Neural Coding

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Outline

- a little about neurons
- a little about point processes
- examples of rate coding
- populations of neurons:
  - correlations
  - population coding and decoding

Neurons

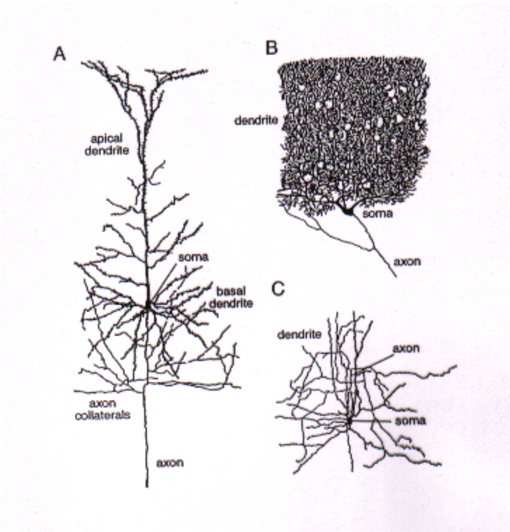
ca 10^{11} neurons/human brain

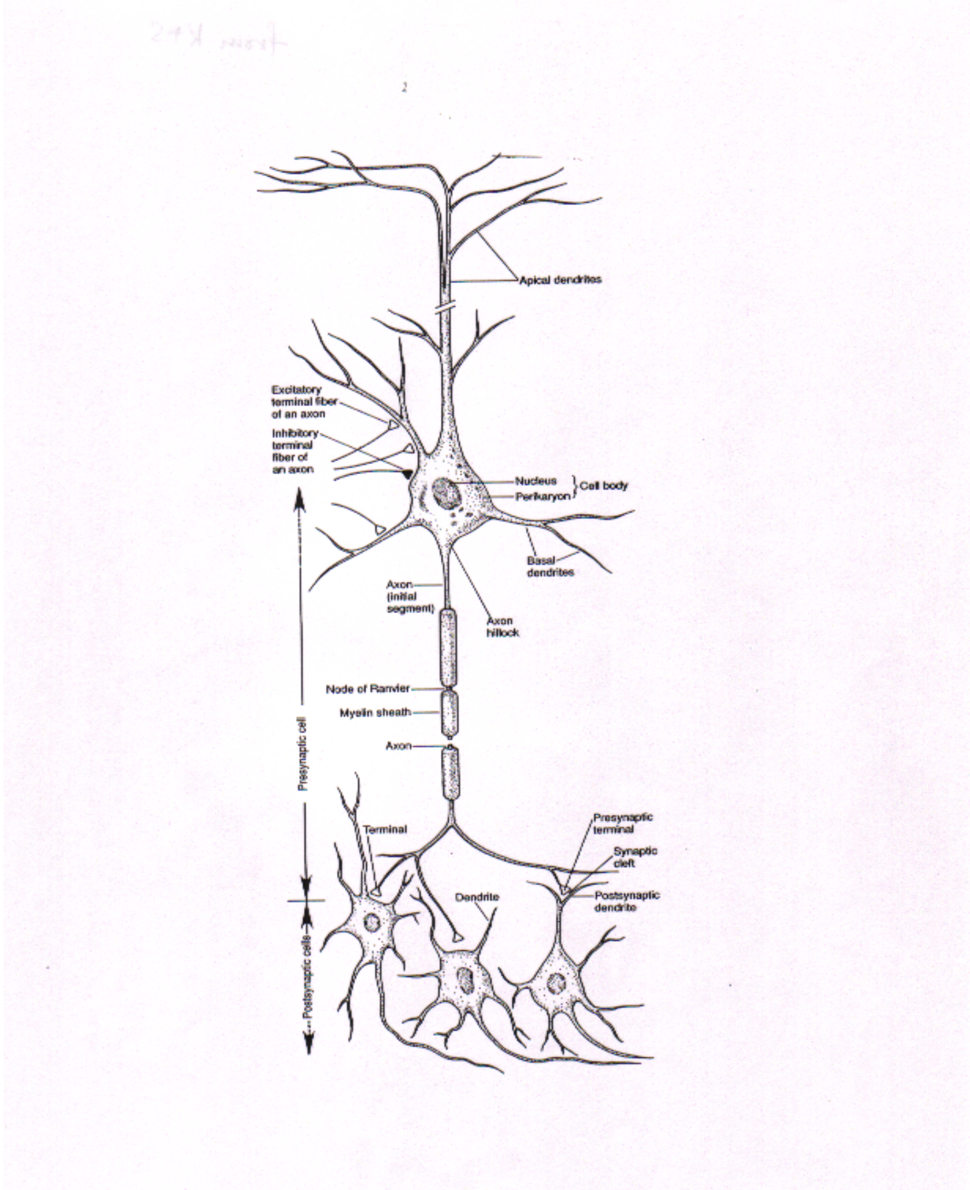
$10^4/mm^3$

soma 10-50 μm

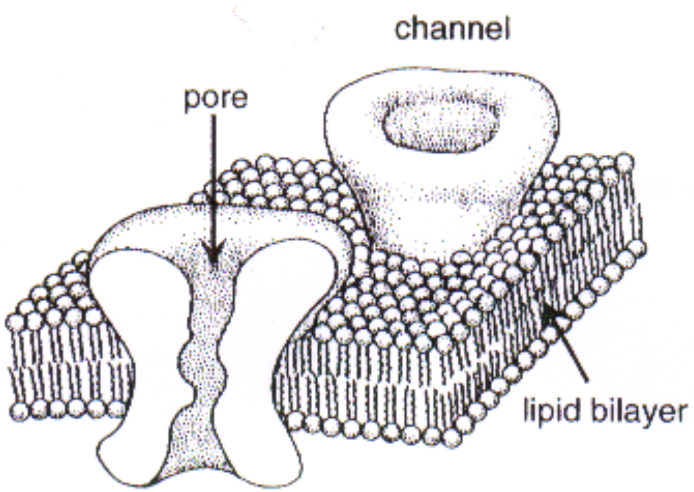
axon length ~ 4 cm

