

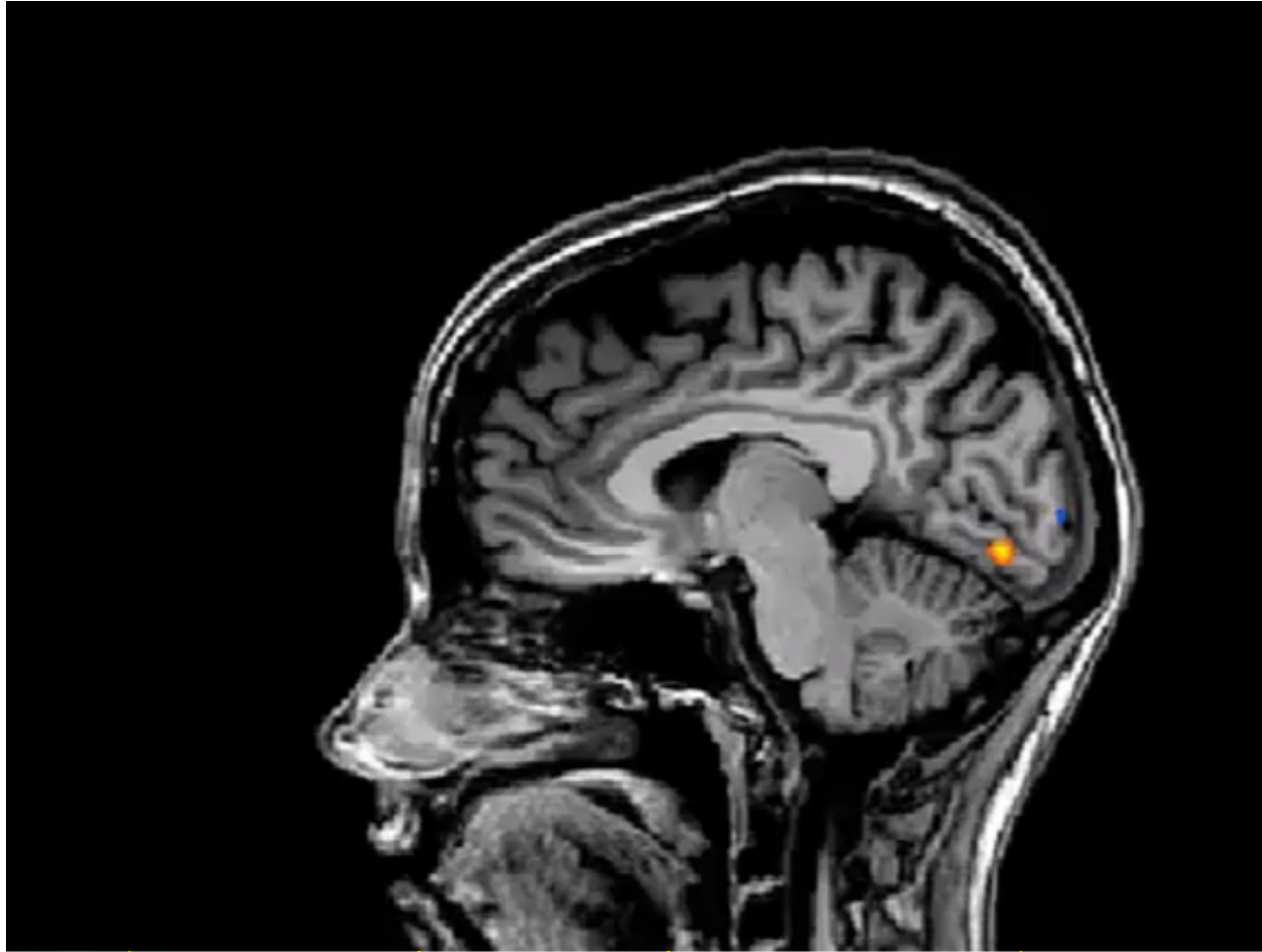
Encoding and decoding neural information

Course of Neuroinformatics

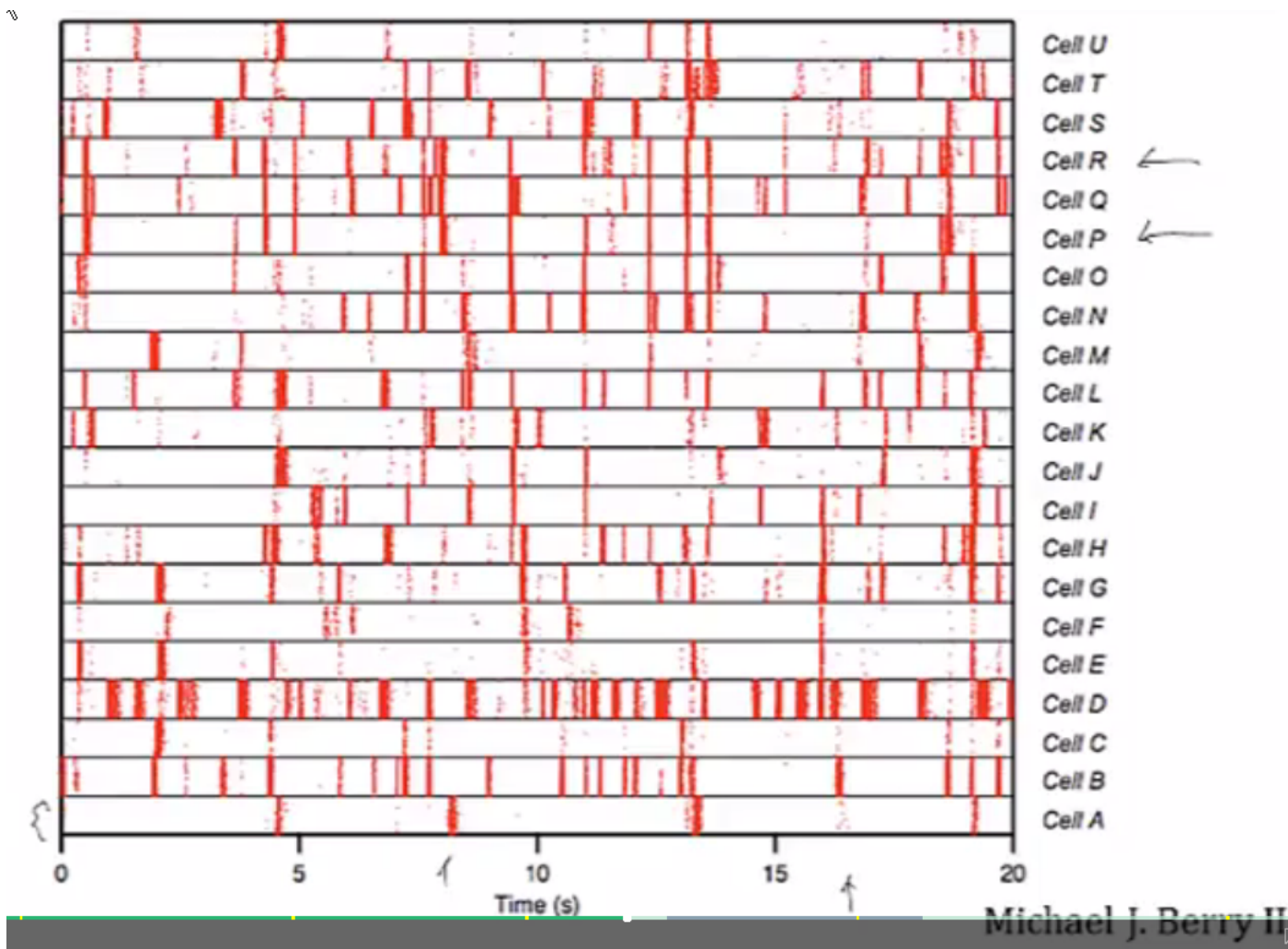
Karla Štěpánová

CIIRC, CTU in Prague

Introduction



Introduction



Introduction

- Encoding
 - How the brain represents information (models to express it)
 - $P(\text{response} | \text{stimulus})$
 - Each neuron different response – only frequency is not enough
- Decoding
 - What was the cause of the given spike pattern of the neuron?
 - Decide whether to behave or not
 - What the brain is doing based on its activity
 - $P(\text{noise}) \gg P(\text{signal})$
- Information theory
 - How much information can be encoded and transferred?
 - Information theory to quantify neural representation

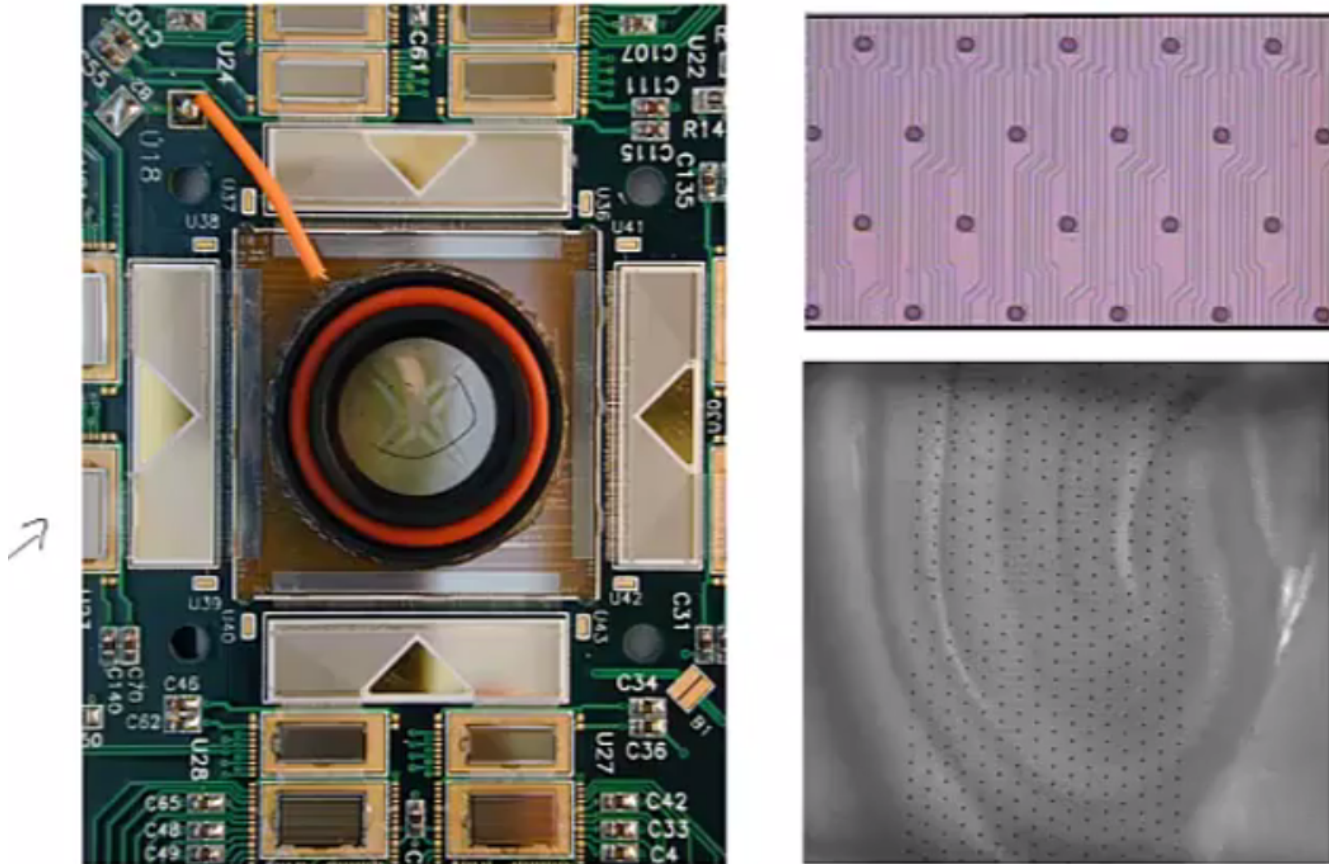
Reading neural code

- Non-invasive – EEG, fMRI



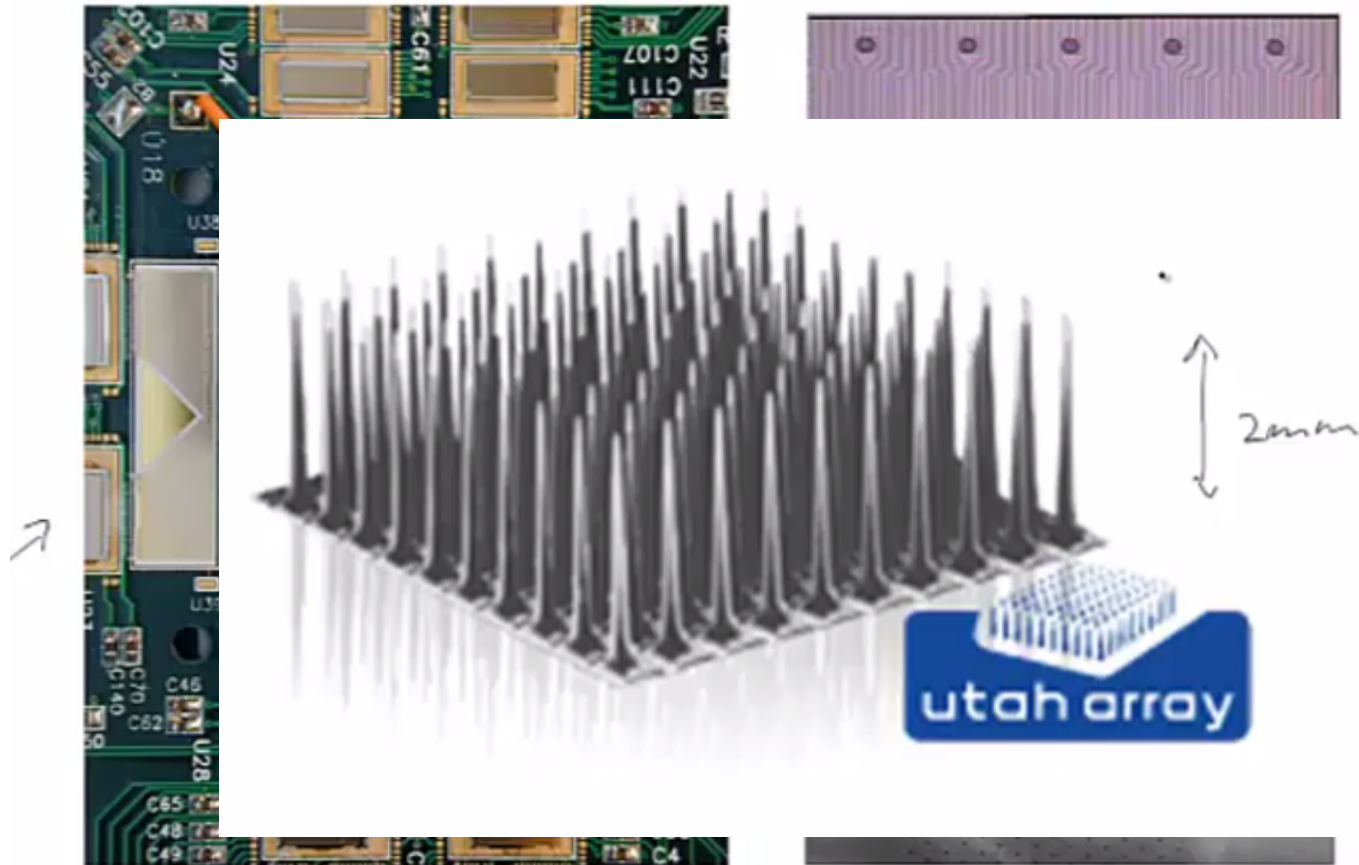
Reading neural code

- EEG
- Multielectrode array (amplifying signals, electrode $10\mu\text{m} \sim$ neuron)



