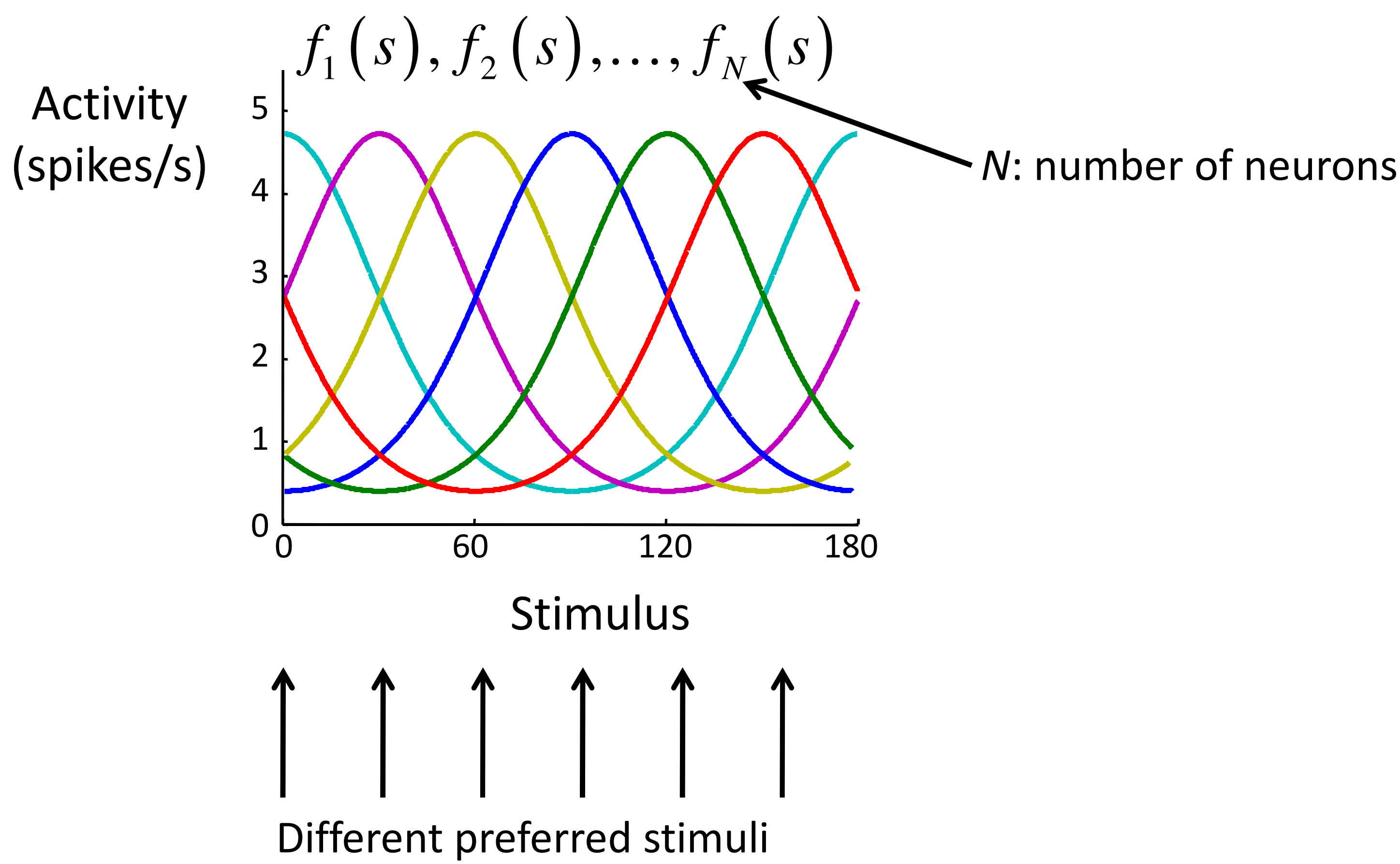
# Single neuron – response variability



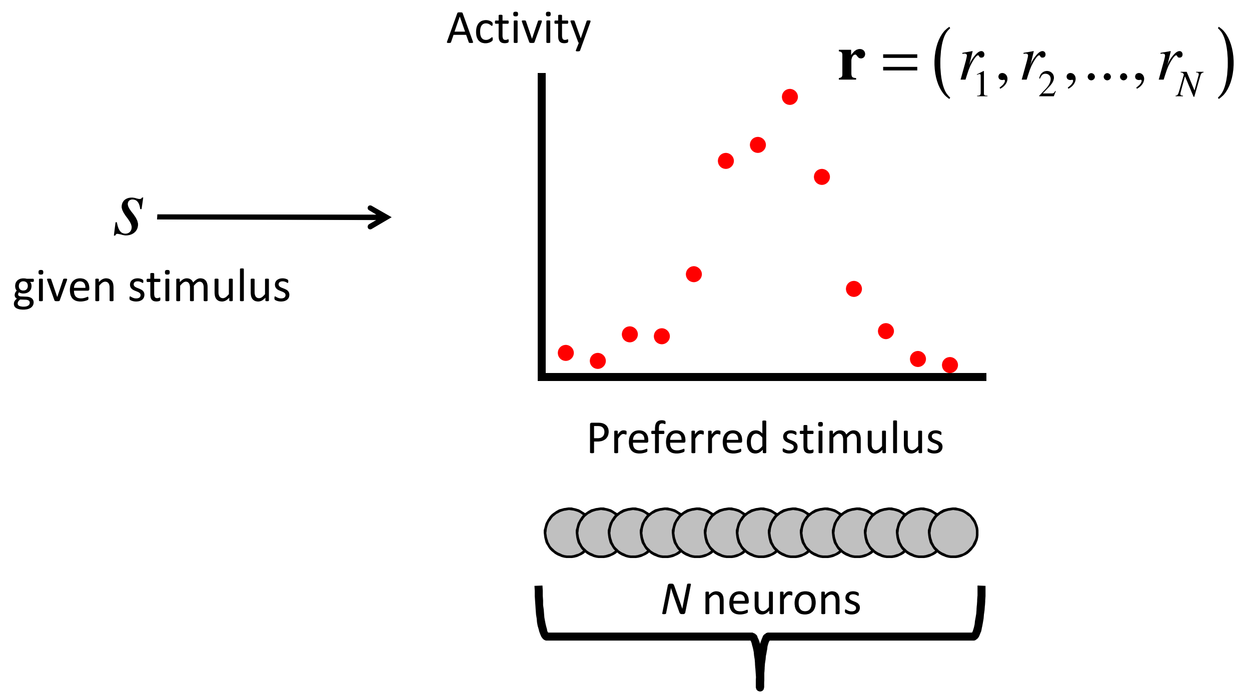

$$p(r \mid s)$$

Variability depends on stimulus

# Population of neurons

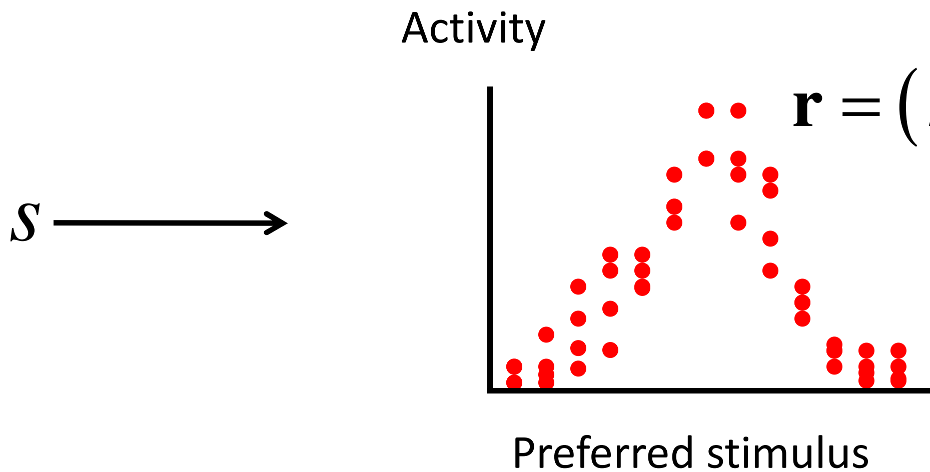


# Population activity on a single trial




These are now different neurons,
not different stimuli!

# Population activity – variability




$$\mathbf{r} = \left(r_1, r_2, \ldots, r_N\right)$$

Response distribution
(noise distribution): $p\left(\mathbf{r} \mid s\right)$

# Independent Poisson variability

One neuron:

$$p(r \mid s) = \frac{e^{-f(s)} f(s)^r}{r!}$$

Population:

$$p(\mathbf{r} \mid s) = \prod_{i=1}^{N} \frac{e^{-f_i(s)} f_i(s)^{r_i}}{r_i!}$$

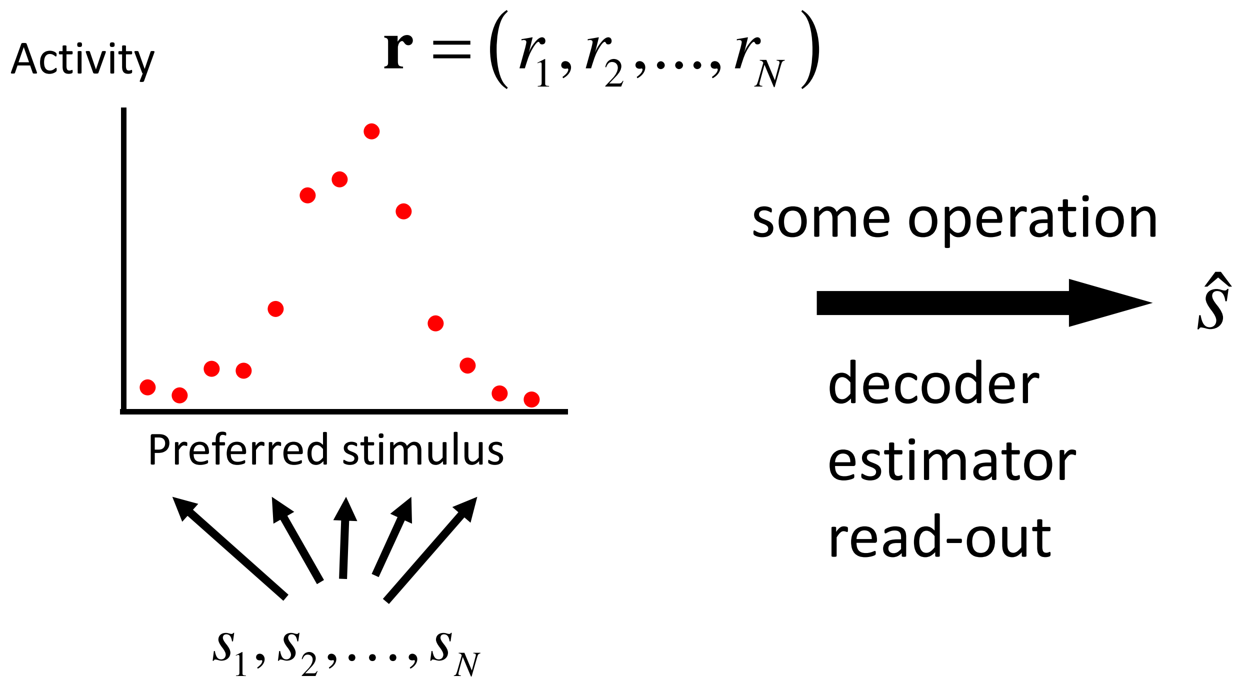
# Population codes in the brain

- Primary visual cortex (orientation, spatial frequency)
- MT (motion direction, velocity)
- IT (human faces, objects)
- SC (saccade direction)
- Primary motor cortex (arm movement direction)
- Hippocampus in rat (self location)
- Cercal interneurons in cricket (wind direction)
- Prefrontal cortex (numerosity)

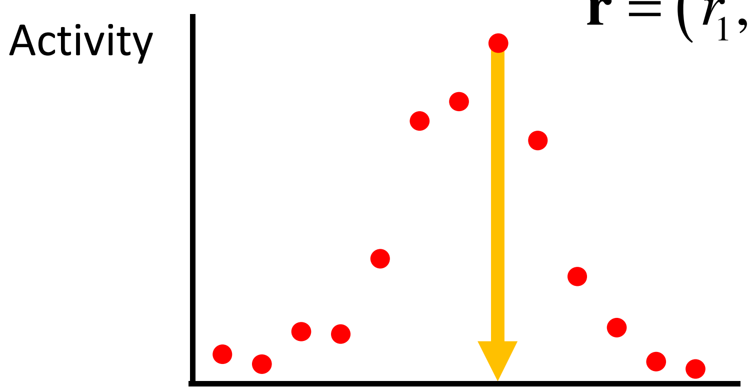
Why population coding and not single-neuron coding? …


stimulus
$s$
encoding
population
activity $\mathbf{r}$
decoding
stimulus
estimate $\hat{s}$