total axon length/mm^3 ~ 400 m



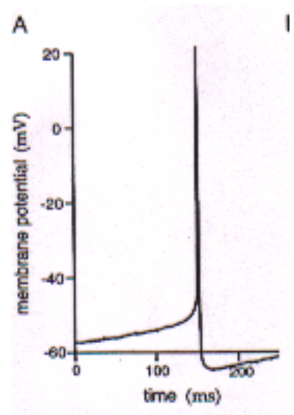


Cell membrane, ion channels, action potentials

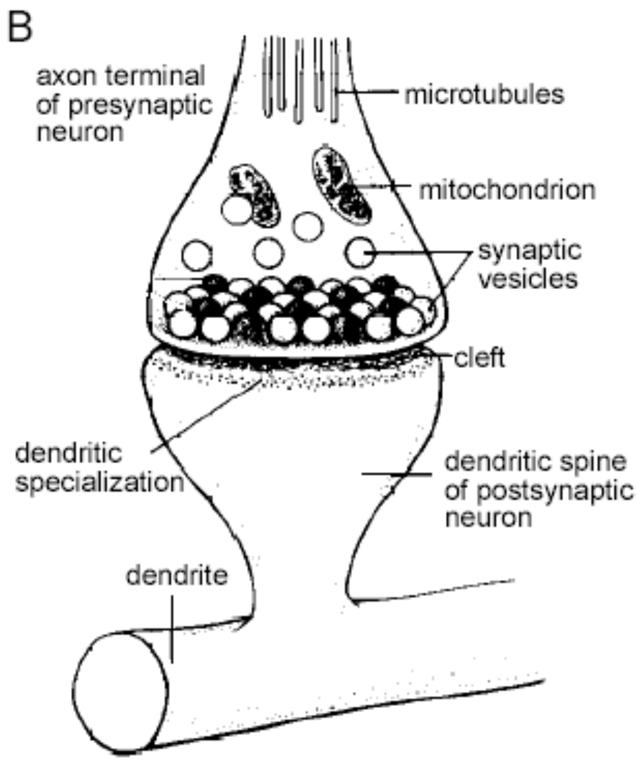


Membrane potential: rest at ca -70 mv
Na-K pump maintains excess K inside,
Na outside

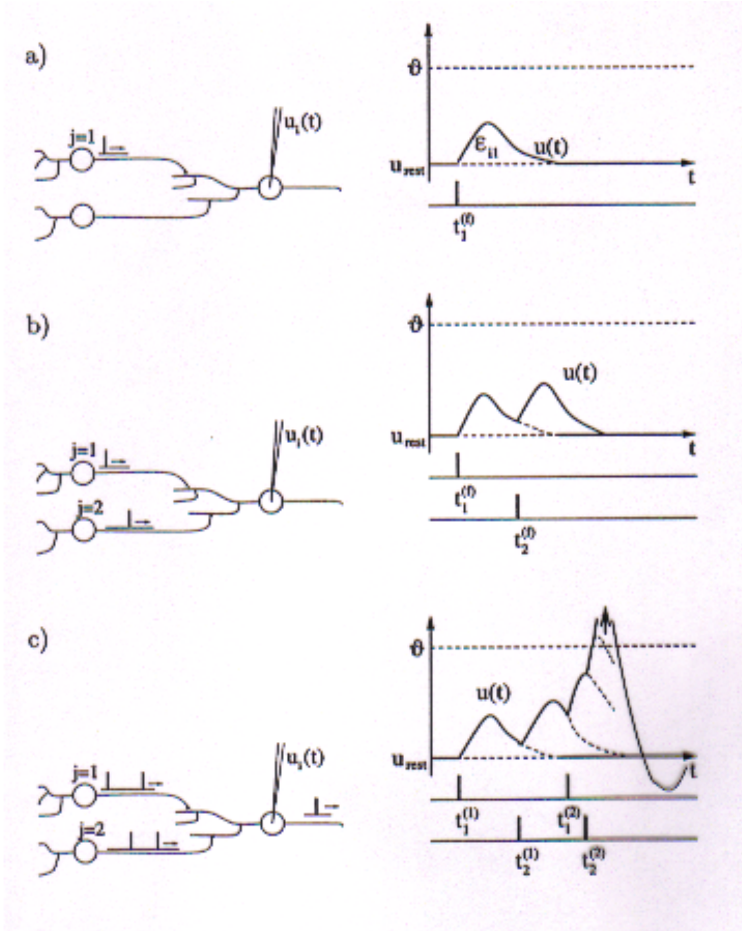
Na in: V rises,
more channels open
→ "spike"



Communication: synapses

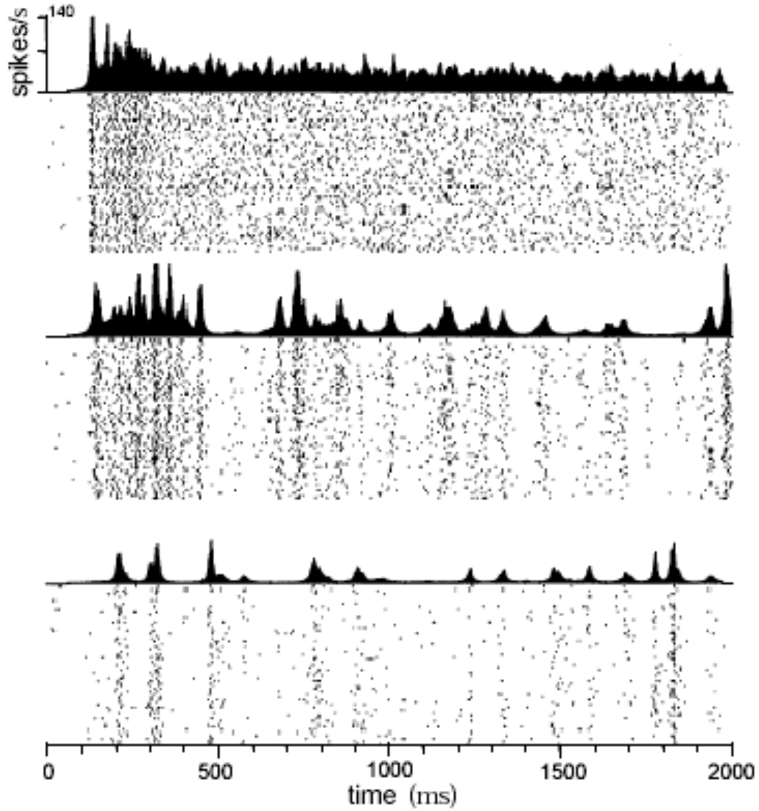


Integrating synaptic input:

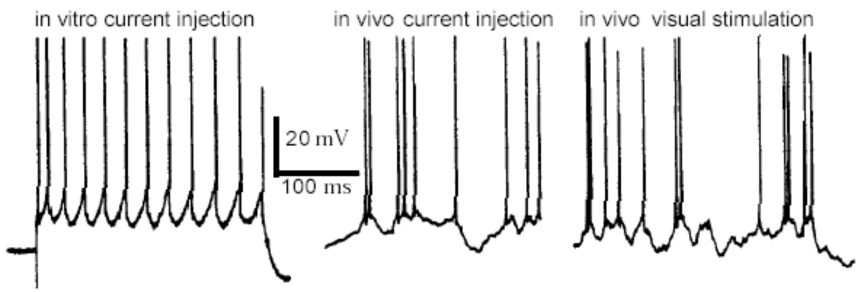


Neuronal communication: noisy spike trains

Motion-sensitive neuron in visual area MT: spike trains evoked by multiple presentations of moving random-dot patterns



Intracellular recordings of membrane potential:
Isolated neurons fire regularly;
neurons *in vivo* do not:



Spike trains: Poisson process model

Homogeneous Poisson process: r = rate = prob of firing per unit time,
i.e., $r\Delta t =$ prob of spike in interval $[t, t+\Delta t) \qquad (\Delta t \to 0)$

Survivor function: probability of not firing in $[0,t)$: $\qquad S(t)$

$$r = \frac{-dS(t)/dt}{S(t)} \qquad \Rightarrow \qquad S(t) = \mathrm{e}^{-rt}$$

Probability of firing for the first time in $[t,\, t+\Delta t)/\,\Delta t$:

$$P(t) = -\frac{dS(t)}{dt} = r\mathrm{e}^{-rt}$$

(interspike interval distribution)

Homogeneous Poisson process (2)

Probability of exactly 1 spike in $[0,T)$:

$$P_T(1) = \int_0^T dt\; r\mathrm{e}^{-rt} \cdot \mathrm{e}^{-r(T-t)} = rT\mathrm{e}^{-rT}$$

Probability of exactly 2 spikes in $[0,T)$:

$$P_T(2) = \int_0^T dt_2 \int_0^{t_2} dt_1\; r\mathrm{e}^{-rt_1} \cdot r\mathrm{e}^{-r(t_2-t_1)} \cdot \mathrm{e}^{-r(T-t_2)} = \tfrac{1}{2}(rT)^2\mathrm{e}^{-rT}$$

… Probability of exactly n spikes in $[0,T)$:

$$P_T(n) = \frac{1}{n!}(rT)^n\mathrm{e}^{-rT}$$

Poisson distribution

Poisson distribution

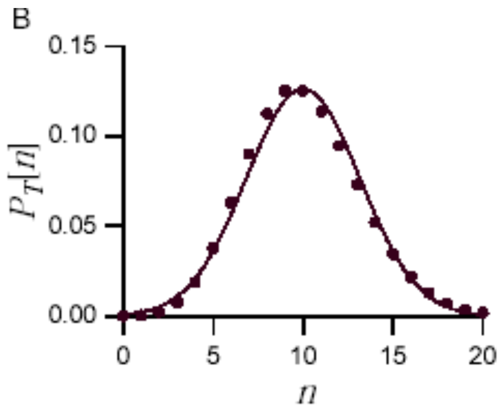
Probability of n spikes in interval of duration T:

$$P_T(n) = \frac{(rT)^n}{n!} e^{-rT}$$

Mean count: $\bar{n} = rT$

variance: $\overline{(n - \bar{n})^2} = rT = \bar{n}$ i.e., $\bar{n} \pm \sqrt{\bar{n}}$ spikes

large rT: → Gaussian



Poisson process (3): correlation function

Spike train: $$S(t) = \sum_f \delta(t - t_f)$$

mean: $$\langle S(t) \rangle = r$$

Correlation function:

$$C(\tau) = \langle (S(t) - r)(S(t+\tau) - r) \rangle = r\delta(\tau)$$

Stationary renewal process

Defined by ISI distribution $P(t)$

Relation between $P(t)$ and $C(t)$: define $C_+(t) \equiv \frac{1}{r}(C(t) + r^2)\Theta(t)$

$$C_+(t) = P(t) + \int_0^t dt' P(t') P(t-t') + \cdots$$

$$= P(t) + \int_0^t dt' P(t') C_+(t-t')$$

Laplace transform: $C_+(\lambda) = P(\lambda) + P(\lambda) C_+(\lambda)$

Solve: $C_+(\lambda) = \dfrac{P(\lambda)}{1 - P(\lambda)}$

Fano factor

$$F = \frac{\overline{(n-\bar{n})^2}}{\bar{n}}$$ spike count variance / mean spike count

$$F = 1$$ for stationary Poisson process

$$\bar{n} = \int_0^T \langle S(t) \rangle dt = rT$$

$$\overline{(\delta n)^2} = \int_0^T dt \int_0^T dt' \langle \delta S(t) \delta S(t') \rangle = T \int_{-\infty}^{\infty} C(\tau) d\tau$$ → $$F = \frac{\int_{-\infty}^{\infty} C(\tau) d\tau}{r}$$

$$F = CV^2$$ for stationary renewal process
(exercise: prove this)

Nonstationary point processes

Nonstationary Poisson process: time-dependent rate $r(t)$

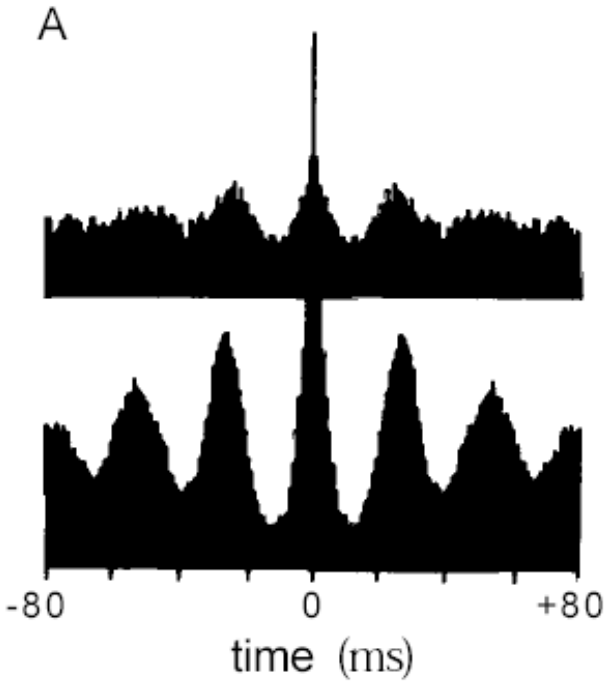
Still have Poisson count distribution, $F=1$