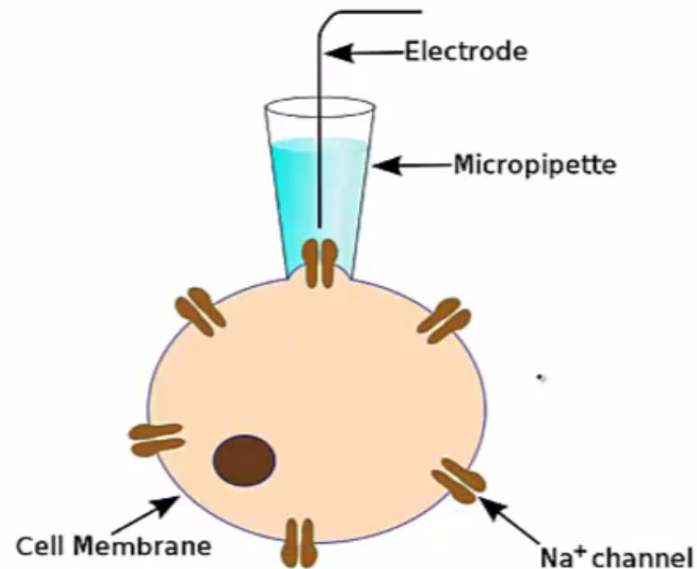
Reading neural code

- EEG
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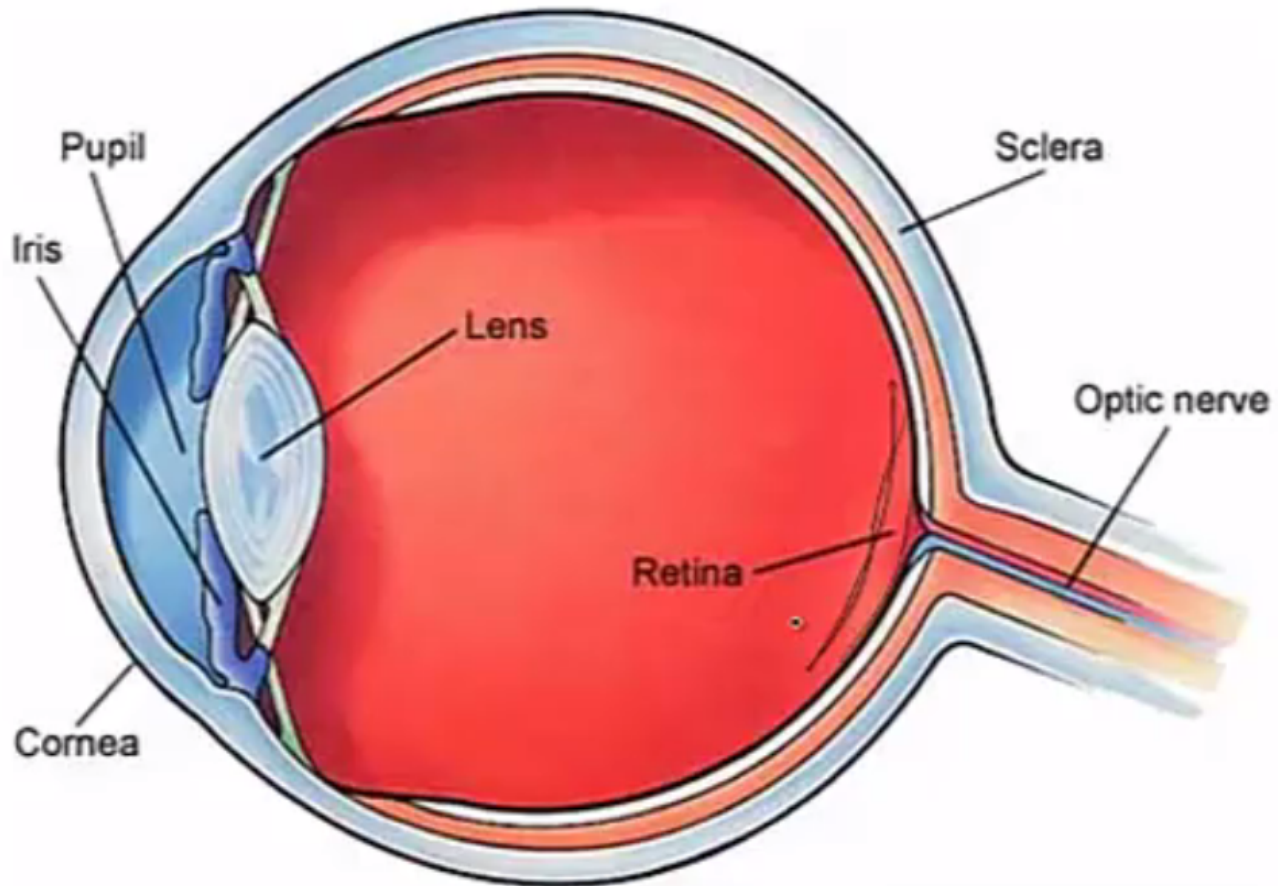


Reading neural code

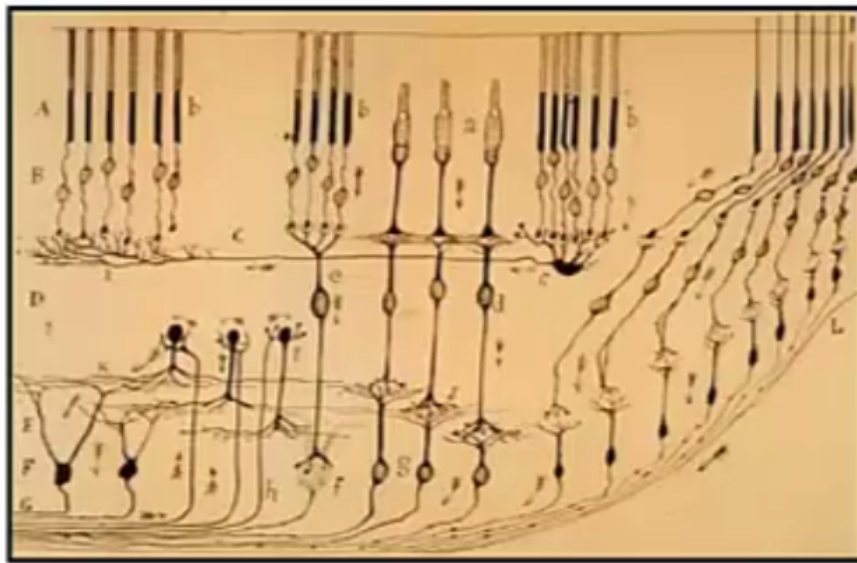
- EEG
- Multielectrode array (amplifying signals, electrode $10\mu\text{m} \sim$ neuron)
- Single neuron recordings



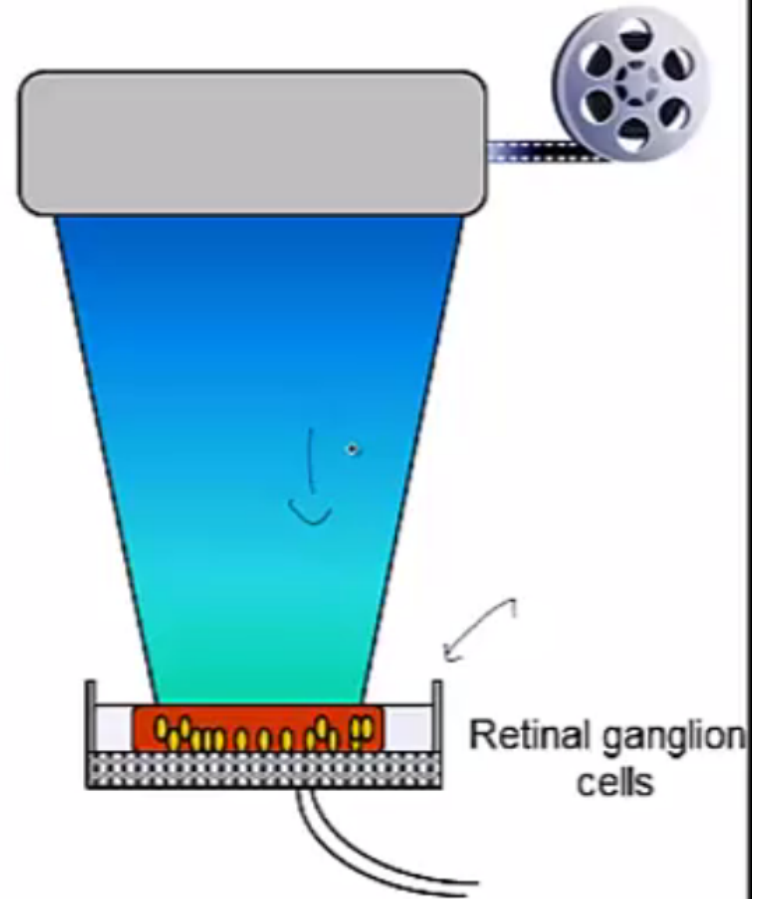
Encoding



Encoding



Ramon y Cajal, 1901



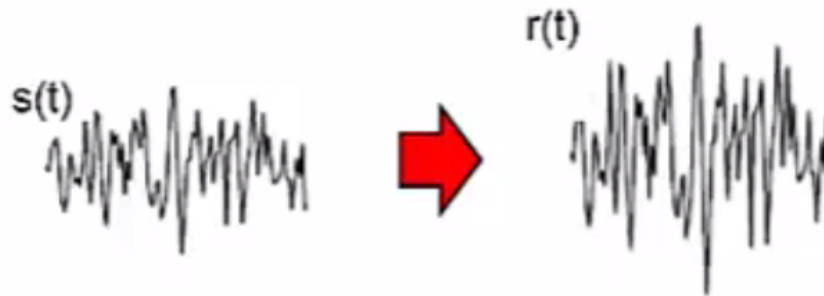
Encoding

- $P(\text{response} \mid \text{stimulus}) - r(t)$ given a stimulus

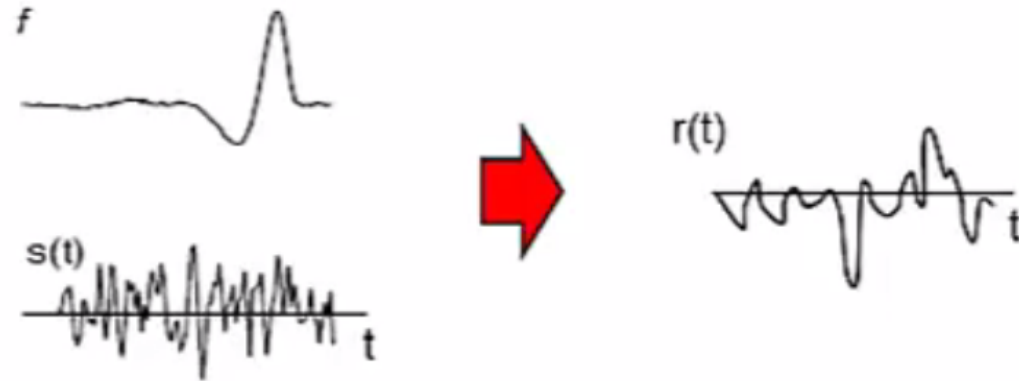
Encoding

- $P(\text{response} \mid \text{stimulus}) - r(t)$ given a stimulus
- Linear response

$$r(t) = \phi s(t) \quad \sim \quad \phi s(t - \tau)$$



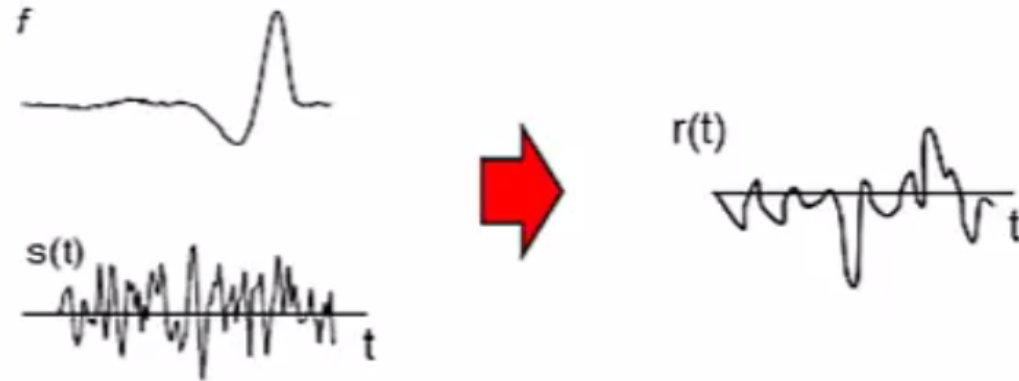
Encoding – temporal filtering



Linear filter:

$$r(t) = \sum_{k=0}^n s_{t-k} f_k$$
$$r(t) = \int_{-\infty}^t d\tau s(t - \tau) f(\tau)$$

Encoding – temporal filtering

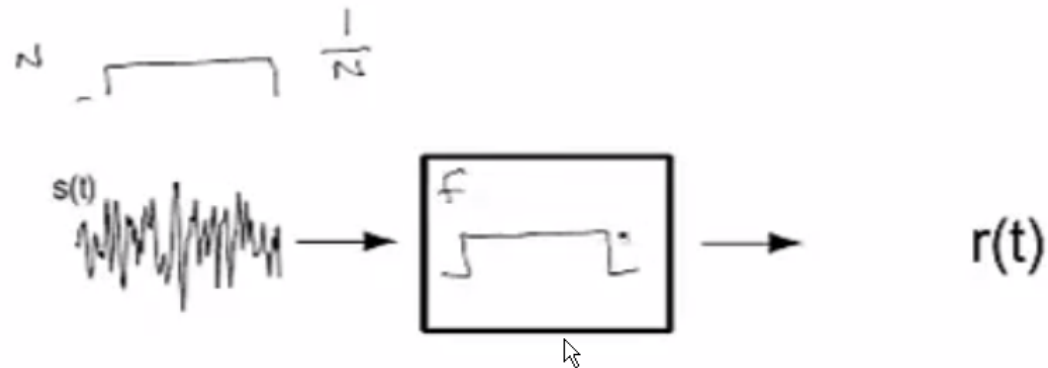


Linear filter:

$$r(t) = \sum_{k=0}^n s_{t-k} f_k$$
$$r(t) = \int_{-\infty}^t d\tau s(t - \tau) f(\tau)$$

Encoding – temporal filtering

- Running average

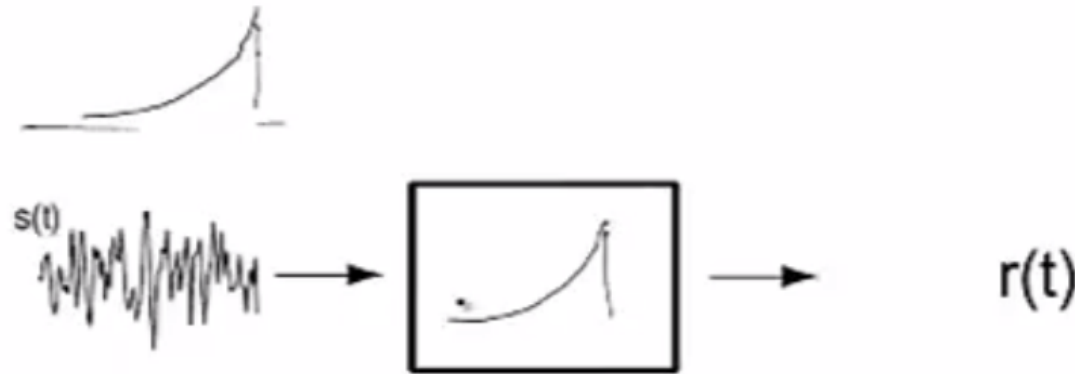


Linear filter:

$$r(t) = \sum_{k=0}^n s_{t-k} f_k$$

Encoding – temporal filtering

- Leaky average – differential filter (high output for quick increase in signal, not if held high)

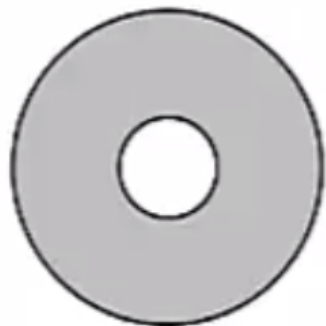


Linear filter:

$$r(t) = \sum_{k=0}^n s_{t-k} f_k$$

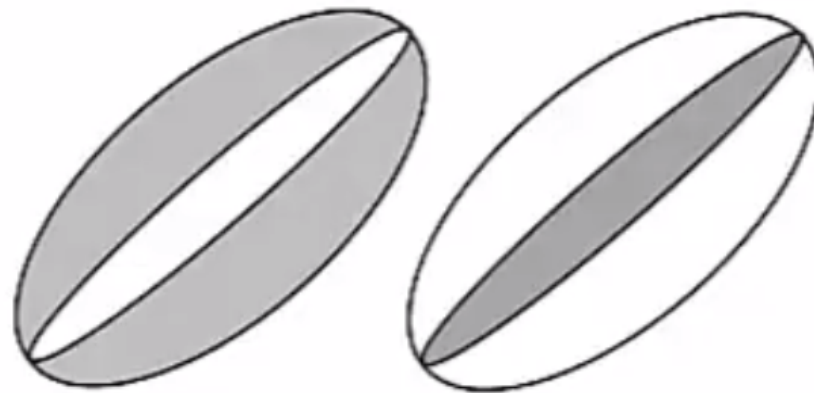
Encoding – spatial filtering

57



retina

.