# Decoding population activity



# Winner-take-all decoder

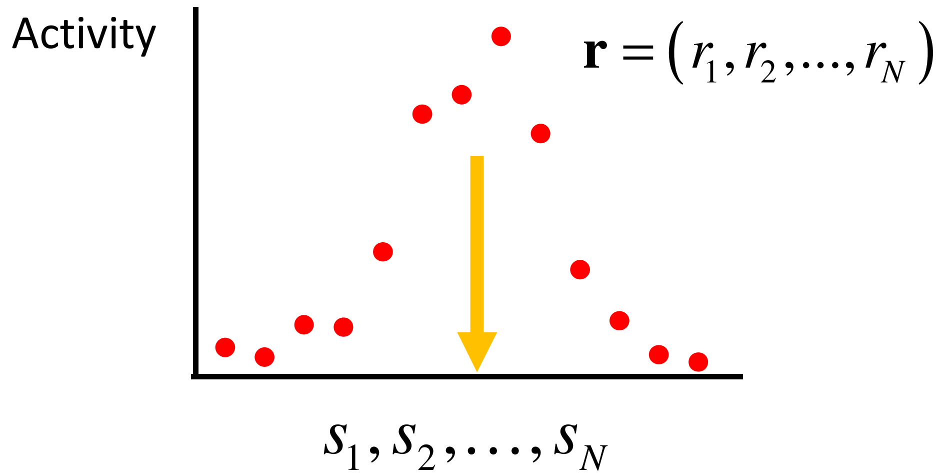



$$\mathbf{r} = \left(r_1, r_2, \ldots, r_N\right)$$

$$s_1, s_2, \ldots, s_N$$

$$\hat{s} = s_j : \;\; j = \underset{i}{\operatorname{argmax}}\, r_i$$

# Center-of-mass decoder



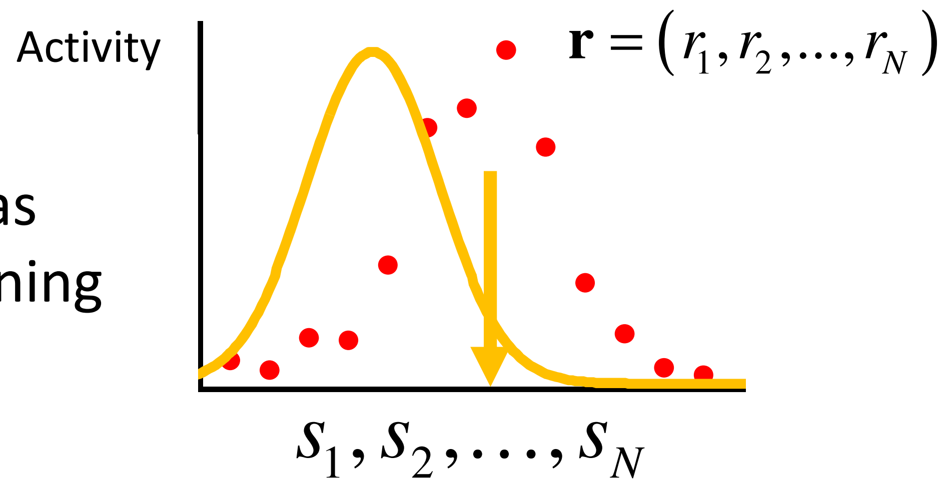

weight factors

preferred stimuli of neurons

$$\hat{s} = \frac{\sum_i r_i s_i}{\sum_i r_i}$$

# Template-matching decoder

template has shape of tuning curve



# Exercise

Show that in good approximation, minimizing the sum squared distance between the template and the population pattern is equivalent to

$$\hat{s} = \underset{s}{\operatorname{argmax}}\ \mathbf{r} \cdot \mathbf{f}\left(s\right).$$

$$\hat{s} = \underset{s}{\operatorname{argmin}} \sum_{i=1}^{N} \left(r_i - f_i\left(s\right)\right)^2$$

# Maximum-likelihood decoder

- Does not only use **r** and **f**(*s*), but also noise distribution $p(\mathbf{r}|s)$ (e.g. independent Poisson)
- Find the value of *s* that maximizes the likelihood of *s*, i.e. $p(\mathbf{r}|s)$

$$\hat{s} = \underset{s}{\operatorname{argmax}}\; p(\mathbf{r} \mid s)$$

- Experimental disadvantage: need to know (or assume) $p(\mathbf{r}|s)$

# Exercise

$$\hat{s} = \underset{s}{\operatorname{argmax}}\ p(\mathbf{r} \mid s)$$

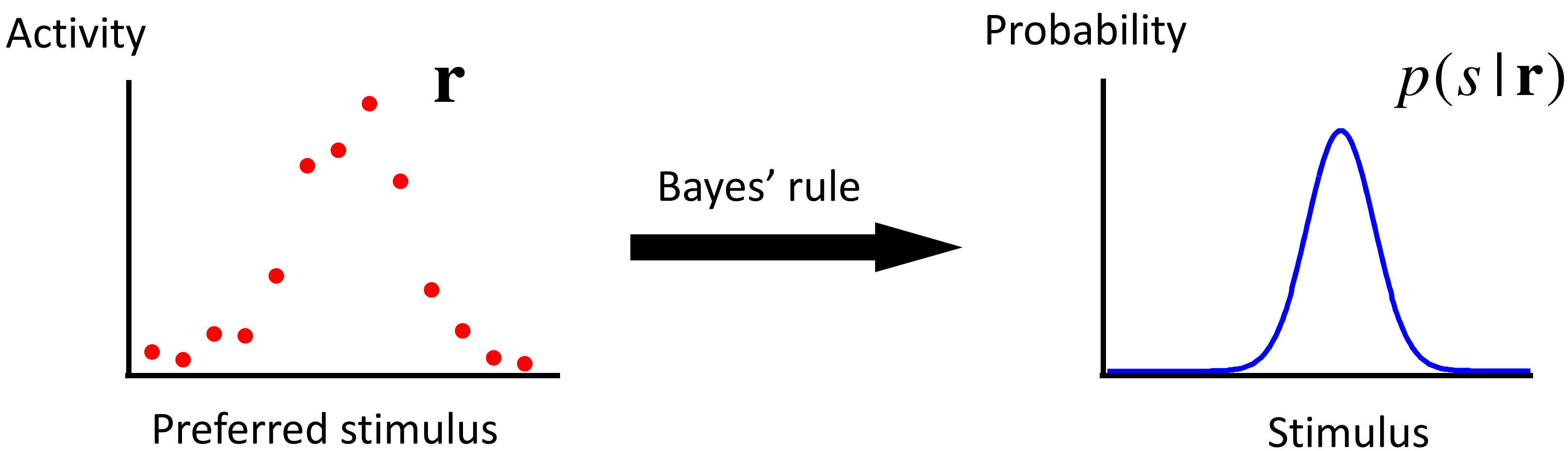
If neuronal noise is independent and normally distributed with fixed variance, the maximum-likelihood decoder is equivalent to a decoder we already know. Which one?