Nonstationary renewal process: time-dependent ISI distribution

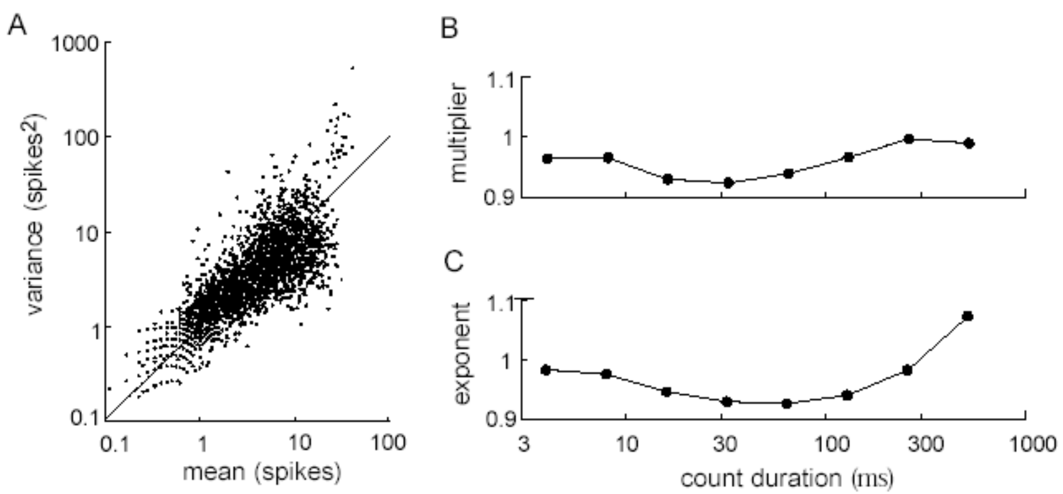
$P(t) \rightarrow P_{t_0}(t)$ = ISI probability starting at t_0

Experimental results (1)

Correlation functions

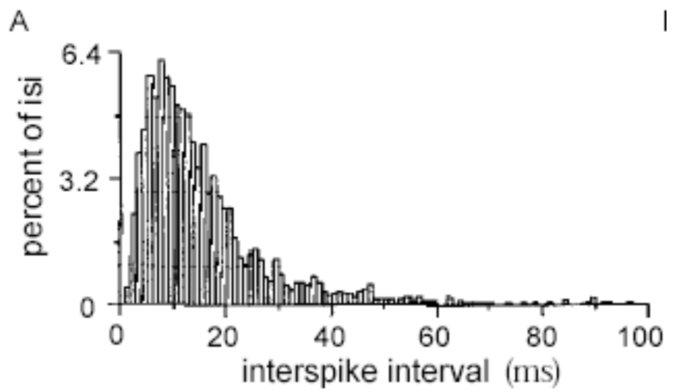


Count variance vs mean

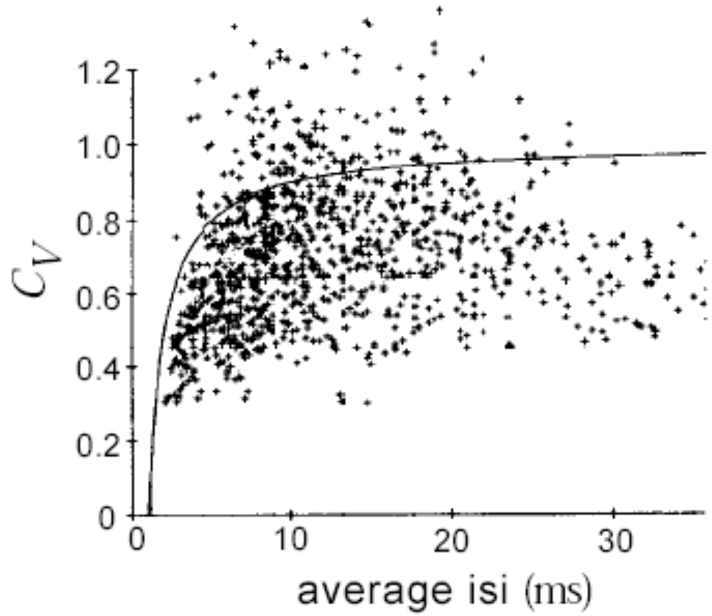


Experimental results (2)