Visual cortex

Encoding – spatial filtering

$$r(t) = \sum_{k=0}^n s_{t-k} f_k$$

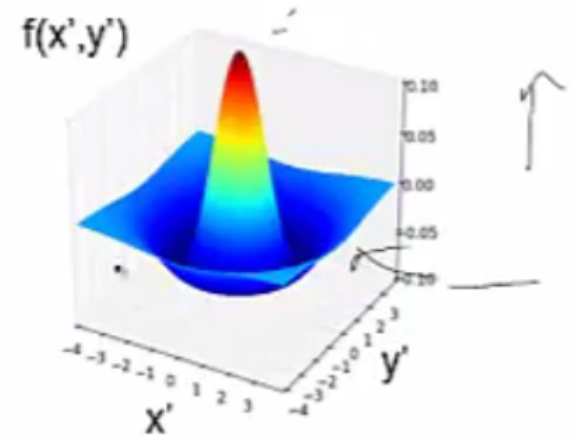
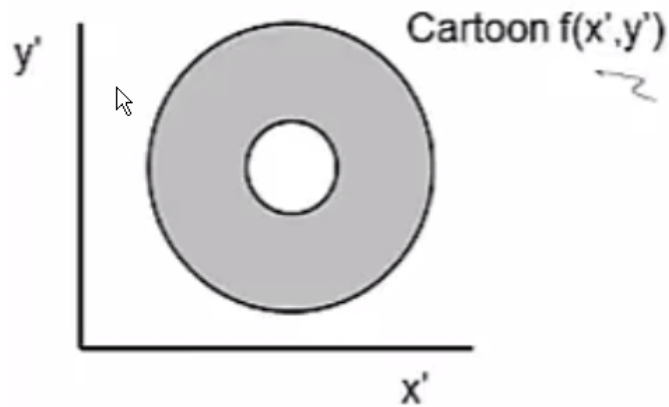
Temporal filter



$$r(x, y) = \sum_{x'=-n, y'=-n}^n s_{x-x', y-y'} \underline{f_{x', y'}}$$

Encoding – spatial filtering

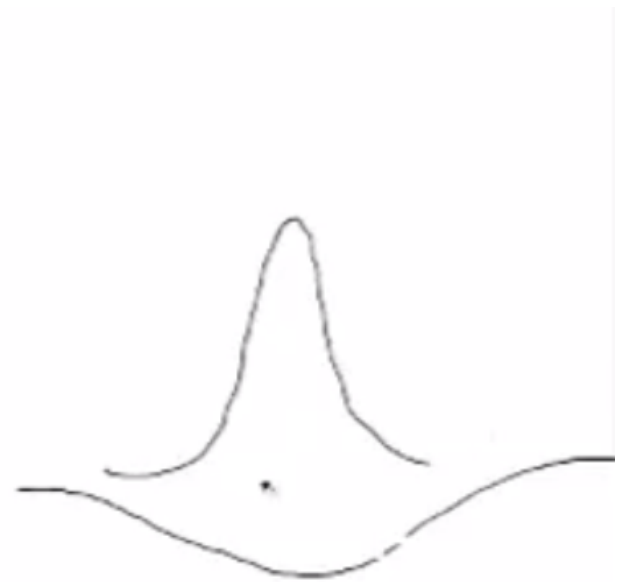
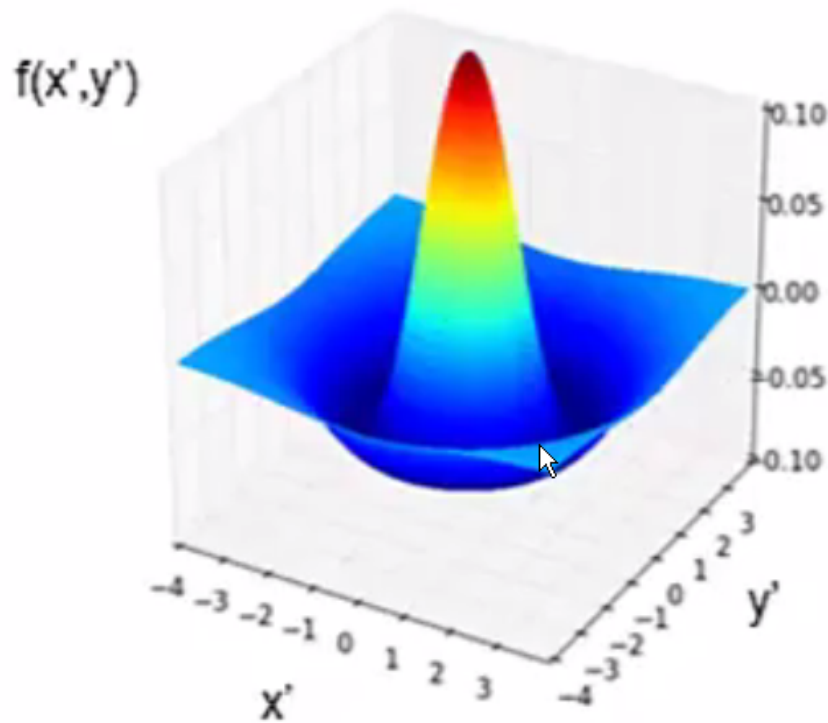
- Retinal receptive fields



$$r(x,y) = \sum_{x'=-n,y'=-n}^n S_{x-x',y-y'} f_{x',y'}$$

Encoding – spatial filtering

- Retinal receptive fields



Encoding – spatial filtering

- Retinal receptive fields

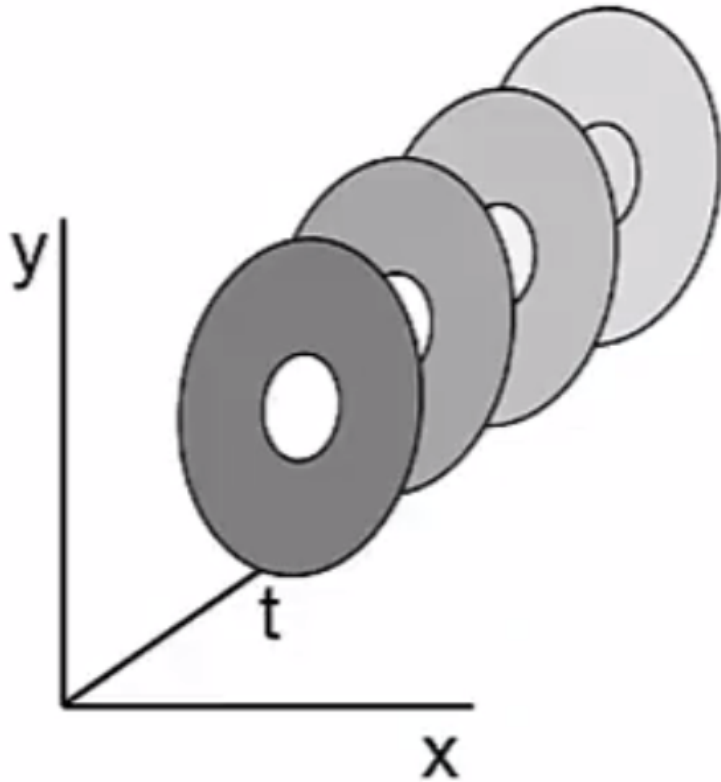


Original image



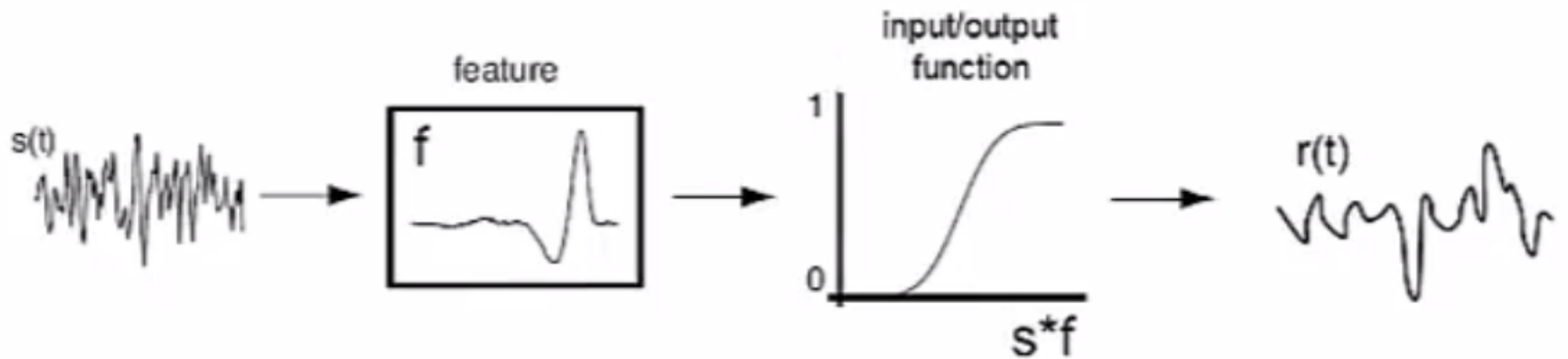
Filter "Difference of Gaussians" applied

Encoding – spatiotemporal filtering



$$r_{x,y}(t) = \iiint dx' dy' d\tau f(x',y',\tau) s(x-x',y-y',t-\tau)$$

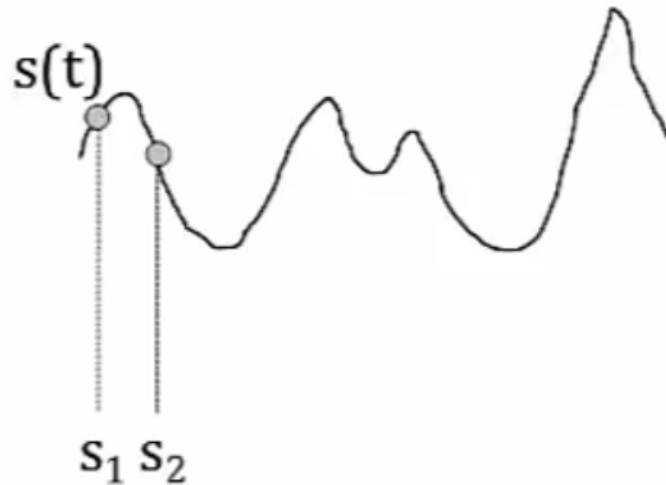
Encoding – temporal filtering



Linear filter & nonlinearity: $r(t) = g(\int s(t-\tau) f(\tau) d\tau)$

Encoding – feature selection

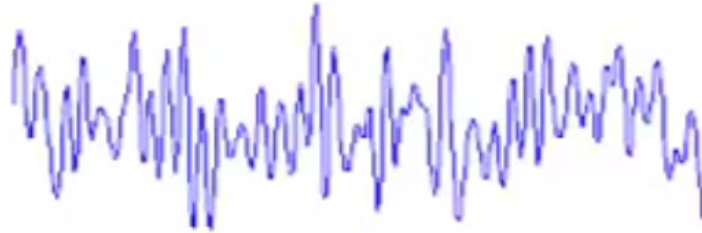
- One stimulus 300 000 values – impossible to handle
- Sample responses of the system to many stimuli to characterize $P(\text{response} \mid \text{stimulus}) \rightarrow P(\text{response} \mid s_1)$
- Pick up small set of relevant dimensions
 - Discretize $P(\text{response} \mid \{s_1, \dots, s_n\})$



Encoding – feature selection

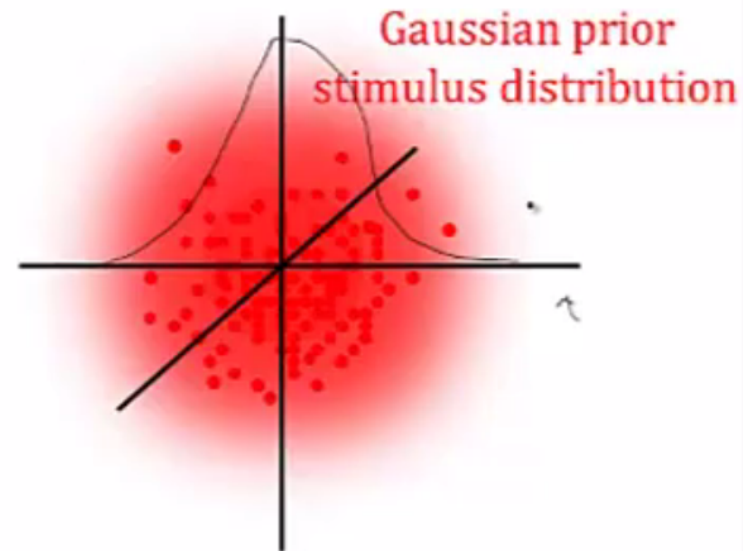
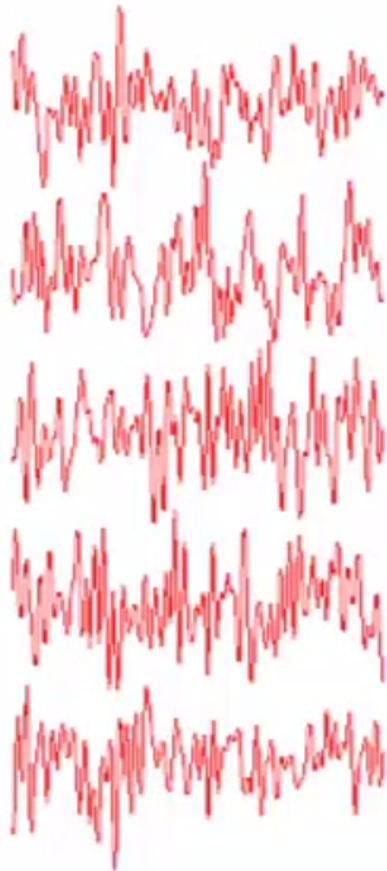
- Gaussian white noise as an input

Gaussian white noise



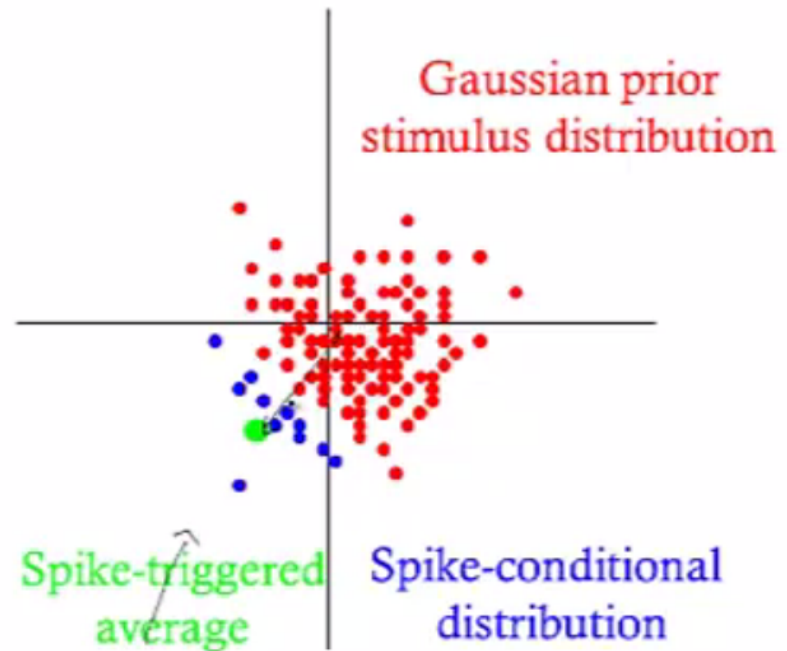
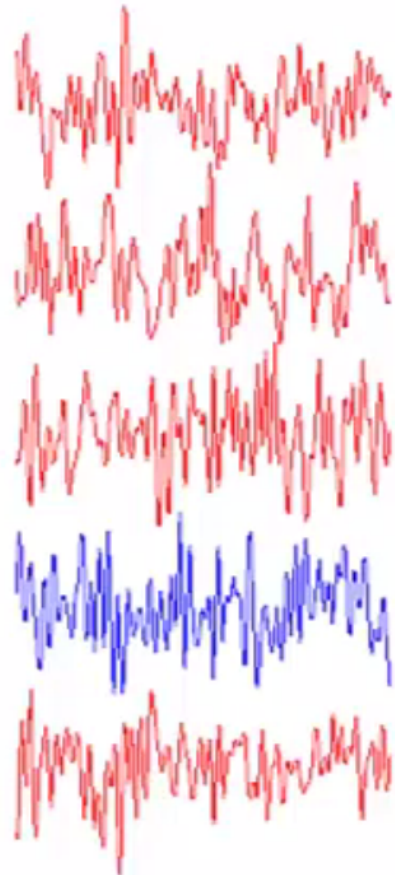
Encoding – feature selection

- Gaussian white noise as an input
 - 100 dimensions (time values) – Gaussian dist. along any axis



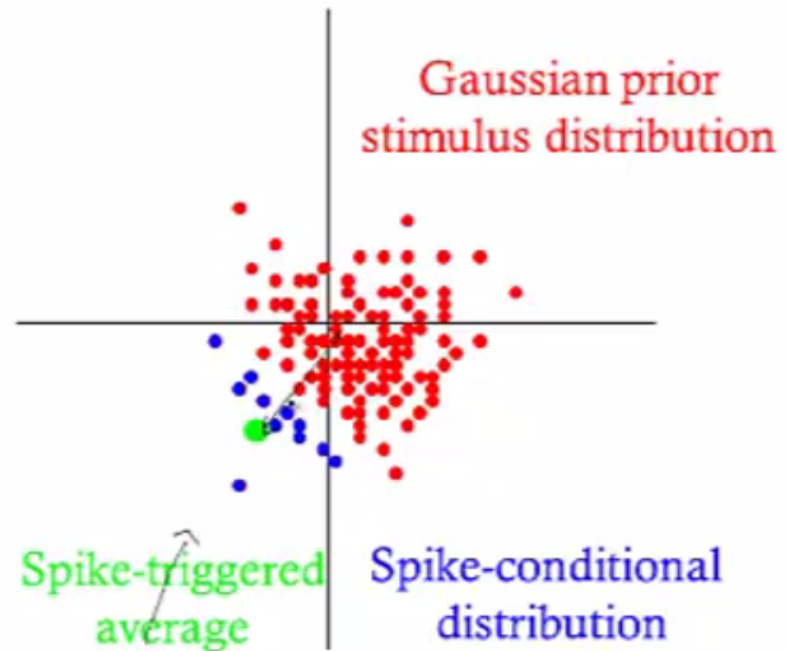
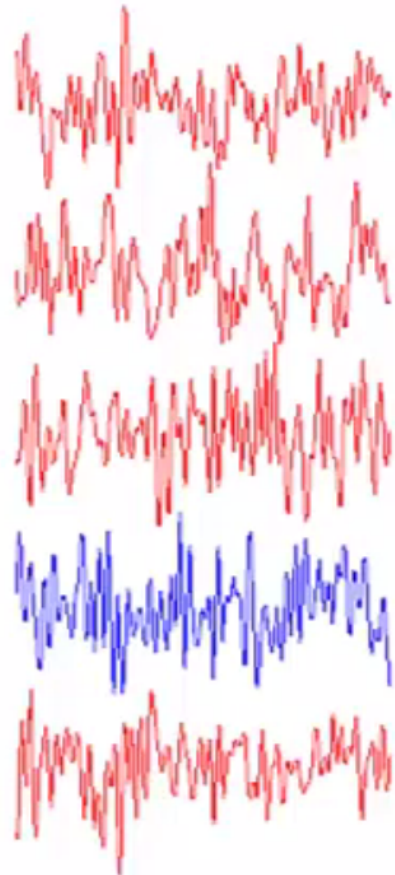
Encoding – feature selection