# Bayesian decoding

- Bayes' rule:

$$p(s \mid \mathbf{r}) \propto p(\mathbf{r} \mid s)\, p(s)$$

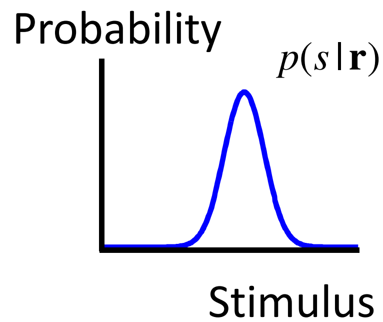
posterior likelihood prior



# Bayesian decoders

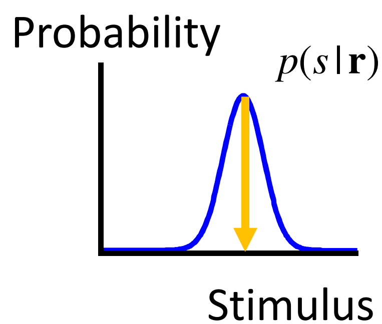
- Bayes' rule:

$$p(s\,|\,\mathbf{r}) \propto p(\mathbf{r}\,|\,s)\,p(s)$$




- Decoders based on the posterior:
  - Maximum-a-posteriori decoder

$$\hat{s} = \underset{s}{\operatorname{argmax}}\; p(s\,|\,\mathbf{r})$$




  - Decoders minimizing expected cost

$$\hat{s} = \underset{s}{\operatorname{argmin}} \int p(s'\,|\,\mathbf{r})\,C(s,s')\,ds'$$

expected value

cost function

# Cost functions

- Sum squared error:

$$C(\hat{s}, s) = (\hat{s} - s)^2$$

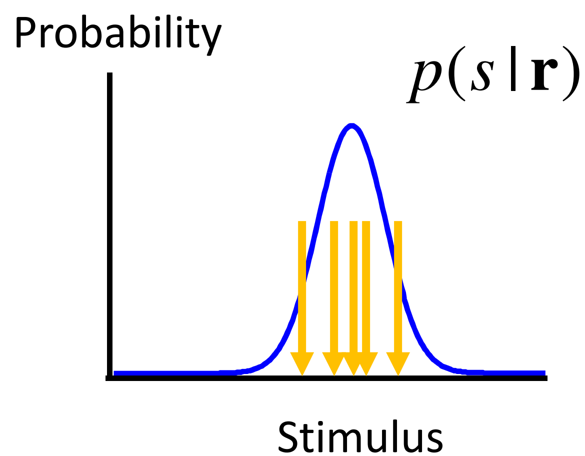
- Leads to *mean* of posterior (can be different from mode):

$$\hat{s} = \int s \, p(s \mid \mathbf{r}) \, ds$$

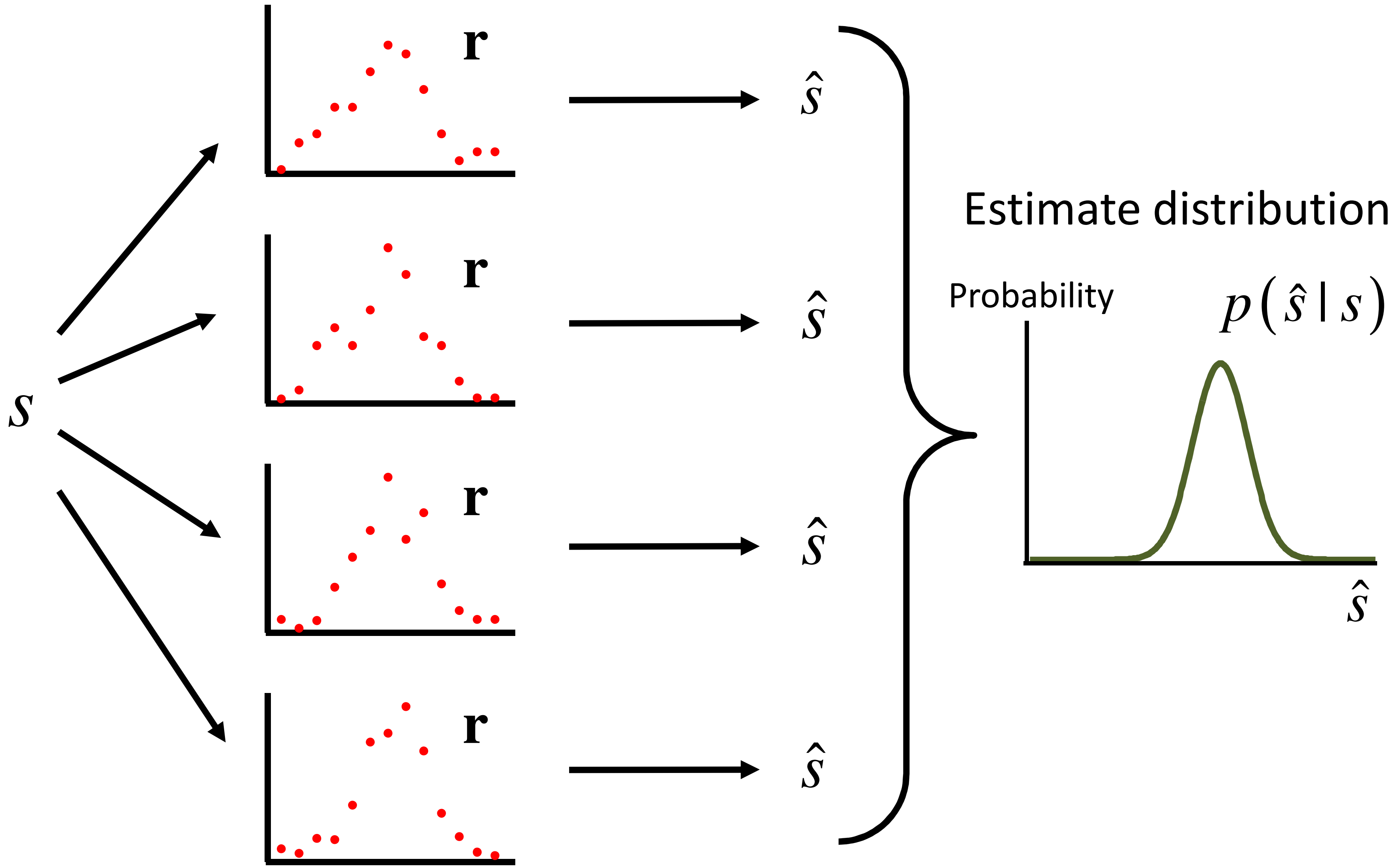
- Exercise: show this.
- Other cost function: absolute error (exercise).