ISI distribution



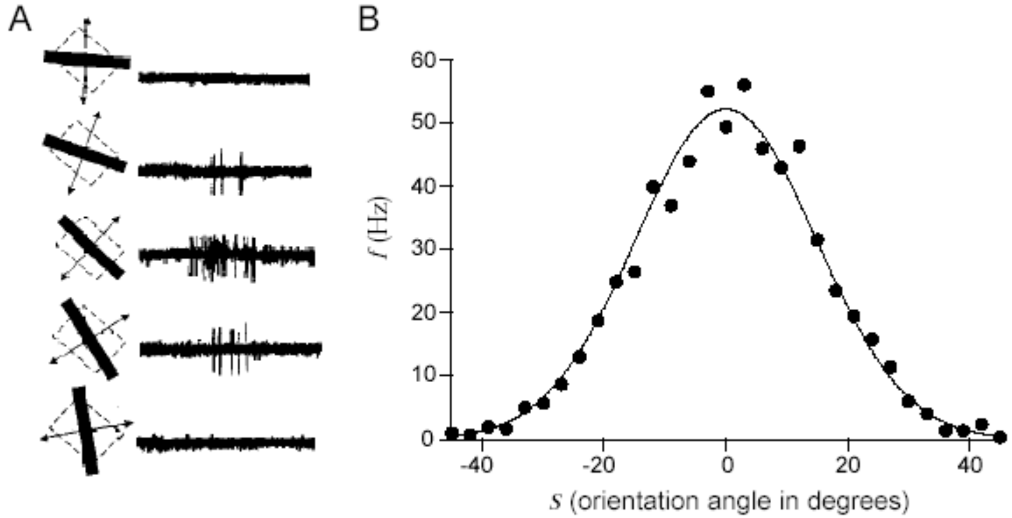
CV's for many neurons



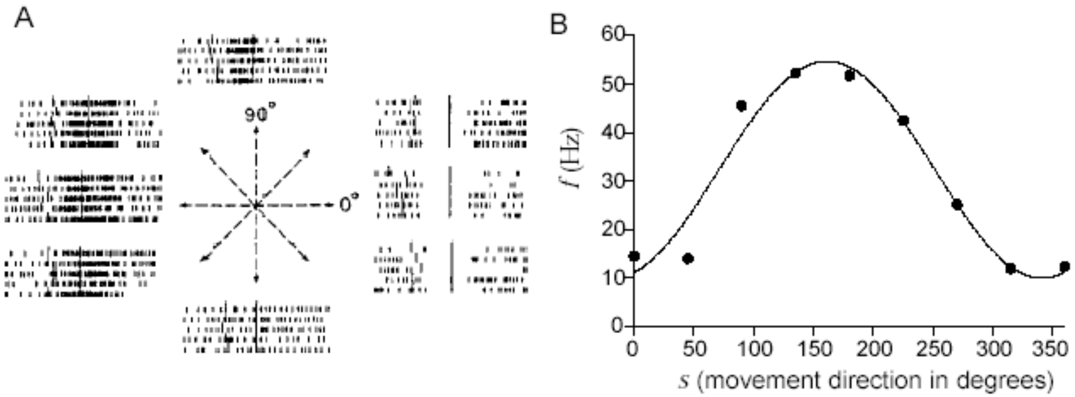
Neuronal firing is not exactly Poisson, but it is (surprisingly) close to it. **(~10% effects)**

Rate coding: examples

Visual cortical neuron: variation of rate with orientation of stimulus

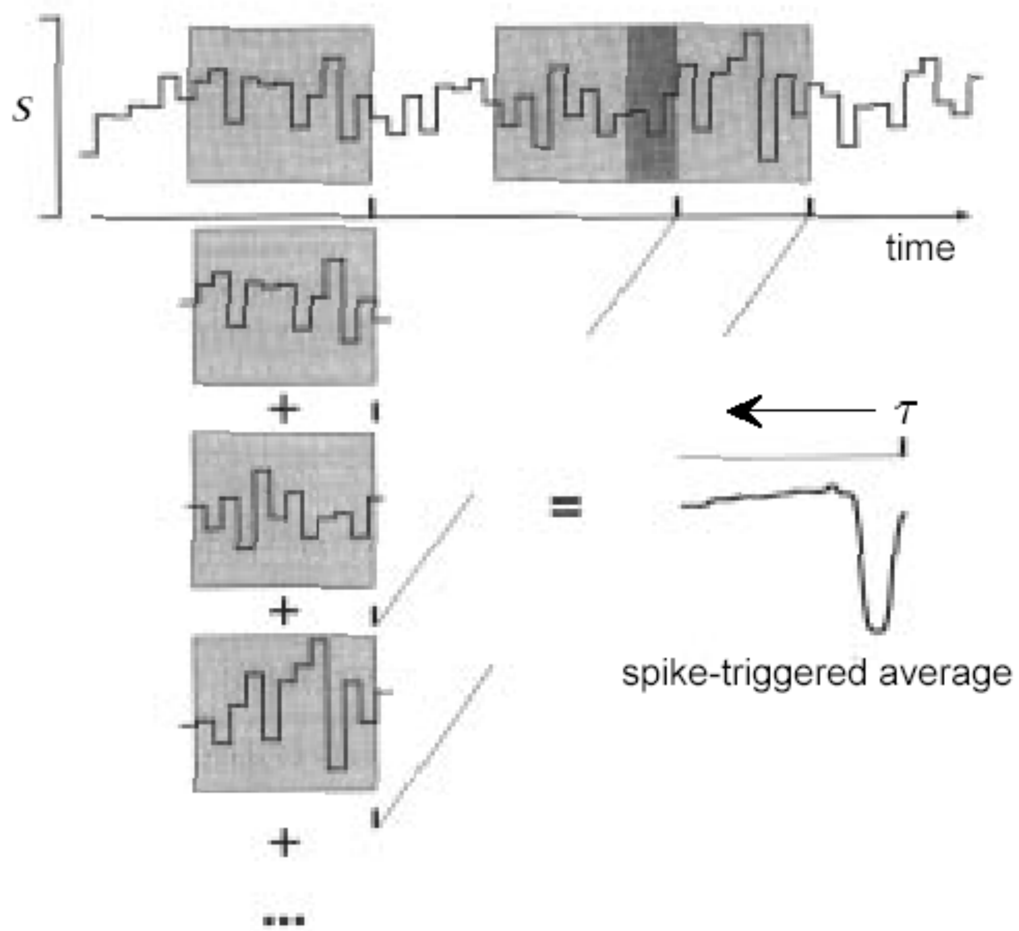


Motor cortical neuron: variation of rate with direction of movement



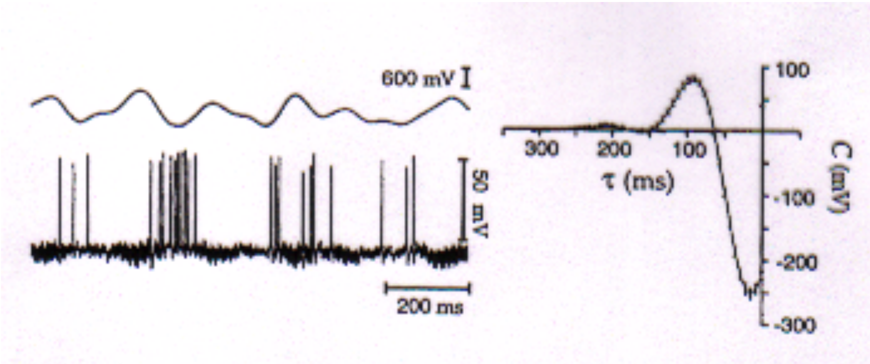
Quantifying the response of sensory neurons

spike-triggered average stimulus ("reverse correlation")