- Gaussian white noise as an input –
 - some stimuli will trigger spikes



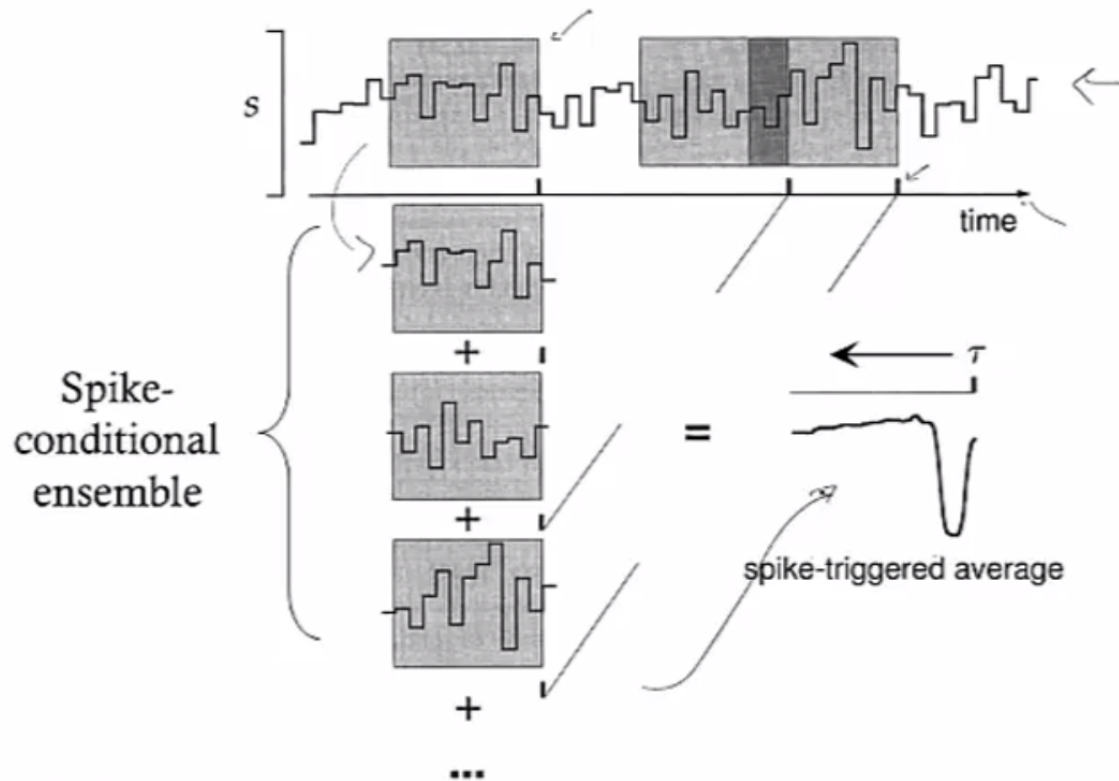
Encoding – feature selection

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Encoding – feature selection

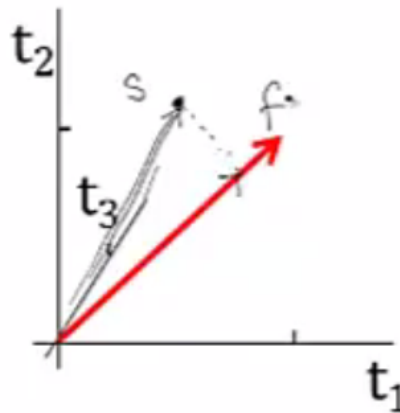
- Gaussian white noise as an input –
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Encoding – feature selection

- Linear filtering
 - takes stimulus and project it to lower dimensional space

Stimulus feature f is a vector in a high-dimensional stimulus space



Linear filtering = convolution = projection

Encoding – feature selection

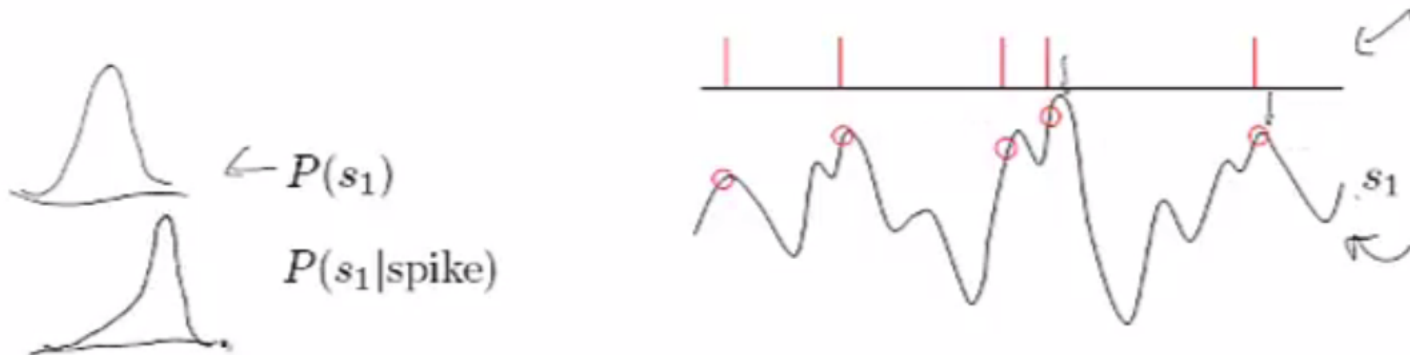
- Input/Output function with respect to this extracted feature

The input/output function is:

$$P(\text{spike}|\text{stimulus}) \xrightarrow{\text{red arrow}} P(\text{spike}|s_1)$$

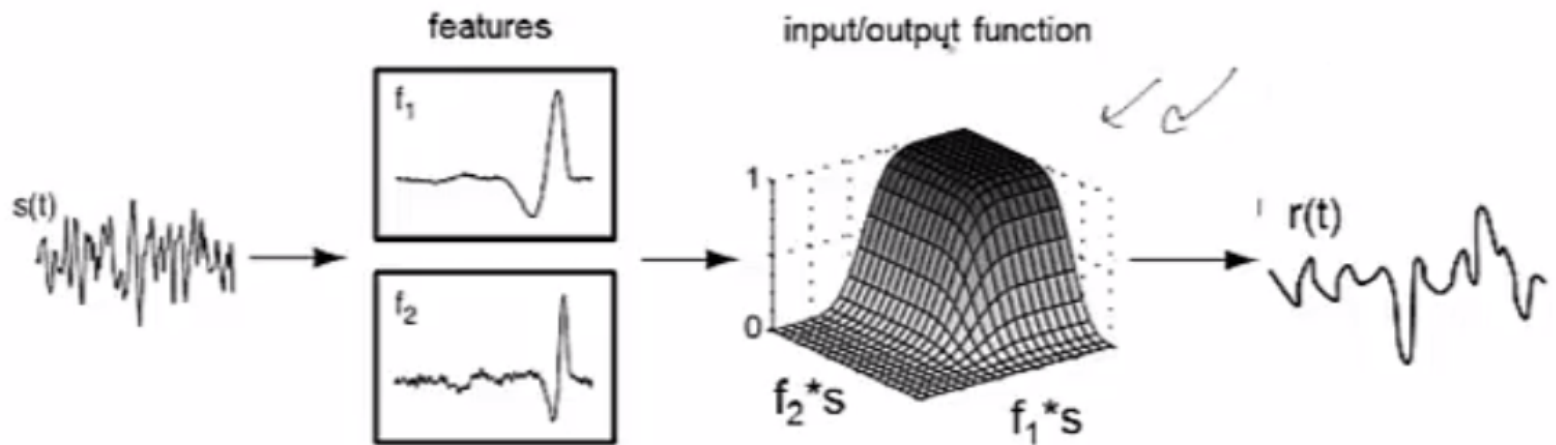
This can be found from data using Bayes' rule:

$$P(\text{spike}|s_1) = \frac{P(s_1|\text{spike}) \overbrace{P(\text{spike})}^{\text{spike-conditioned}}}{\underbrace{P(s_1)}_{\text{prior}}}$$



Encoding – feature selection

- Input/Output function with respect to this extracted feature



Linear filters & nonlinearity: $r(t) = g(f_1*s, f_2*s, \dots, f_n*s)$

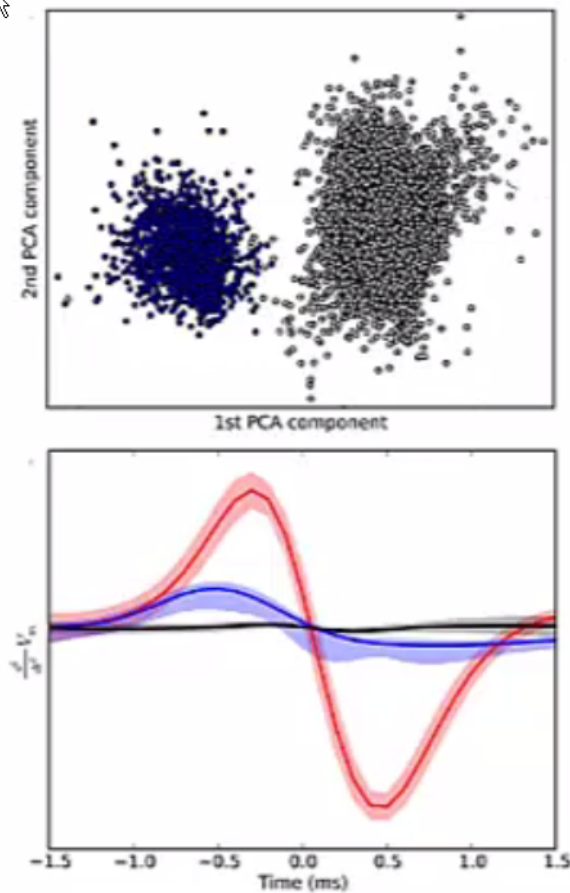
Encoding – feature selection

- PCA
 - eigenfaces from which we can create any face (lin.combination)



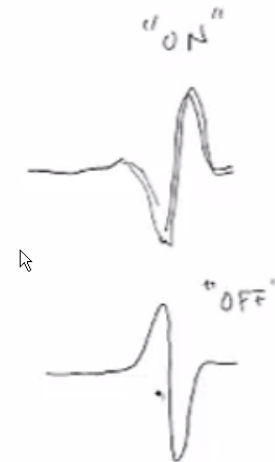
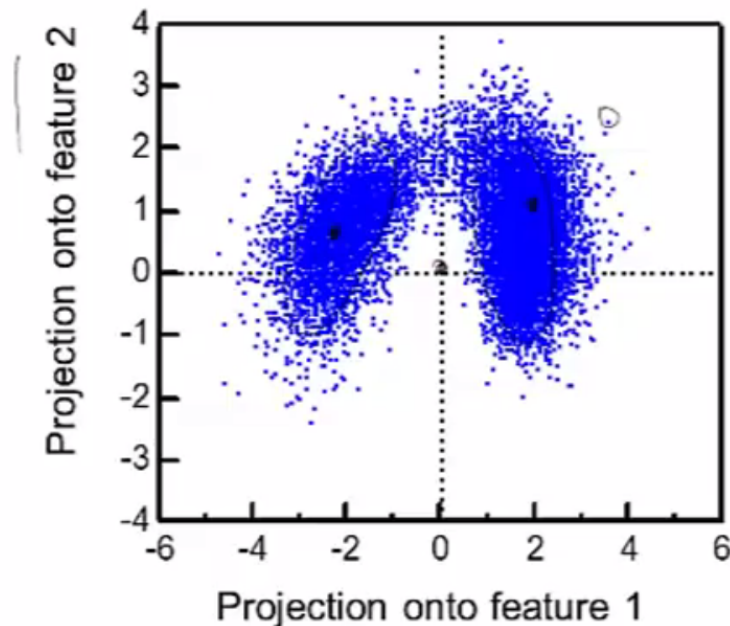
Encoding – feature selection

- PCA
 - Spike sorting (Koepsel et al., 2009)



Encoding – feature selection

- PCA
 - Spike sorting (Fairhall et al., 2007) – response to light changes of visual neurons

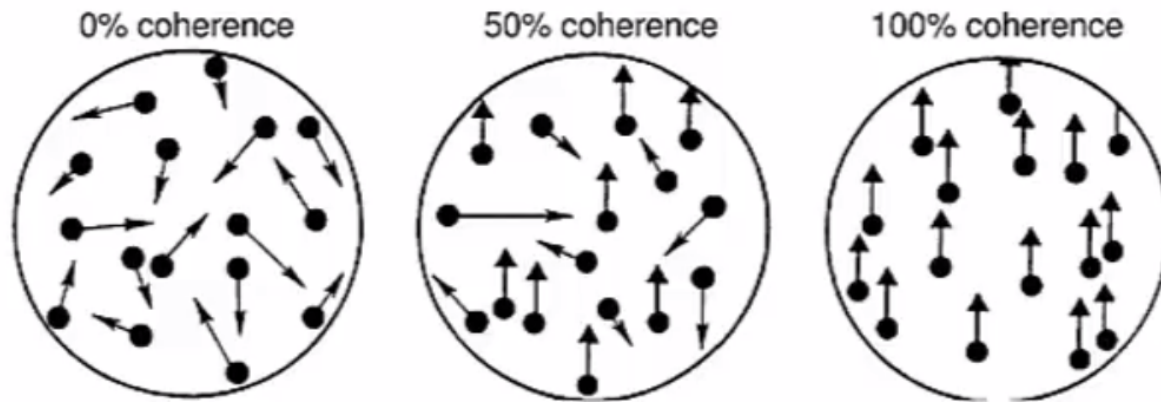


Decoding

- Neural response \rightarrow what was the stimulus
- Predictable from neural activity
- Signal detection theory

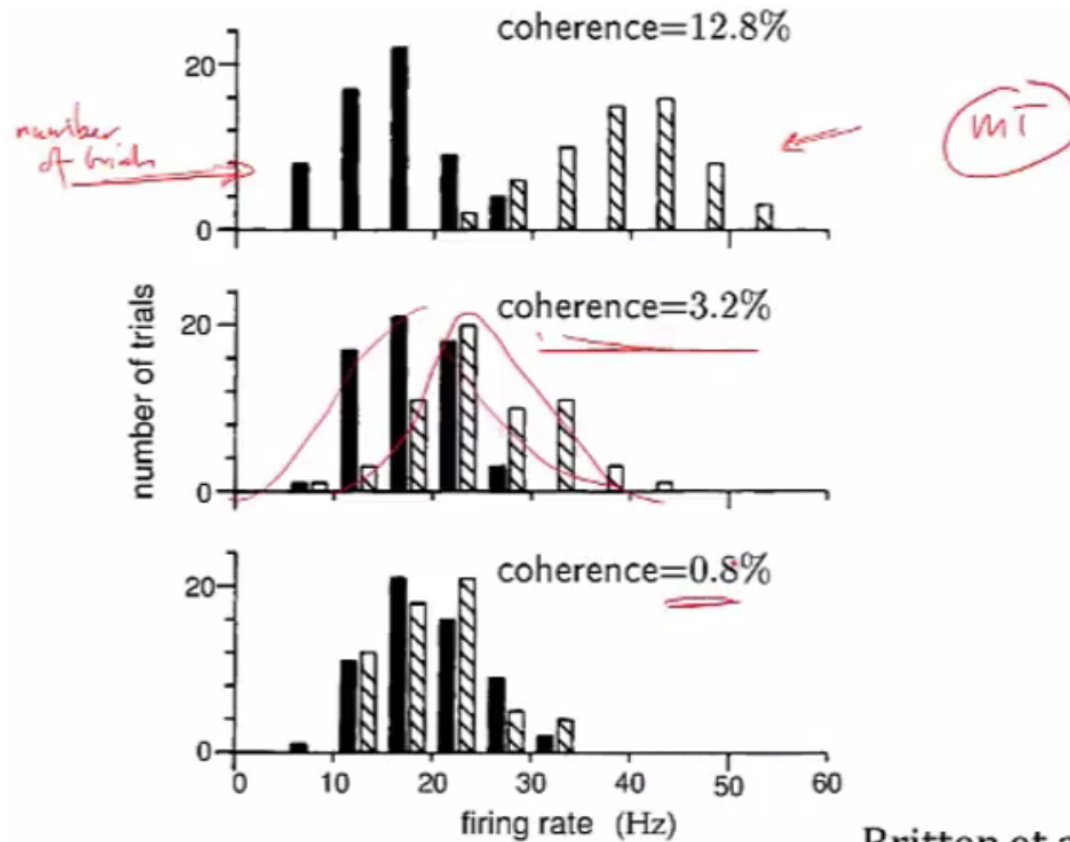
Decoding

- Monkey – neurons sensitive to visual motion
 - Different coherence of input (nmb of dots moving together)