# Sampling decoder

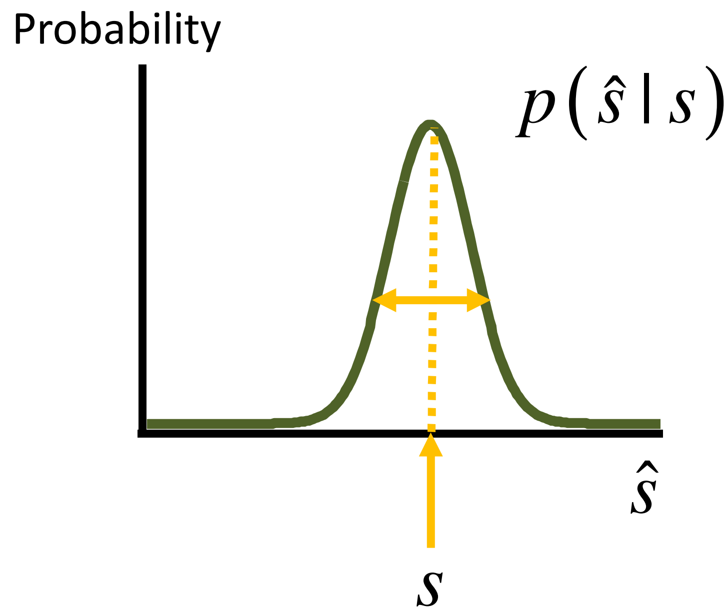
Draw a random number from the posterior distribution → stochastic (non-deterministic) decoder



# How to judge a decoder?



# Good decoders




- Unbiased
- Low variance
- Can be implemented by a neural network.

# Cramer-Rao bound

- Variance of decoder cannot be lower than a fixed number.
- This number depends on the noise distribution.

$$\sigma^2_{\text{any decoder}} \geq \frac{1}{I(s)}$$

Cramer-Rao bound

$$I(s) = -\left\langle \frac{\partial^2}{\partial s^2} \log p(\mathbf{r} \mid s) \right\rangle$$

Fisher information

# Fisher information

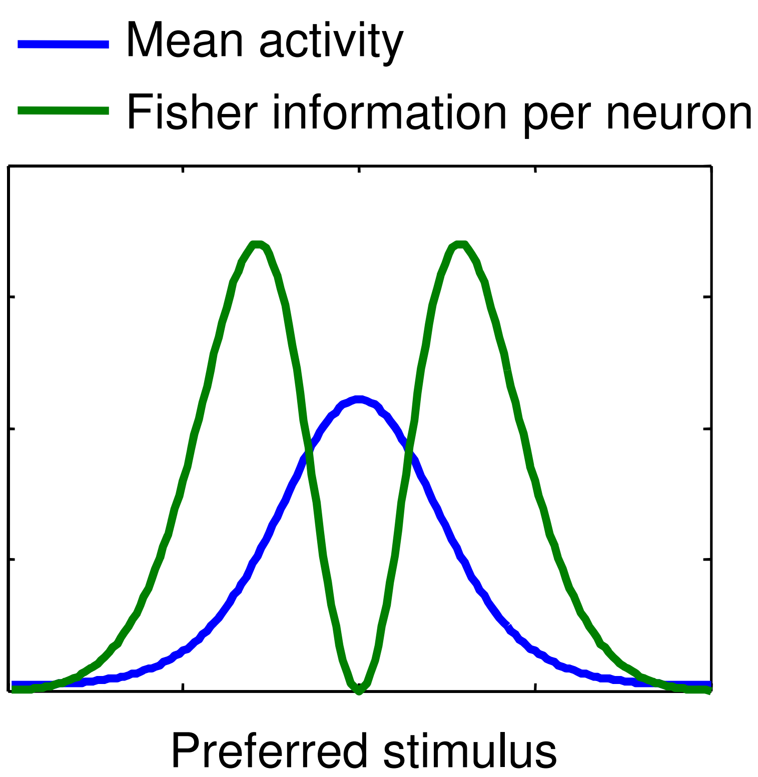
Independent Poisson variability:

$$I(s) = \sum_{i=1}^{N} \frac{f_i'(s)^2}{f_i(s)}$$

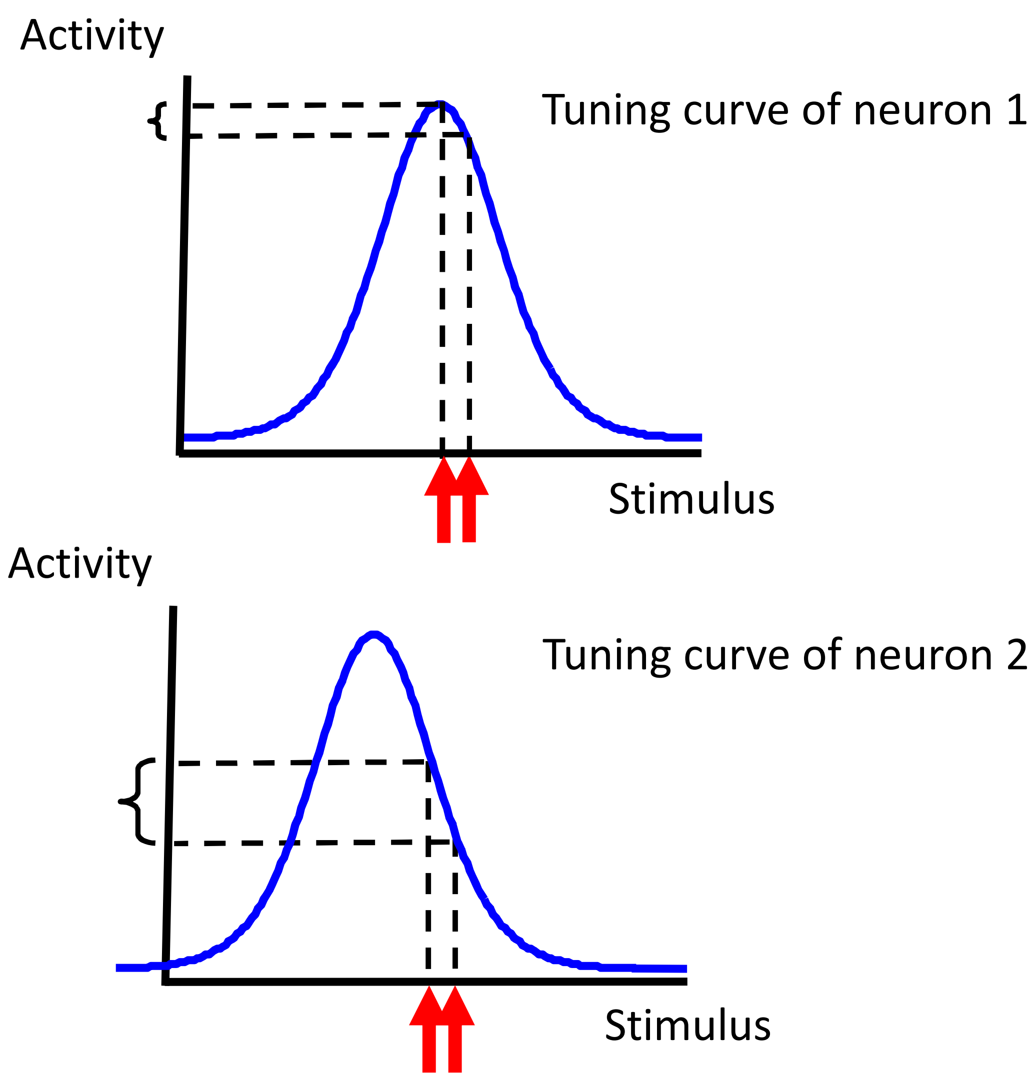
Contribution of neuron *i*:

$$I_i(s) = \frac{f_i'(s)^2}{f_i(s)}$$

*I*(*s*) independent of *s*



# Fisher information per neuron



# Fisher information and discriminability

true separation of stimuli to be discriminated

$$d' = \delta s \sqrt{I(s)}$$

Fisher information

discriminability
(signal detection theory measure)