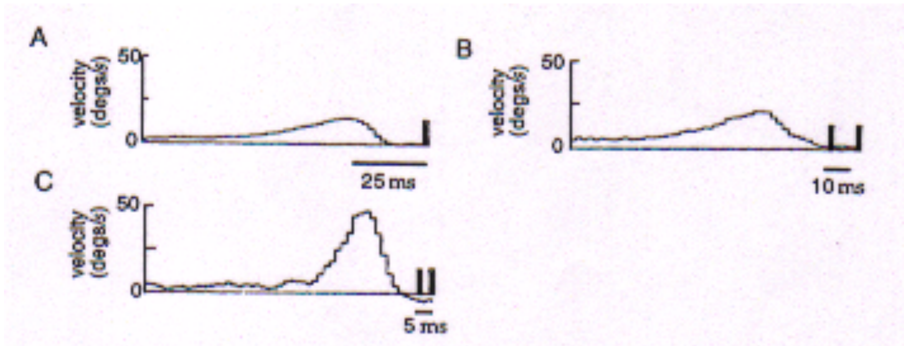


Examples of reverse correlation

Electric sensory neuron in electric fish:
s(t) = electric field



Motion-sensitive neuron in blowfly Visual system:
s(t) = velocity of moving pattern in visual field



Note: non-additive effect for spikes very close in time ($\Delta t < 5$ ms)

Populations of neurons

How independent are different neurons?

Two kinds of correlations: “signal correlations” and “noise correlations”:

notation: stimuli *s*, responses ***r*** (e.g., spike counts if we use Poisson model), trials α

signal correlation: ~ How similar are mean responses? (I.e., how similar are tuning curves):

$$C^{12}_{signal} = \left\langle \left(\left\langle r^1_{s\alpha} \right\rangle_\alpha - \left\langle r^1_{s\alpha} \right\rangle_{s\alpha} \right) \left(\left\langle r^2_{s\alpha} \right\rangle_\alpha - \left\langle r^2_{s\alpha} \right\rangle_{s\alpha} \right) \right\rangle_s$$

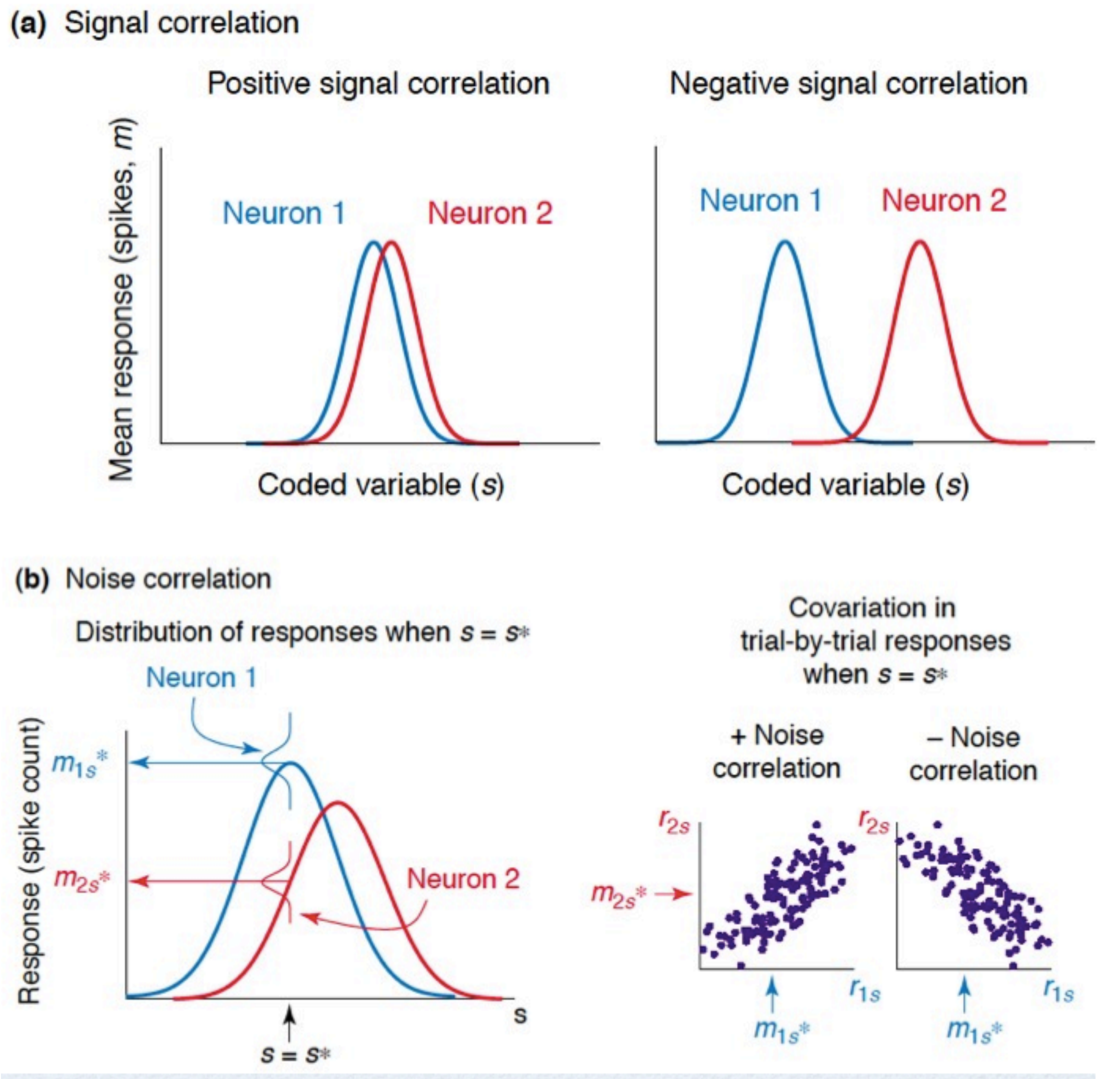
$$= \left\langle \left(m^1_s - \left\langle m^1_s \right\rangle_s \right) \left(m^2_s - \left\langle m^2_s \right\rangle_s \right) \right\rangle_s , \quad m^1_s = \left\langle r^1_{s\alpha} \right\rangle_\alpha$$

noise correlation: how similar across trials are fluctuations of responses of 1 and 2 to a stimulus?