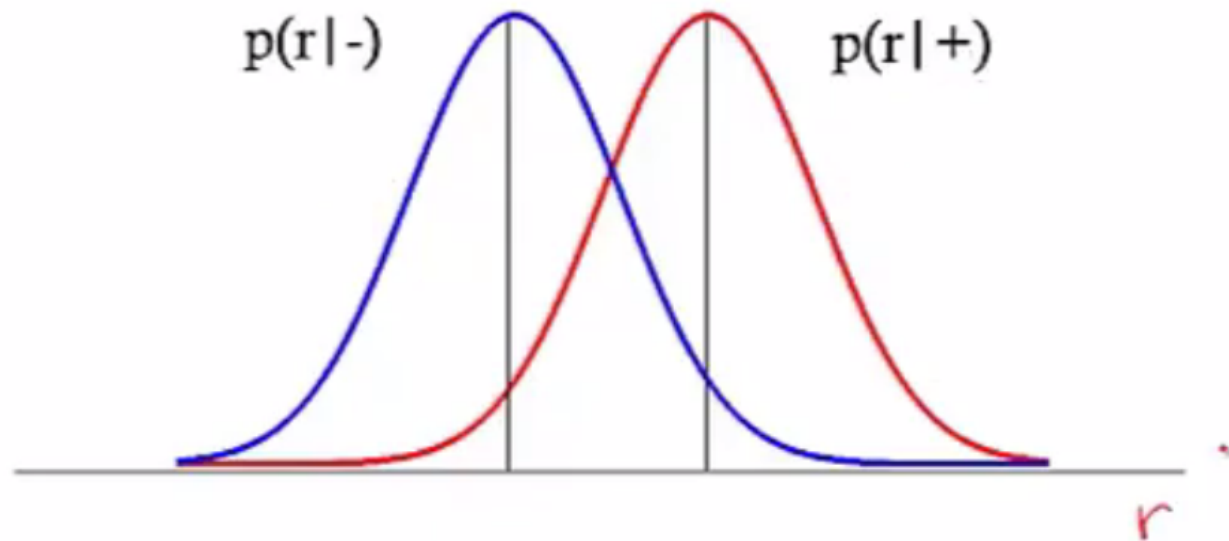
Decoding

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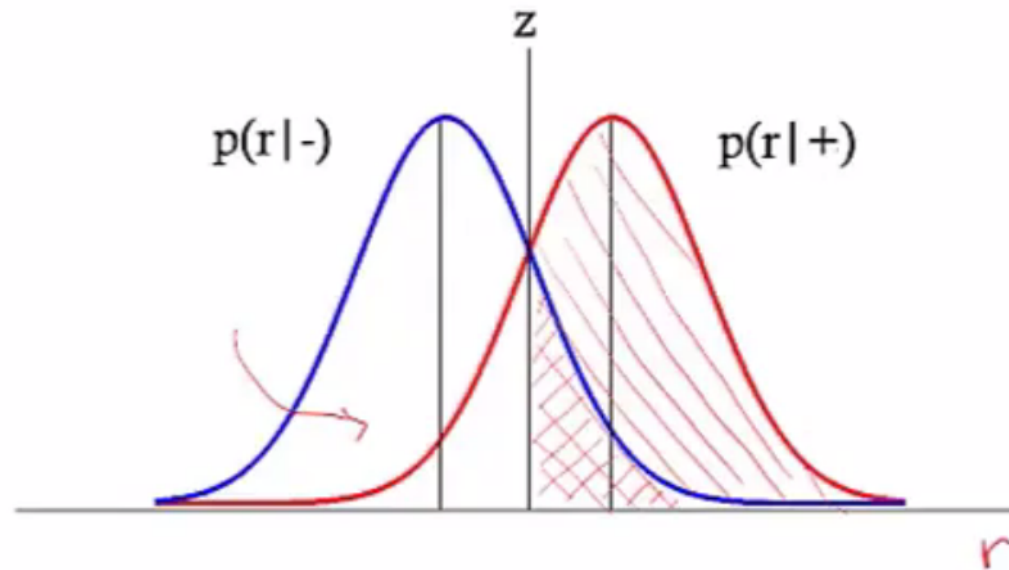
Decoding

- Monkey – neurons sensitive to visual motion
 - Different coherence of input (nmb of dots moving together)
 - Moving up vs. moving down



Decoding

- Monkey – neurons sensitive to visual motion
 - Threshold – maximum probability of correct answer



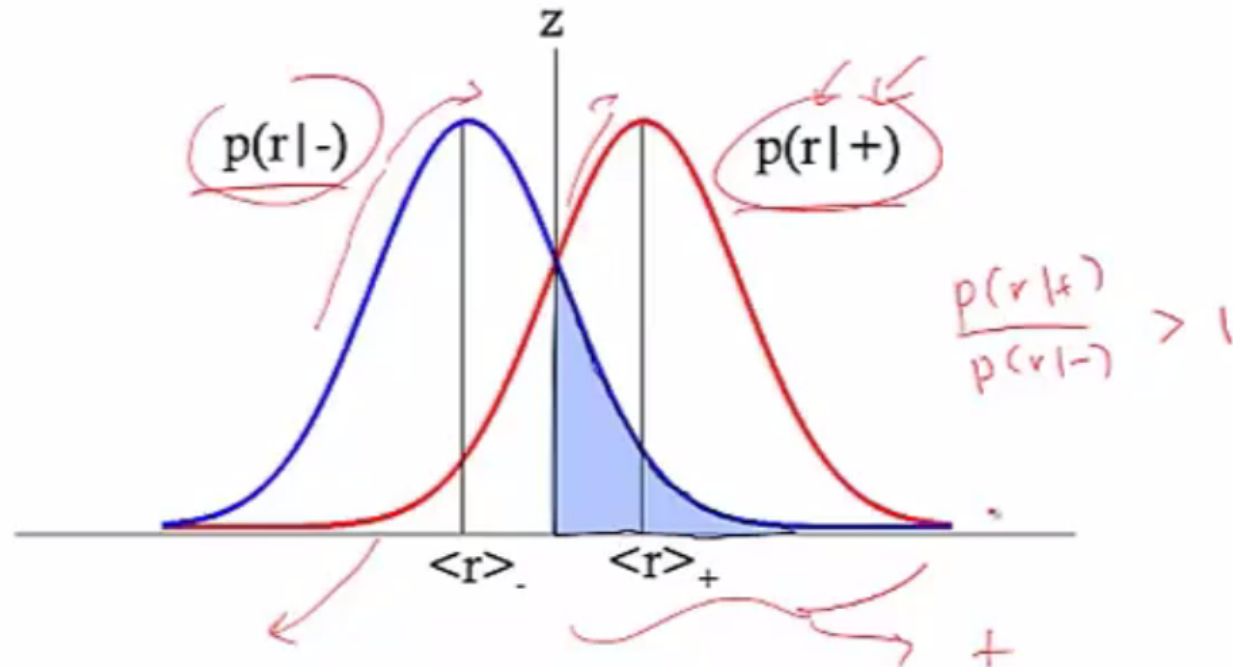
$$P(r \geq z | -)$$

$$P(r \geq z | +)$$

$$P_{\text{corr}} = p(+)\ P(r \geq z | +) + p(-)\ (1 - P(r \geq z | -))$$

Decoding

- Likelihood ratio – Neymann-Pearson lemma

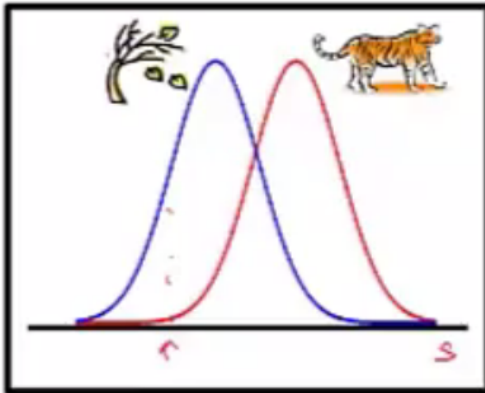


The likelihood ratio test is the most efficient statistic, in that it has the most power for a given size

Decoding

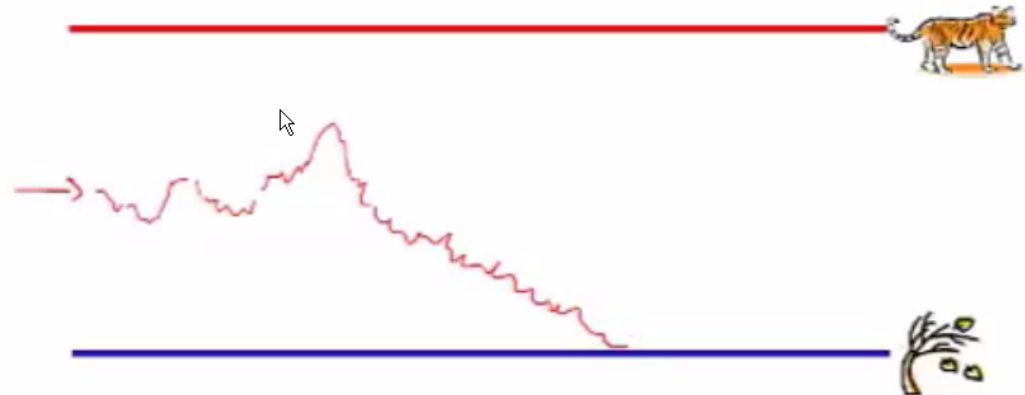
- Sequence of observations – accumulated evidence

Now let's say we don't have to decide immediately...



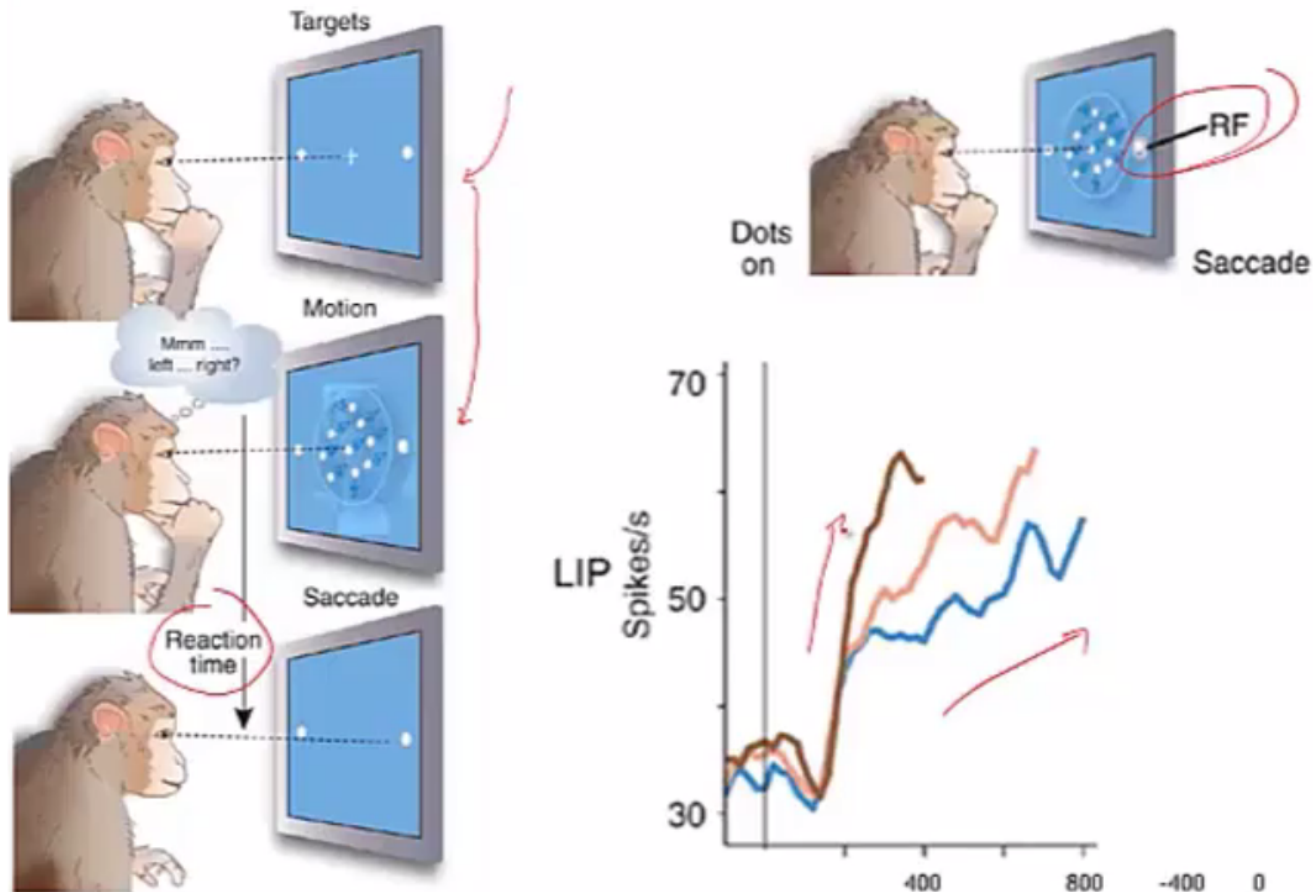
$$L(s) = \frac{P(s|\text{tiger})}{P(s|\text{breeze})} \} < 1$$

$$\log L(s) < 0$$



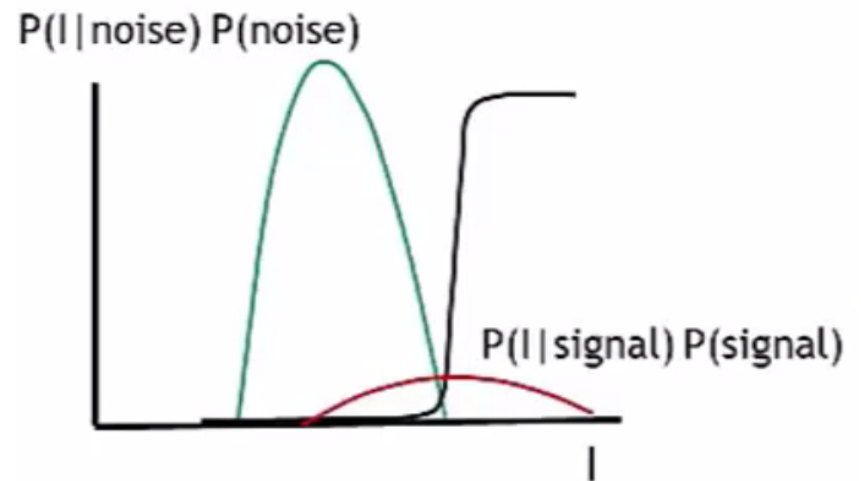
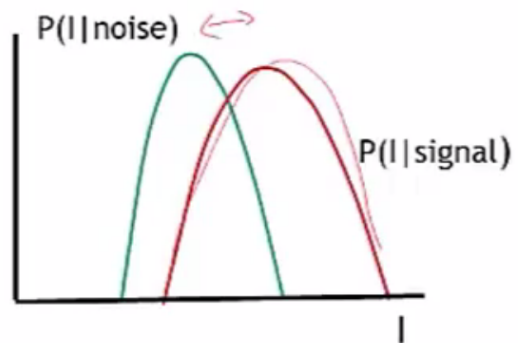
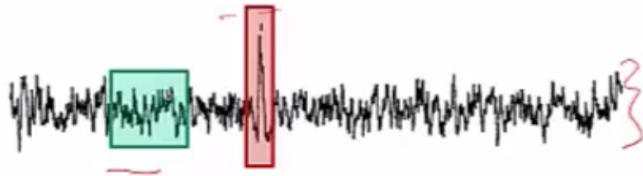
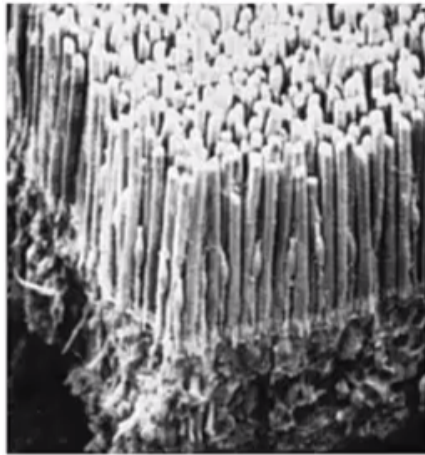
Decoding

- Sequence of observations – accumulated evidence
 - Kiani et.al, 2006



Decoding

- Priors \rightarrow changes decisions (retina: $P(\text{noise}) = 99.9\%$)



Decoding

- Priors \rightarrow changes decisions (retina: $P(\text{noise}) = 99.9\%$)
- Costs



Cut your losses: answer + when $\text{Loss}_+ < \text{Loss}_-$.

i.e. $L_+P[- | r] < L_-P[+ | r]$.