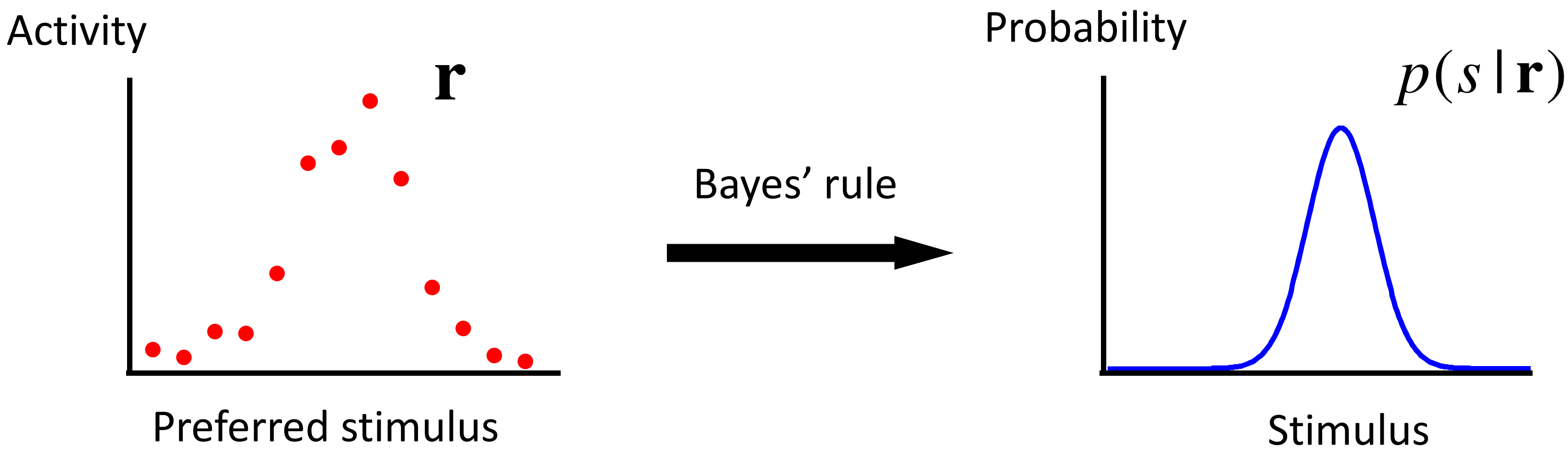
# Efficient Decoding

- An efficient decoder is one that achieves the Cramer-Rao lower bound.

$$\sigma^2_{\text{efficient decoder}} = \frac{1}{I(s)}$$

- Fisher information is a decoder-independent measure of the "quality" of a population code.
- The ML decoder is asymptotically unbiased and efficient → "best possible decoder".

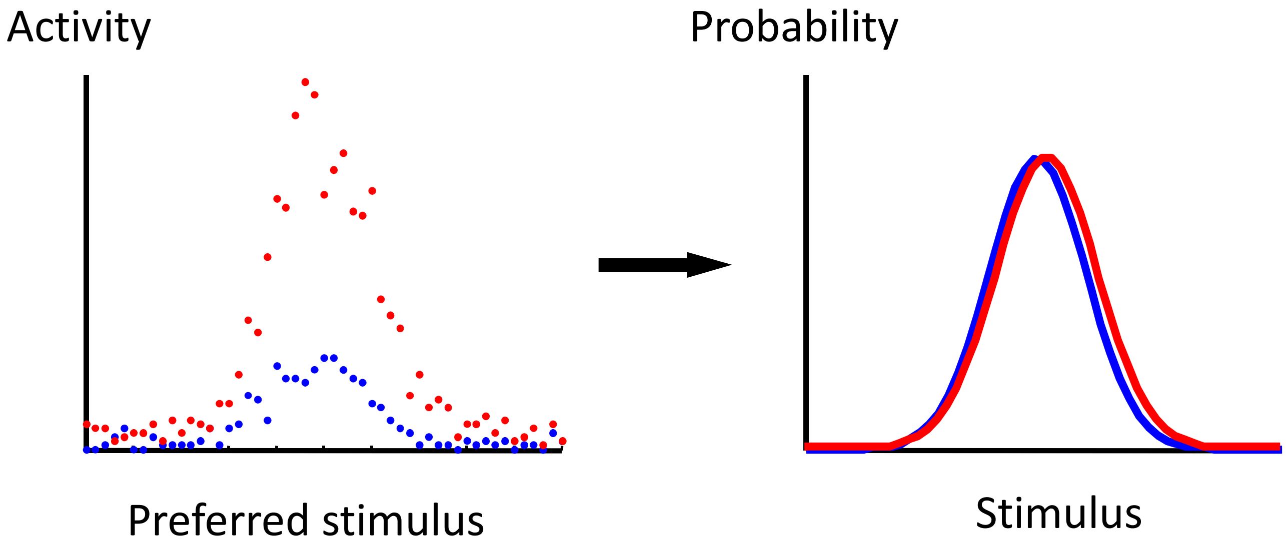
# Decoding probability distributions




Allows for probabilistic inference

# Alternative probabilistic codes

$$f_i(s) = A \cdot \Pr(s = s_i)$$



# Binary stimuli

- Was the motion to the left or to the right?
- Is A bigger than B?
- Were A and B the same or different?
- Was the target present or absent?

$$p(s=0 \mid \mathbf{r}) = \frac{p(\mathbf{r} \mid s=0)\, p(s=0)}{p(\mathbf{r})}$$

*s* = 0, 1

$$p(s=1 \mid \mathbf{r}) = \frac{p(\mathbf{r} \mid s=1)\, p(s=1)}{p(\mathbf{r})}$$

# Binary stimuli – Log odds

$$L = \log \frac{p(s=1 \mid \mathbf{r})}{p(s=0 \mid \mathbf{r})} = \log \frac{p(\mathbf{r} \mid s=1)}{p(\mathbf{r} \mid s=0)} + \log \frac{p(s=1)}{p(s=0)}$$

↑ log odds = log posterior ratio

↑ log likelihood ratio

↑ log prior ratio

Measure of certainty / confidence in binary decisions

# Thursday

- Noise correlations in encoding and decoding
- Generalized linear models

- Reading:
    1. **Averbeck, Latham, Pouget (2006)**
    ***Neural correlations, population coding, and computation.***
    **Nat Rev Neurosci 7(5): 358-66.**
    2. Ginzburg and Sompolinsky (1994)
    *Theory of correlations in stochastic neural networks.*
    Physical Review E 50(4): 3171-91.
    3. Pillow et al. (2008)
    *Spatio-temporal correlations and visual signalling in a complete neural population*. Nature 454 (7207): 995-9.