$$C^{12}_{noise} = \left\langle \left(r^1_{s\alpha} - \left\langle r^1_{s\alpha} \right\rangle_\alpha \right) \left(r^2_{s\alpha} - \left\langle r^2_{s\alpha} \right\rangle_\alpha \right) \right\rangle_{s\alpha}$$

$$= \left\langle \left(r^1_{s\alpha} - m^1_s \right) \left(r^2_{s\alpha} - m^2_s \right) \right\rangle_{s\alpha} ,$$

Signal and noise correlation



Effects of noise correlation on information transmission

Transmitted (mutual) information:

$$I(s,r) = H(s) - \langle H(s \mid r) \rangle_r = -\sum_s p(s) \log p(s) + \sum_r p(r) \sum_s p(s \mid r) \log p(s \mid r)$$

reduction in entropy of stimulus set from knowing response

$$= H(r) - \langle H(r \mid s) \rangle_s = -\sum_r p(r) \log p(r) + \sum_s p(s) \sum_r p(r \mid s) \log p(r \mid s)$$

reduction in entropy of responses from knowing stimulus

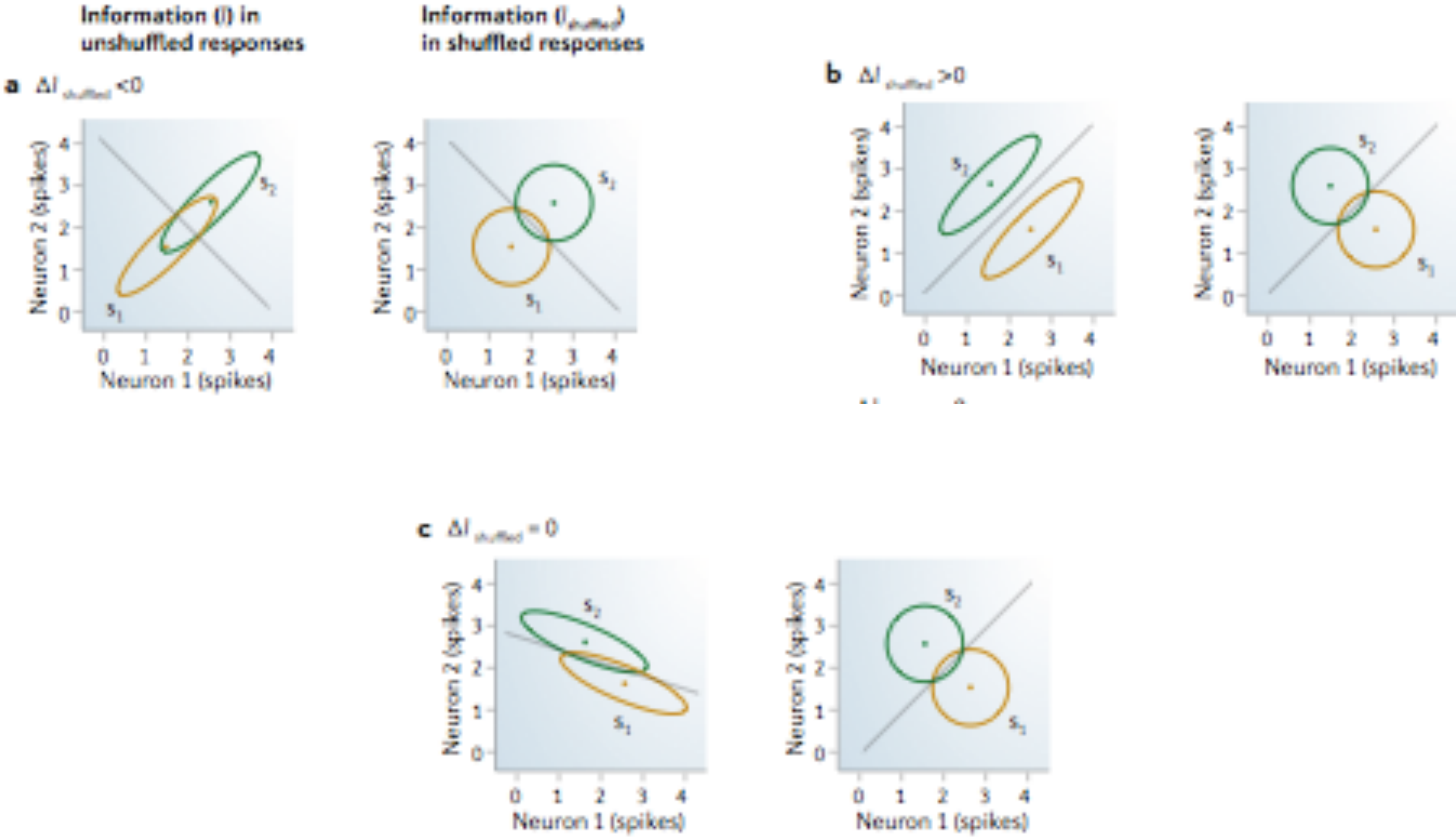
$$= \sum_{rs} p(r,s) \log \frac{p(r,s)}{p(r)p(s)}$$

Symmetric in s and r!

2-neuron, 2-stimulus examples:

Encoding perspective: look at

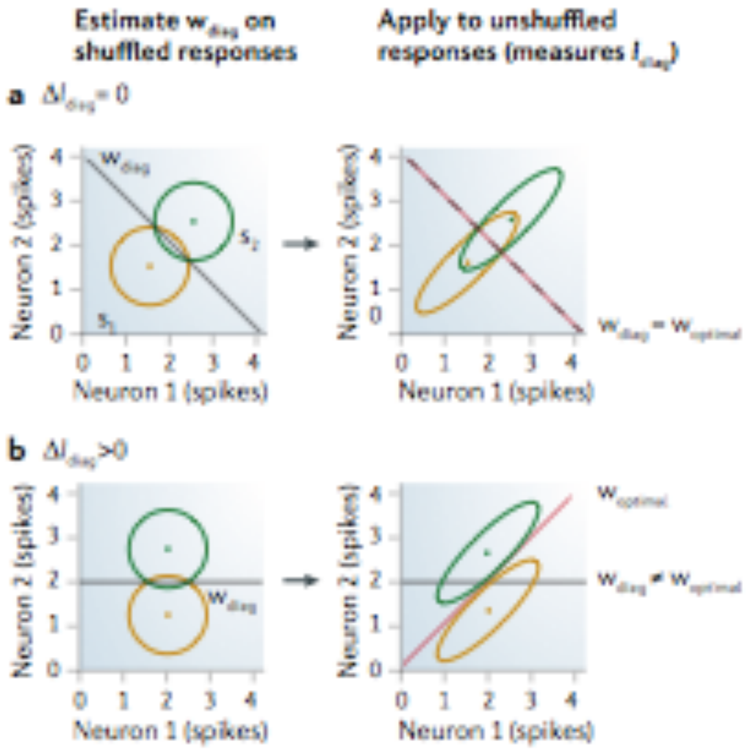
$$\Delta I_{shuffled} = I - I_{shuffled\ responses}$$