Decoding – from populations

- Population vector average (parallel to arm movement)

Pop. vector:

$$\vec{v}_{\text{pop}} = \sum_{a=1}^N \left(\frac{r - r_0}{r_{\text{max}}} \right) \vec{c}_a$$

For sufficiently large N,

$$\langle \vec{v}_{\text{pop}} \rangle = \sum_{a=1}^N (\vec{v} \cdot \vec{c}_a) \vec{c}_a$$

Decoding – from populations

Maximum Likelihood:
 s^* which maximizes $p[\mathbf{r}|s]$

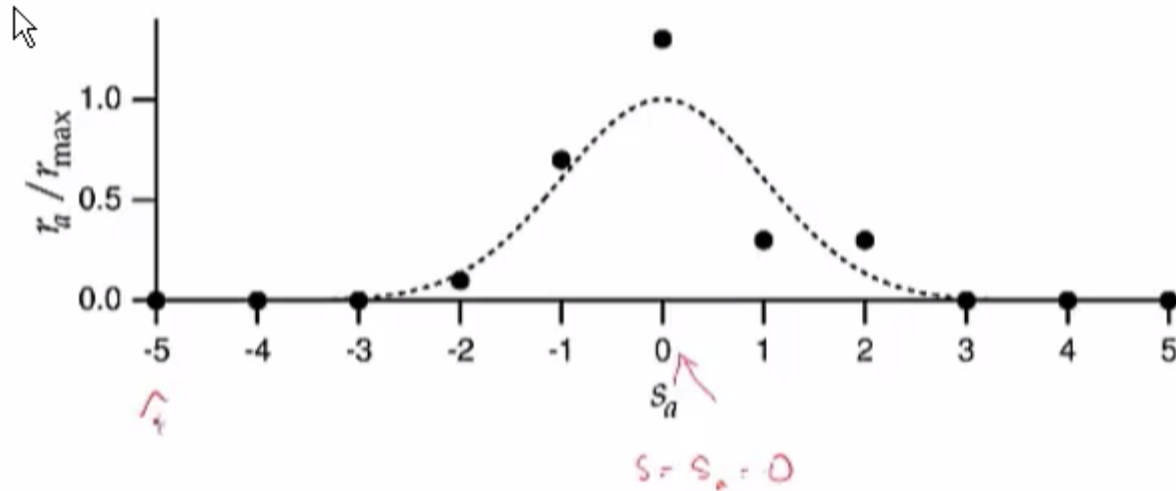
likelihood function

$$p[s|\mathbf{r}] = \frac{p[\mathbf{r}|s]p[s]}{p[\mathbf{r}]}$$

a posteriori distribution

Maximum *a posteriori*:
 s^* which maximizes $p[s|\mathbf{r}]$

Decoding – from populations



Population response of 11 cells with Gaussian tuning curves

$$P[\mathbf{r}|s] = \prod_{a=1}^N \frac{(f_a(s)T)^{r_a T}}{(r_a T)!} \exp(-f_a(s)T)$$

Decoding – stimulus reconstruction

Want an estimator s_{Bayes} $s \leftarrow \hat{v}$

Introduce an error function, $L(s, s_{\text{Bayes}})$; minimize error.

$$\rightarrow \frac{\partial}{\partial s_{\text{Bayes}}} \int ds \underline{L(s, s_{\text{Bayes}})} \underline{p[s|\mathbf{r}]} = 0$$

For least squares cost, $\underline{L(s, s_{\text{Bayes}})} = \underline{(s - s_{\text{Bayes}})^2}$;

$$\frac{\partial}{\partial s_{\text{Bayes}}} \int ds (s - s_{\text{Bayes}})^2 p(s|\mathbf{r}) = 2 \int ds (s - s_{\text{Bayes}}) p(s|\mathbf{r}) = 0$$

$$\int ds s p(s|\mathbf{r}) = \int ds s_{\text{Bayes}}$$

Solution: $s_{\text{Bayes}} = \int ds p[s|\mathbf{r}] s \leftarrow$

Decoding – stimulus reconstruction

Want an estimator s_{Bayes} $s \leftarrow \checkmark$

Introduce an error function, $L(s, s_{\text{Bayes}})$; minimize error.

$$\rightarrow \frac{\partial}{\partial s_{\text{Bayes}}} \int ds \underline{L(s, s_{\text{Bayes}})} \underline{p[s|\mathbf{r}]} = 0$$

For least squares cost, $L(s, s_{\text{Bayes}}) = (s - s_{\text{Bayes}})^2$;

$$\frac{\partial}{\partial s_{\text{Bayes}}} \int ds (s - s_{\text{Bayes}})^2 p(s|\mathbf{r}) = 2 \int ds (s - s_{\text{Bayes}}) p(s|\mathbf{r}) = 0$$

$$\int ds s p(s|\mathbf{r}) = \int ds s_{\text{Bayes}}$$

Solution: $s_{\text{Bayes}} = \int ds p[s|\mathbf{r}] s \leftarrow$

If response is a single spike \rightarrow we just average all stimuli by the probability they appeared given this response

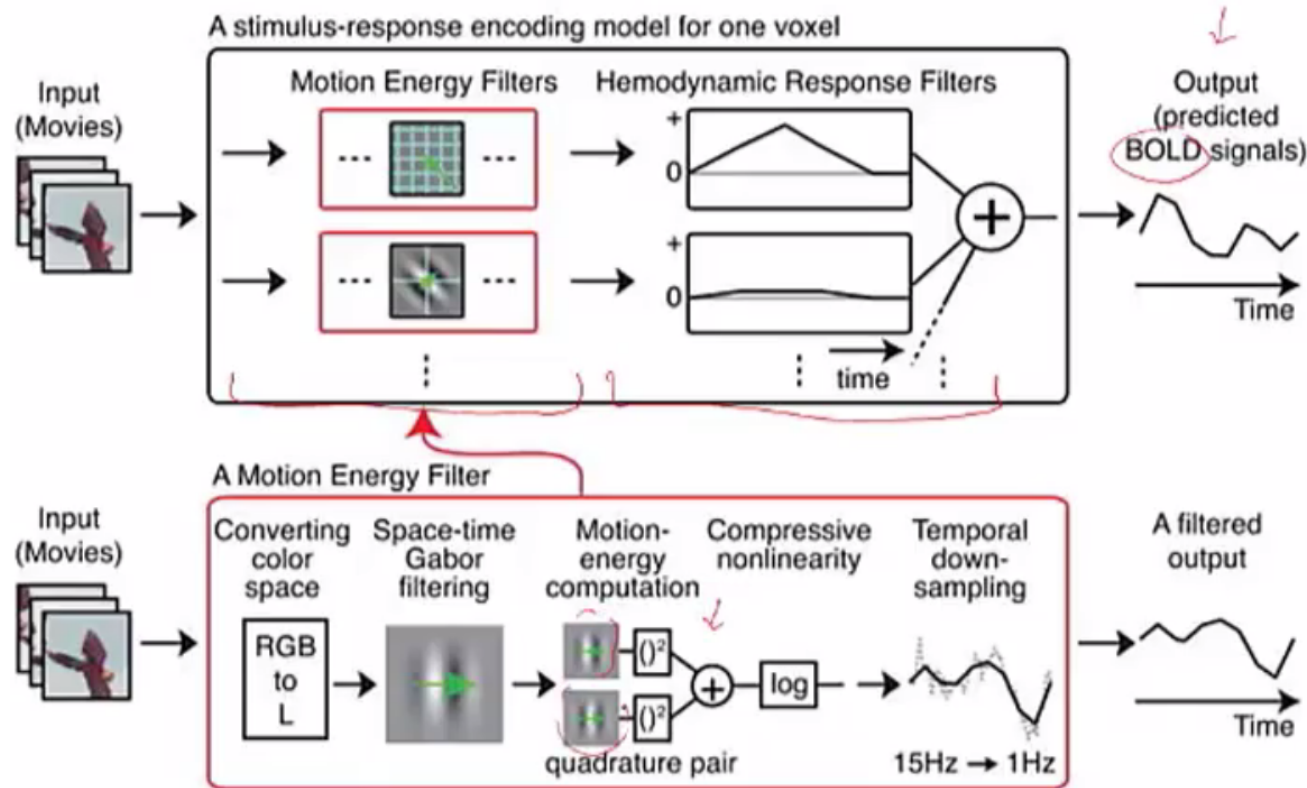
Decoding – stimulus reconstruction

- Yang Dan, Barkley – cat LGN neurons reconstruction

<https://www.youtube.com/watch?v=tFdZ9eGTG5A>

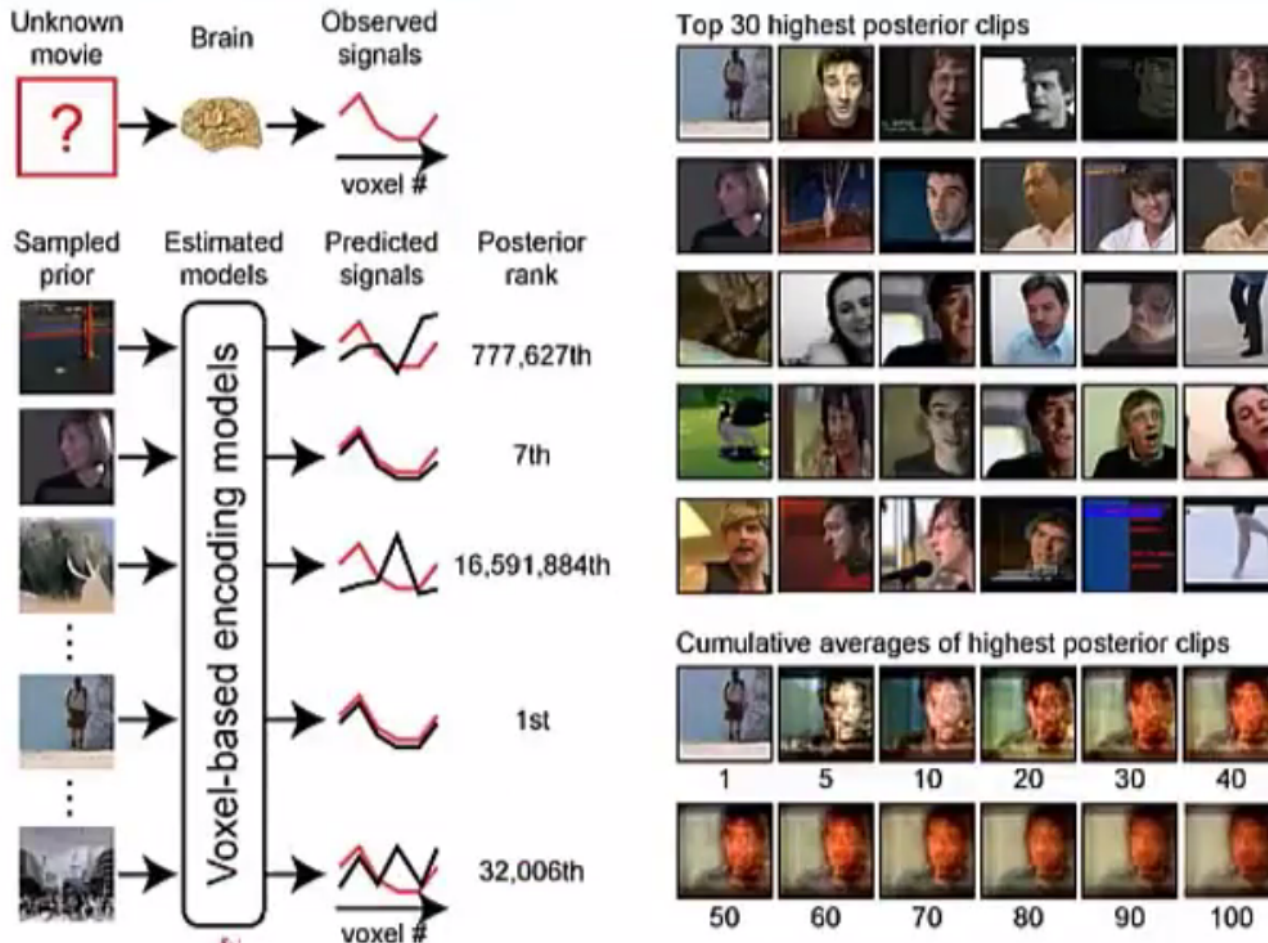
Decoding – stimulus reconstruction

- Nishimoto et al., 2011 (fMRI)



Decoding – stimulus reconstruction

- Nishimoto et al., 2011 (fMRI)

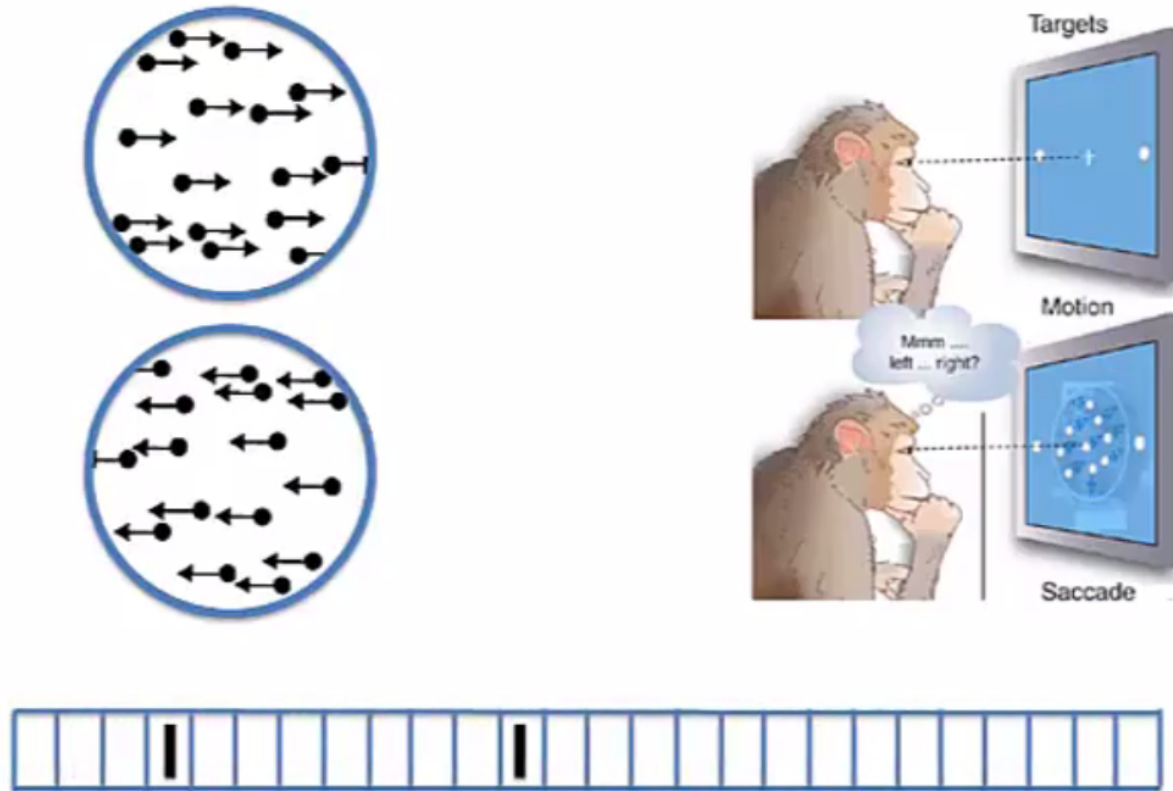


Information theory

- Information transmission limits
 - Problem sparse representation
 - Entropy and information
 - How information tells us about coding

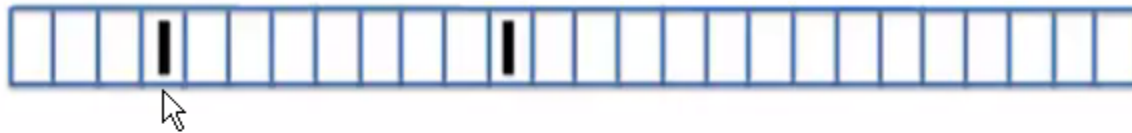
Information theory

- Information (represents this surprise for monkey)



Information theory

- Information that we get from spike/non-spike



$$P(1) = p$$

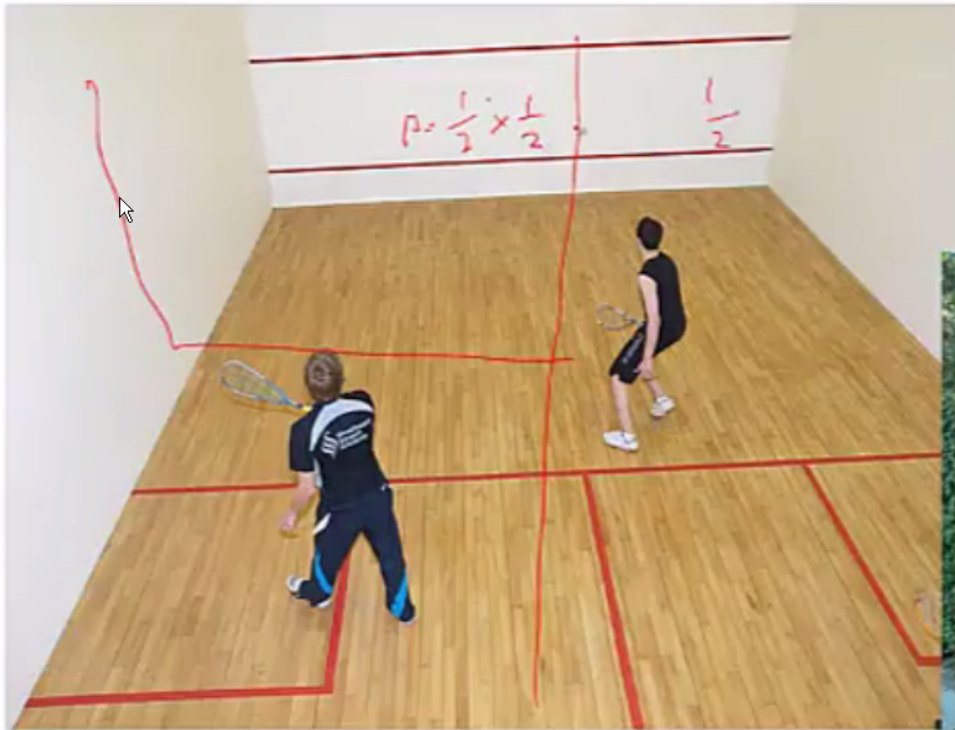
$$P(0) = 1 - p$$

$$\rightarrow \text{information}(1) = -\log_2 p \quad \checkmark$$

$$\text{information}(0) = -\log_2 (1-p)$$

Information theory

- Each bit of information splits space to half

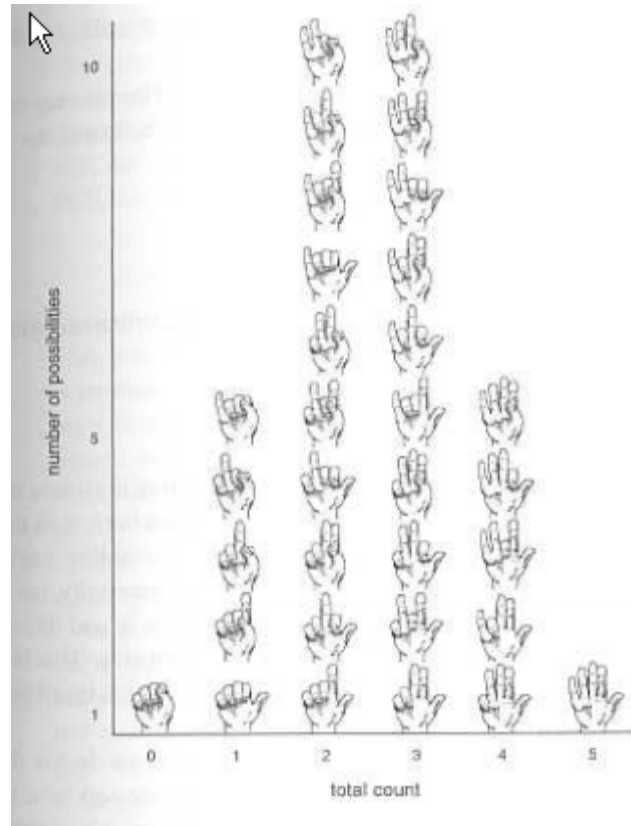


Each *bit* of information specifies location by an additional factor of 2.



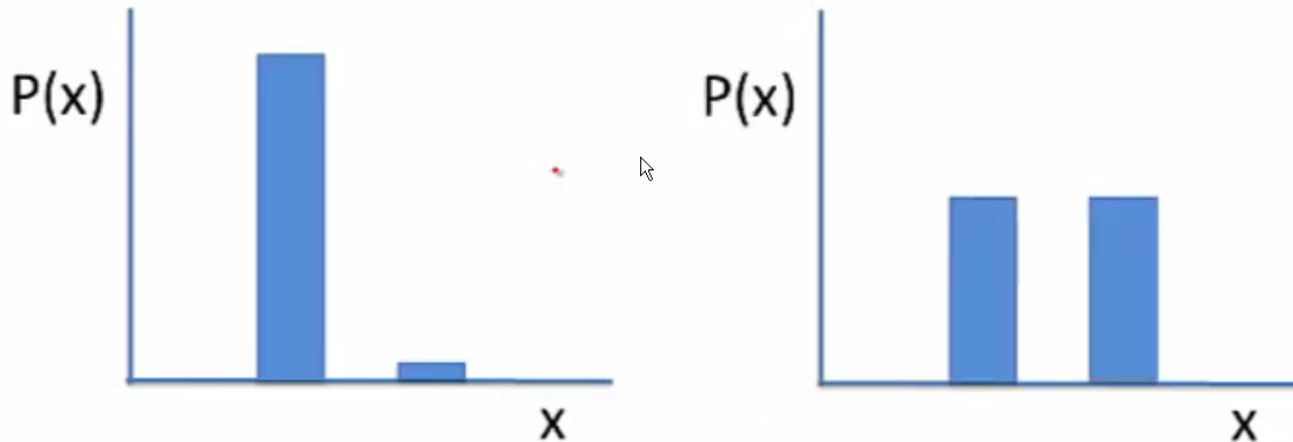
Information theory

- Different encodings



Information theory - Entropy

Entropy – is the expected value (average) of information contained in each message



$$\begin{aligned}\text{Entropy} &= \text{average information} \\ &= - \sum_i p_i \log_2 p_i \\ &= - \int dx p(x) \log_2 p(x)\end{aligned}$$

Units are *bits*

Information theory - Entropy

Entropy – how many questions are needed to find the position of my car?



Information theory - Entropy

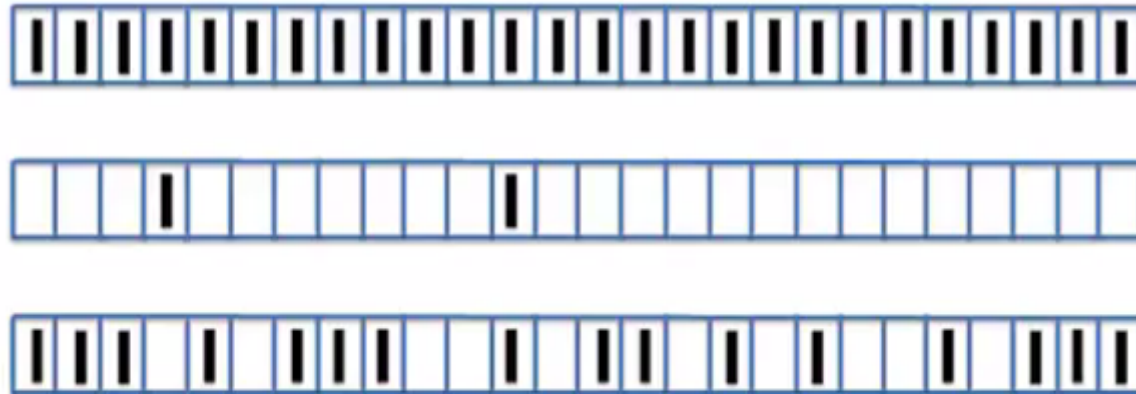
Entropy – how many questions are needed to find the position of my car?



$$\begin{aligned} H &= -\sum p_i \log p_i \\ p_i &= \frac{1}{8} \\ H &= -\sum_{i=1}^8 \frac{1}{8} \log_2 \left(\frac{1}{8} \right) \\ &= \sum \frac{1}{8} \cdot (-3) \quad 8 = 2^3 \\ &= 3 \end{aligned}$$

Information theory - Entropy

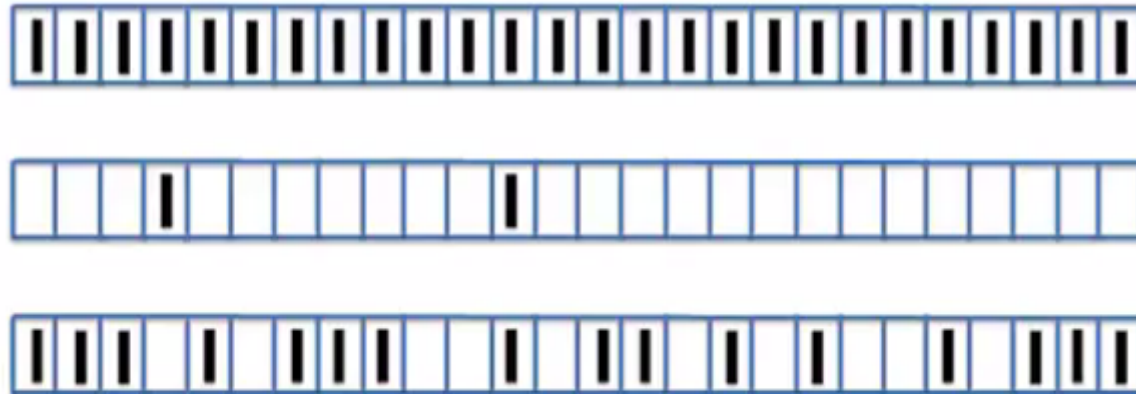
- Which of the messages/encoding can contain the most information?
- Not varying \rightarrow does not provide much information...



Entropy = average information
 $= - \sum_{i=1}^2 p_i \log_2 p_i$

Information theory - Entropy

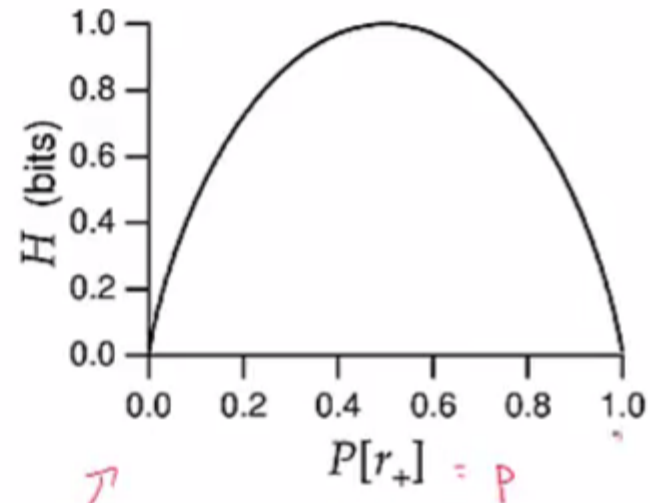
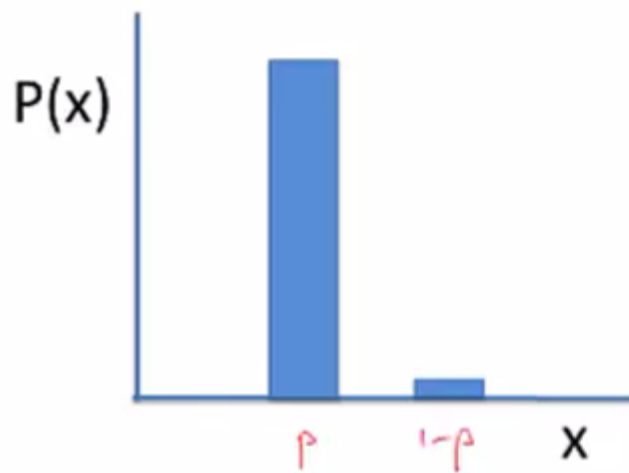
- Large entropy \rightarrow lot of possibility for representing inputs



Entropy = average information
 $= - \sum_{i=1}^2 p_i \log_2 p_i$

Information theory - Entropy

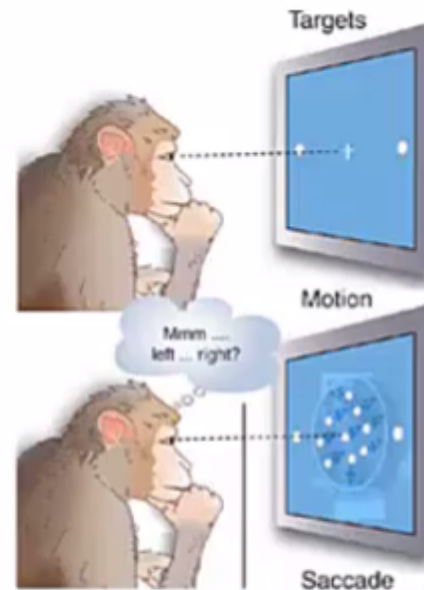
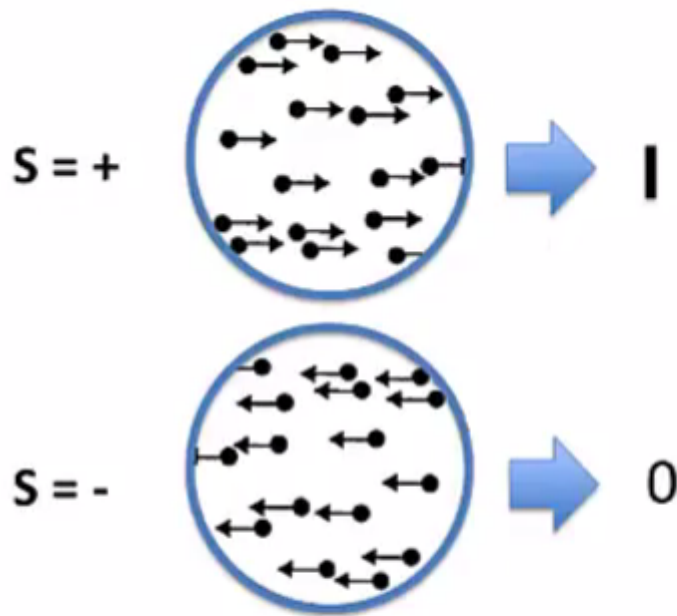
- Maximum entropy for $p = 1/2 \rightarrow$ would be best if uniform distribution (if we could place ball in squash to any place then we need least bits to encode the information)



$$\text{Entropy} = - \sum p_i \log_2 p_i$$

$$= - p \log_2 p - (1-p) \log_2 (1-p)$$

Information theory - Entropy



$\Rightarrow r$

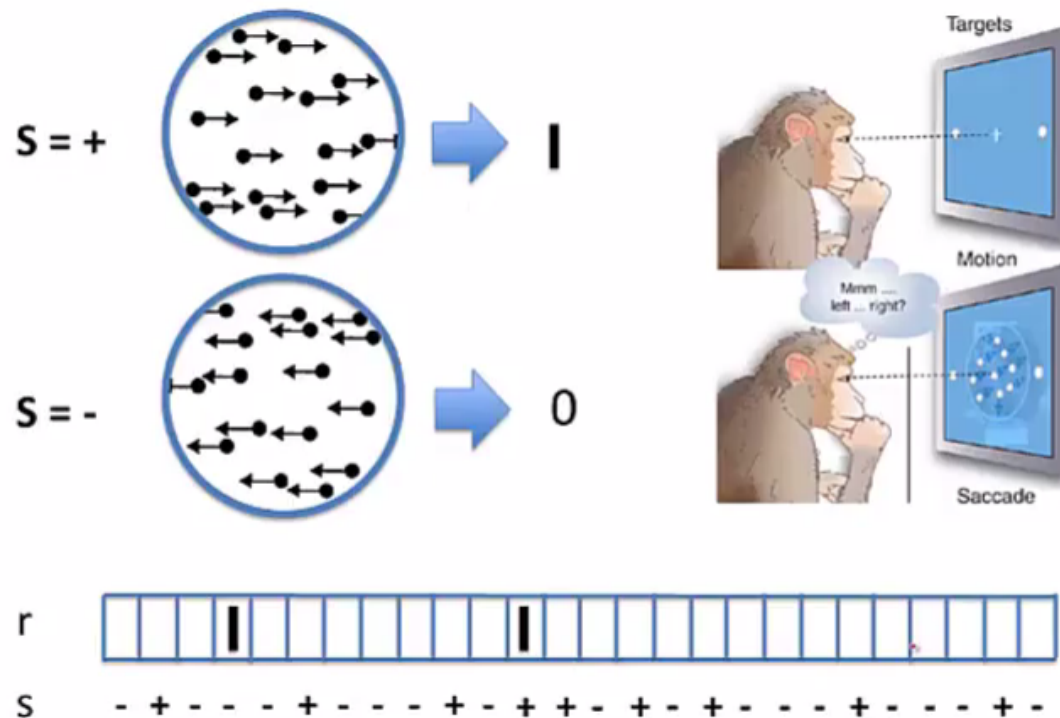


$\Rightarrow S$



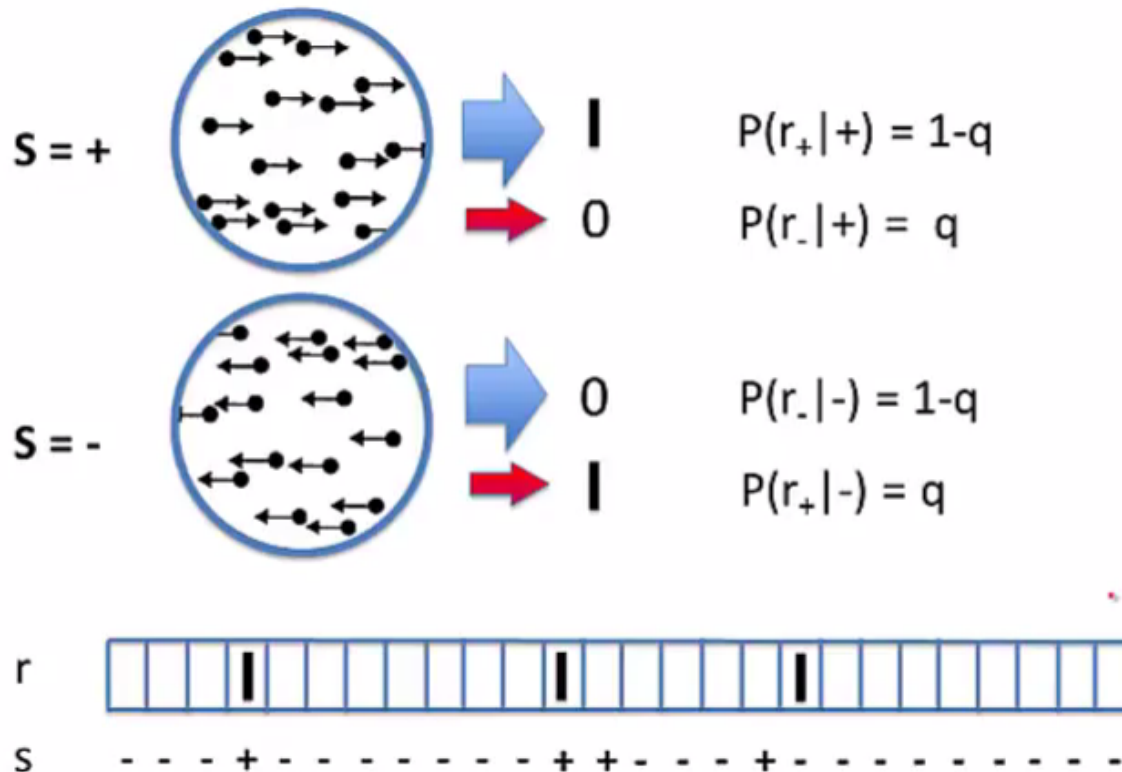
Information theory - Entropy

- Either:
 - Neuron not responding to stimulus
 - bad feature
 - didn't understand what code is doing