Decoding perspective:

Decoding ⇔ drawing a line to separate responses to the two stimuli optimally

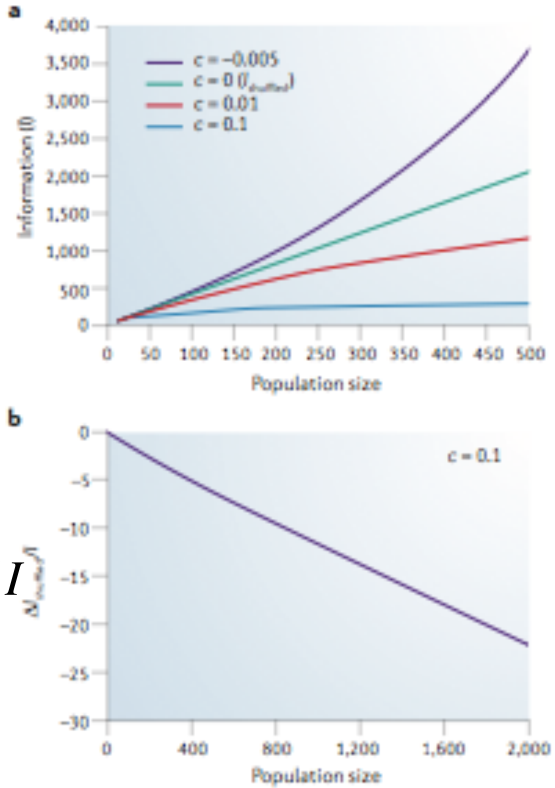
I_{diag}: Find this line using the shuffled data and use it on the unshuffled data.
Look at $\Delta I_{diag} = I - I_{diag}$



More neurons?

encoding perspective:

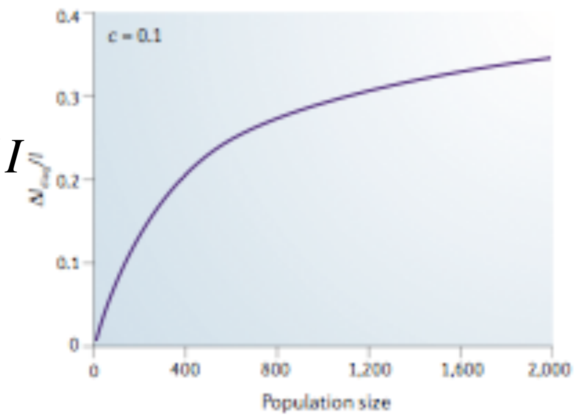
I



$\Delta I_{shuffled} / I$

decoding perspective:

$\Delta I_{diag} / I$



all the above material from Averbeck et al
Nature Rev Neurosci **7** 358-366 (2006)

Population coding and Bayesian inference

Key idea about “noisy neurons”:
Neurons don’t just encode the mean of some quantity badly.
The variability in the response encodes the distribution of that quantity.

Here: how this can work in a simple example with independent Poisson neurons (Ma et al, Nat Neurosci 2006)

firing of neurons: conditional spike count distribution

$$p(\mathbf{r} \mid s) = \prod_i \frac{e^{-f_i(s)} f_i(s)^{r_i}}{r_i!}$$

$f_i(s)$ = tuning curve of neuron i

Use Bayes’s theorem to decode responses:

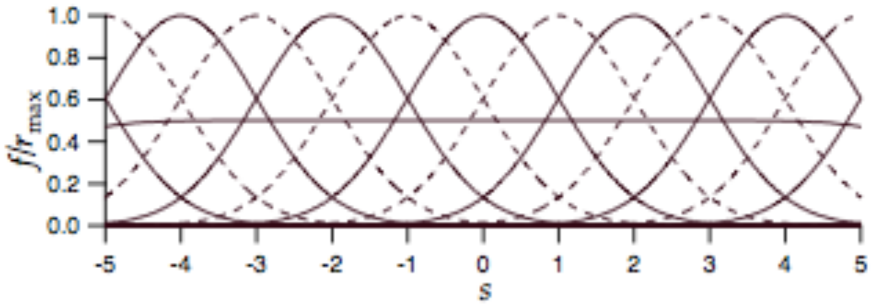
$$p(s \mid \mathbf{r}) \propto \prod_i \frac{e^{-f_i(s)} f_i(s)^{r_i}}{r_i!} p(s)$$

$p(s)$ = prior on s (assumed flat here)

Example: Gaussian tuning curves

$$\log p(s \mid \mathbf{r}) = \sum_i \left[r_i \log f_i(s) - f_i(s) \right] + \text{const} \approx \sum_i r_i \log f_i(s) + \text{const}'$$

tuning curve of neuron i: $$f_i(s) = g \exp\left[-\frac{(s-i)^2}{2\sigma^2} \right]$$



maximize $\log p(s|\mathbf{r})$: $$0 = \sum_i r_i f_i'(s) / f_i(s) = -\frac{1}{\sigma^2} \sum_i r_i (s-i) \Rightarrow s = \frac{\sum_i i r_i}{\sum_i r_i}$$

2nd derivative: $$-\frac{\partial^2 \log p(s \mid \mathbf{r})}{\partial s^2} = -\frac{\partial}{\partial s}\left[-\frac{1}{\sigma^2} \sum_i r_i (s-i) \right] = \frac{\sum_i r_i}{\sigma^2}$$ = 1/variance

i.e., gain = $\Sigma_i r_i$ ~ 1/variance