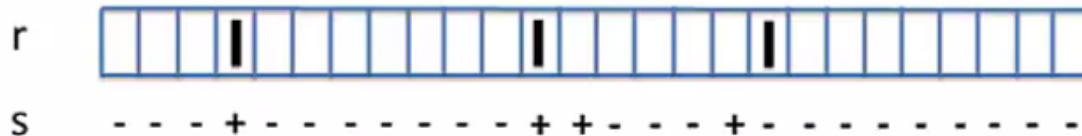
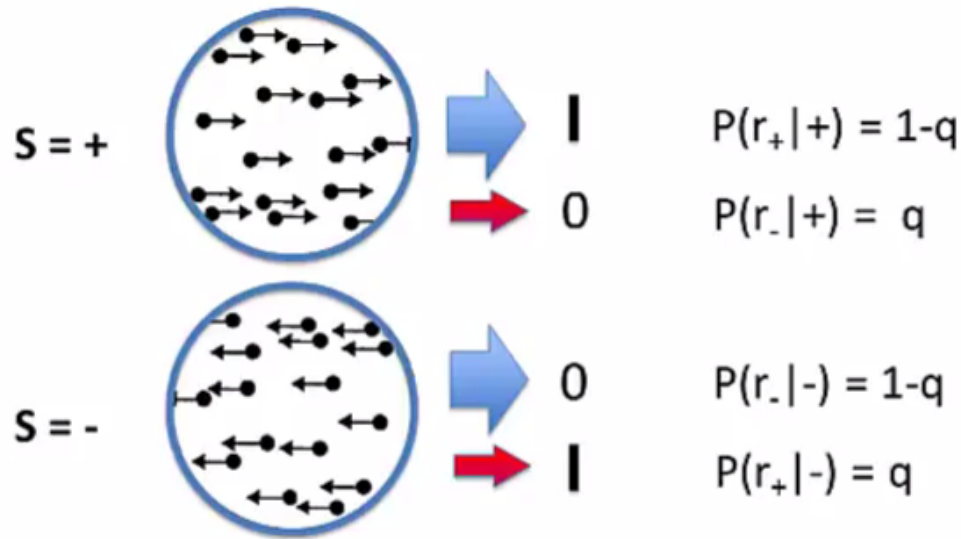
Information theory - Entropy

- How much variability in r is encoding s
 - Possibility of error



Information theory - Entropy

- How much entropy accounts for these errors (noise)



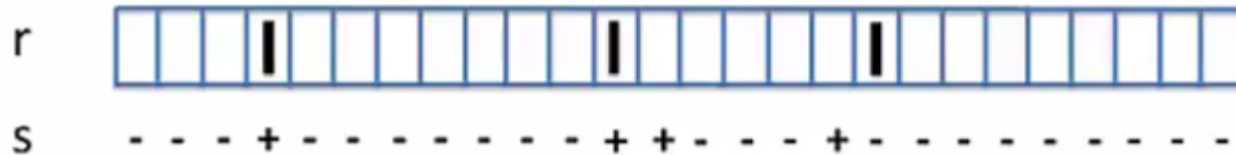
$$H = - \sum_{i=1}^2 p_i \log_2 p_i$$

Total entropy: $H[R] = - P(r_+) \log P(r_+) - P(r_-) \log P(r_-)$

Noise entropy: $H[R|+] = - q \log q - (1-q) \log (1-q)$

Information theory – Mutual information

- The amount of information that the response carries about the stimulus



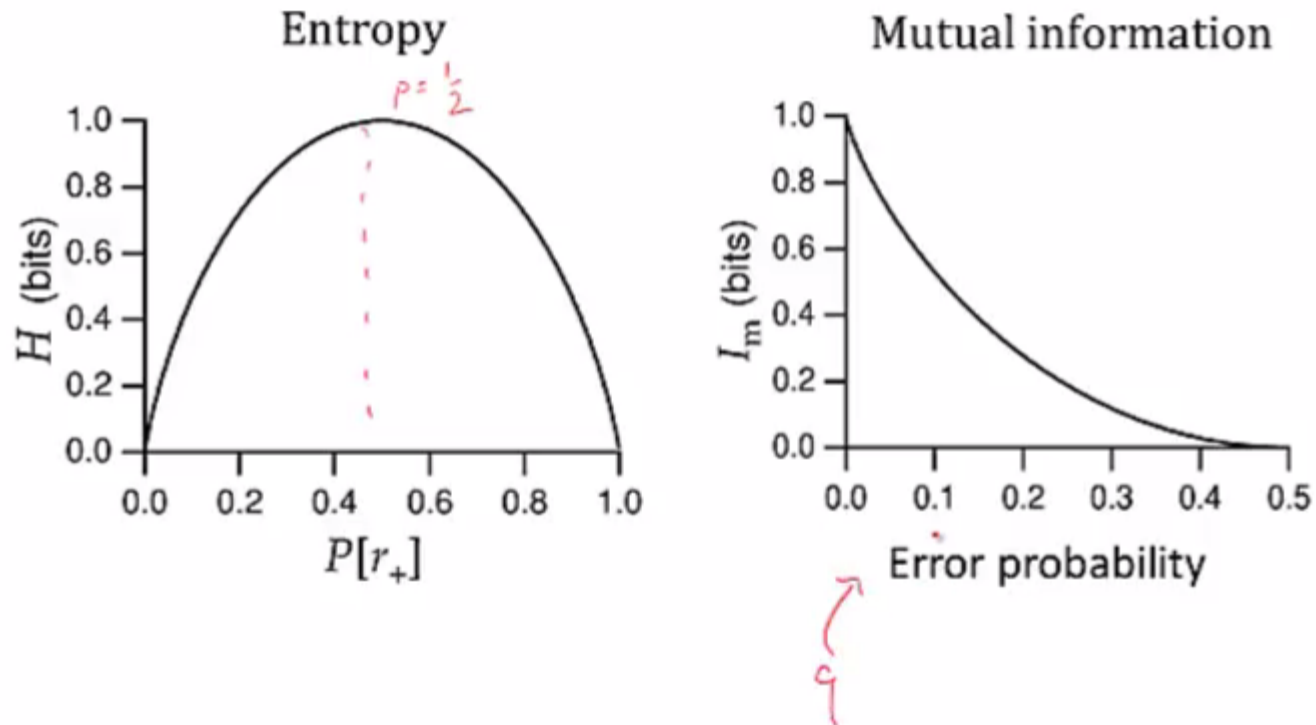
The amount of entropy that is used in coding the stimulus

$$MI(S,R) = \text{Total entropy} - \text{average noise entropy}$$

$$MI = - \sum_r p(r) \log_2 p(r) - \sum_s p(s) [- \sum_r p(r|s) \log_2 p(r|s)]$$

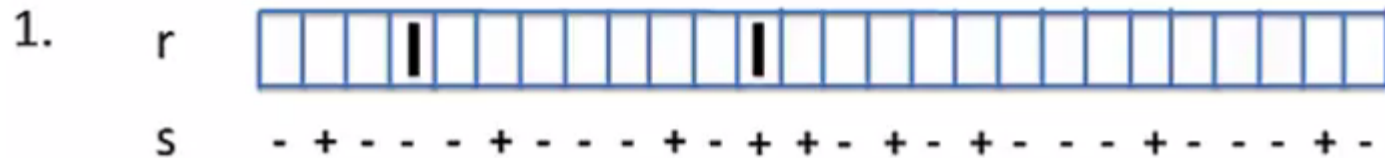
Information theory – Mutual information

- The amount of information that the response carries about the stimulus



Information theory – Mutual information

- The amount of information that the response carries about the stimulus



Response is unrelated to stimulus

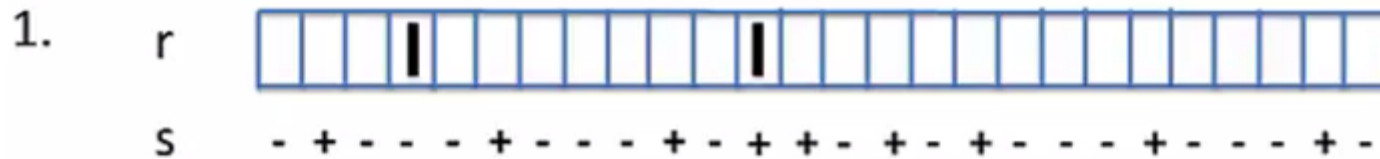
- What is $p(r|s)$?
- What is the MI ?



Response is perfectly predicted by stimulus

Information theory – Mutual information

- The amount of information that the response carries about the stimulus



Response is unrelated to stimulus

- What is $p(r|s)$? = $p(r)$
- What is the MI? = 0



Response is perfectly predicted by stimulus

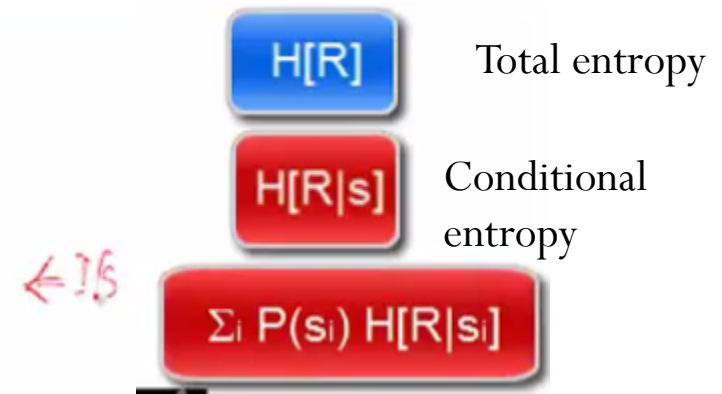
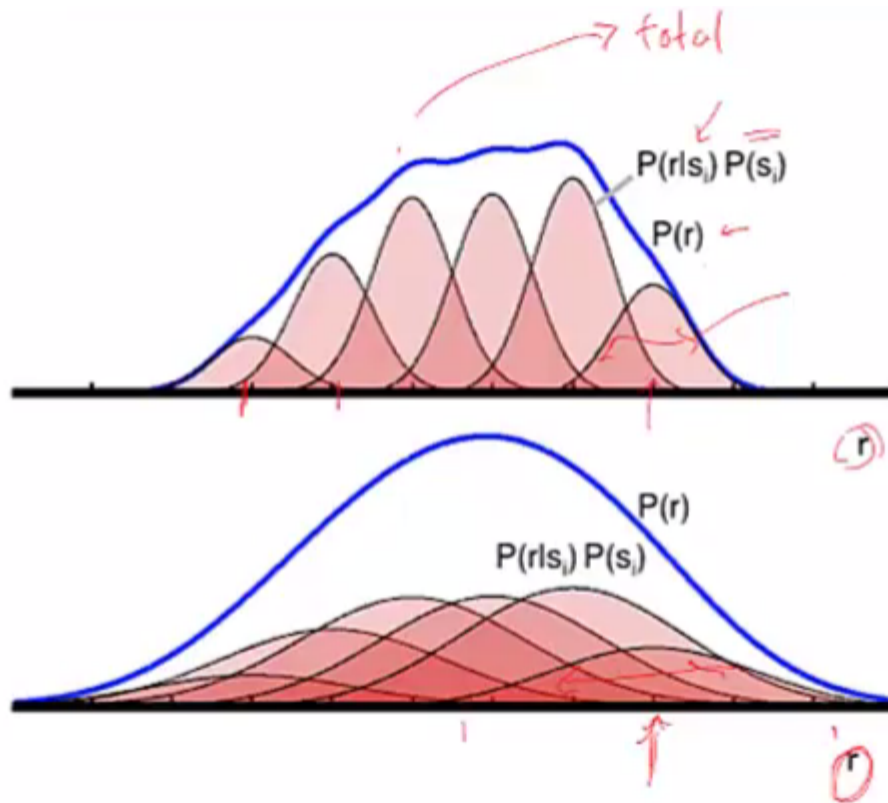
Noise entropy = 0 \rightarrow MI = total entropy of response

Information theory - Entropy

- Information summarizes how much independent two variables are
- Encoding
 - Most coherent form
 - Maximizing entropy

Information theory – Continuous variables

- Which distribution encodes more information about stimulus?



Average cond. entropies over stimulus they drove them

Information theory – Information in spikes

- Information in spike pattern/trains
- Information in single spikes

Information theory – Information in spikes

- Information in spike pattern/trains
- Information in single spikes

Mutual information is the difference between the total response entropy and the mean noise entropy:

$$I(S;R) = H[R] - \sum_s P(s) H[R|s] . \quad \leftarrow$$

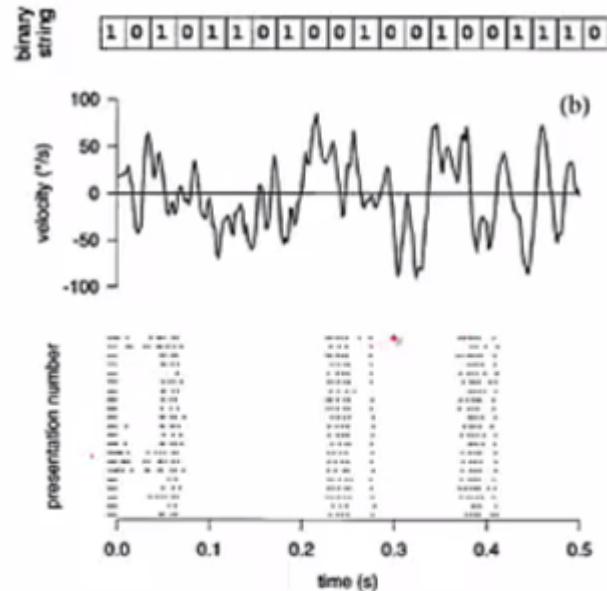
- Take one stimulus s and repeat many times $\rightarrow p(R | s)$
- Compute variability due to noise: noise entropy $H[R | s]$
- Repeat for all s and average: $\sum_s P(s) H[R|s]$
- Compute $P(R) = \sum_s P(s) P(R|s)$ and the total entropy $H[R]$

Information theory – Information in spikes

So far only dealt with single spikes, or firing rates.

What information is carried by patterns of spikes?

Analyze patterns of the code: how informative are they?



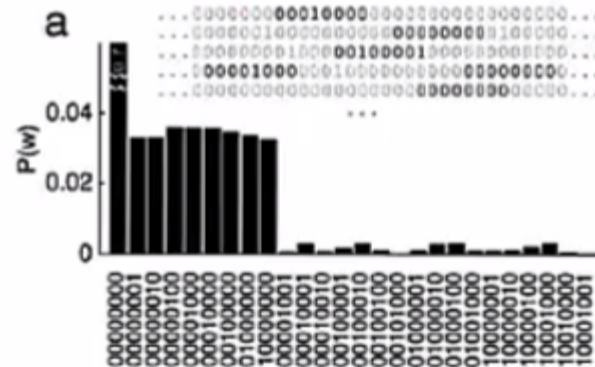
Strong et al., 1997

Information theory – Information in spikes

Entropy:



- Binary words w with letter size Δt , length T .
- Compute $p(w_i)$



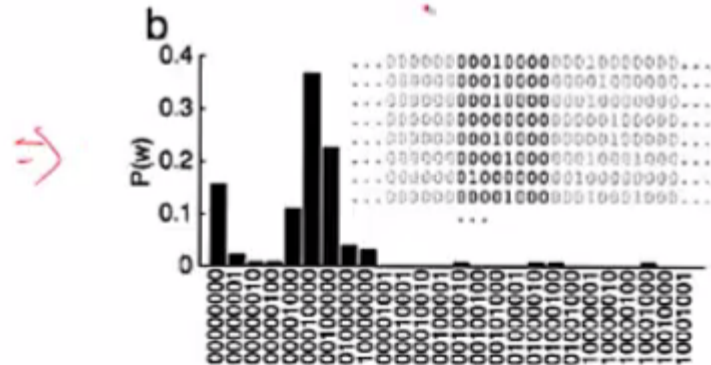
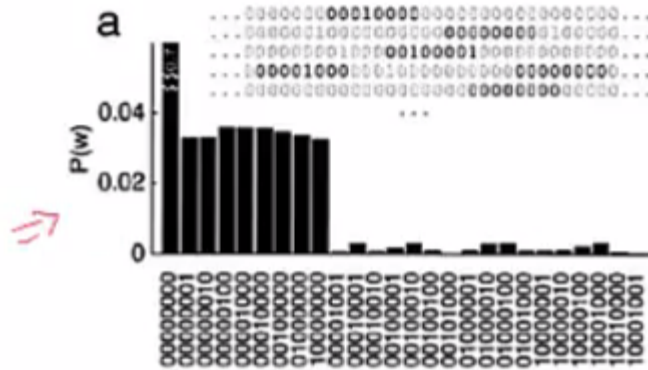
$$H[w] = - \sum p(w_i) \log_2 p(w_i)$$

Entropy of that word distribution

Strong et al., 1997; Reinagel and Reid, 2000

Information theory – Information in spikes

Information :
difference between the total
variability driven by stimuli
and that due to noise, averaged
over stimuli.



Information theory – Information in spikes

Take a stimulus sequence and repeat many times.

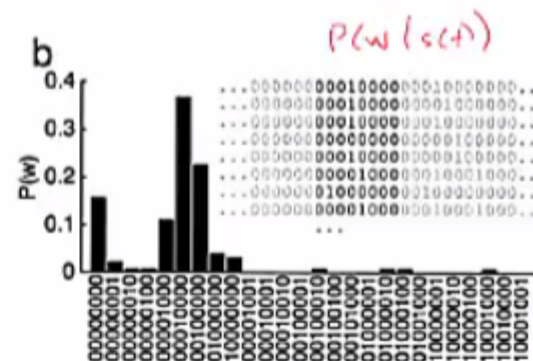
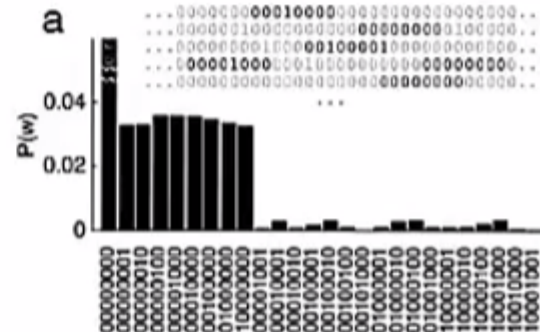
How to sample $P(s)$? ←

Average over $s \rightarrow$ average over time:

For each time in the repeated stimulus, get a set of words $P(w|s(t))$.

$$\underline{H_{\text{noise}}} = \langle H[P(w|s_i)] \rangle_i$$

Choose length of repeated sequence long enough to sample the noise entropy adequately.



Information theory – Information in spikes

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