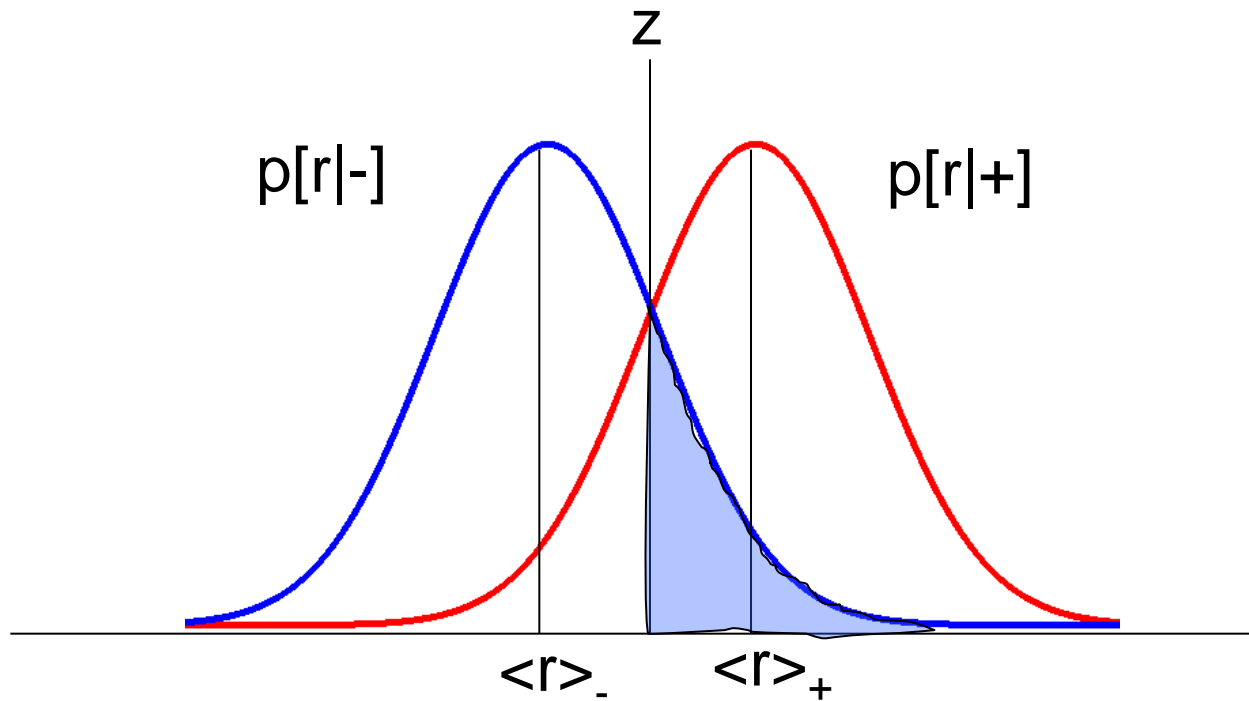


# Signal detection theory

---

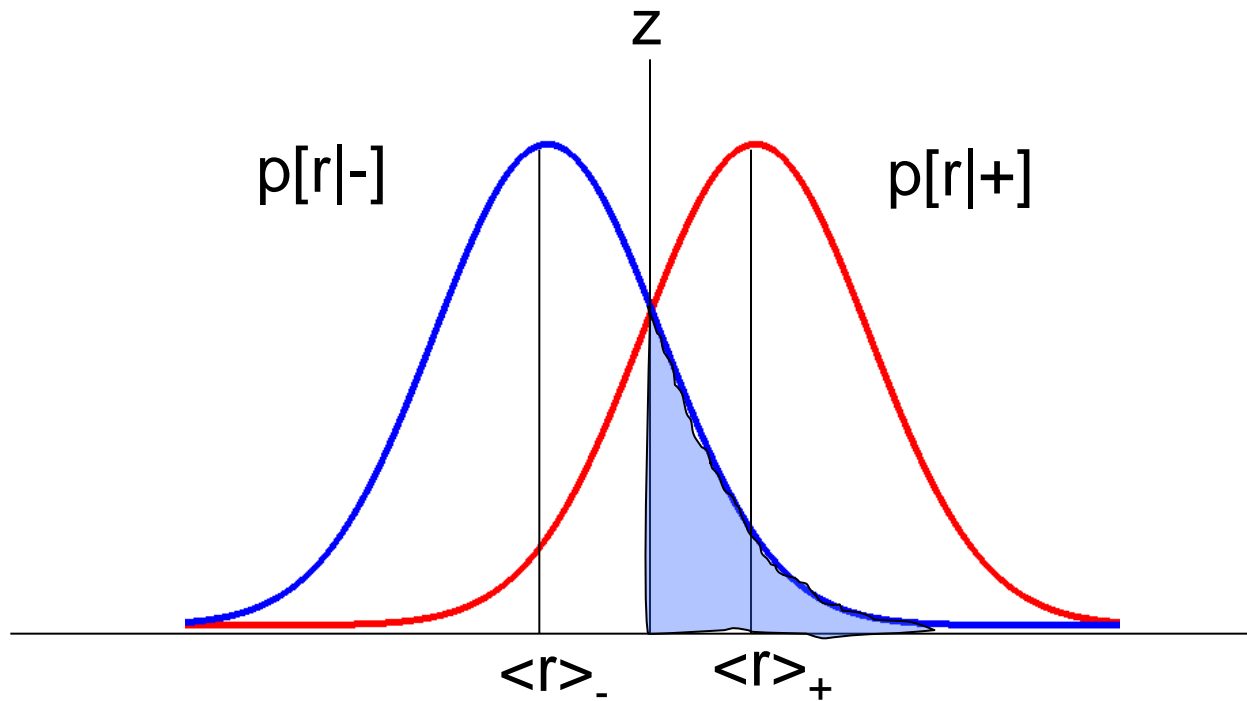


Role of *priors*:

Find  $z$  by maximizing  $P[\text{correct}] = p[+] \beta(z) + p[-](1 - \alpha(z))$

# Is there a better test to use than $r$ ?

---



The optimal test function is the *likelihood ratio*,

$$l(r) = p[r|+] / p[r|-].$$

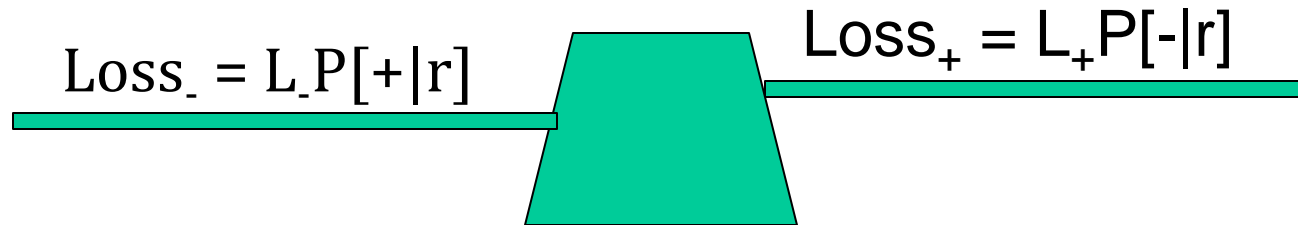
(Neyman-Pearson lemma)

# Building in cost

---

Penalty for incorrect answer:  $L_+$ ,  $L_-$

For an observation  $r$ , what is the expected **loss**?



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

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

Using Bayes',  $P[+|r] = p[r|+]P[+]/p(r)$ ;

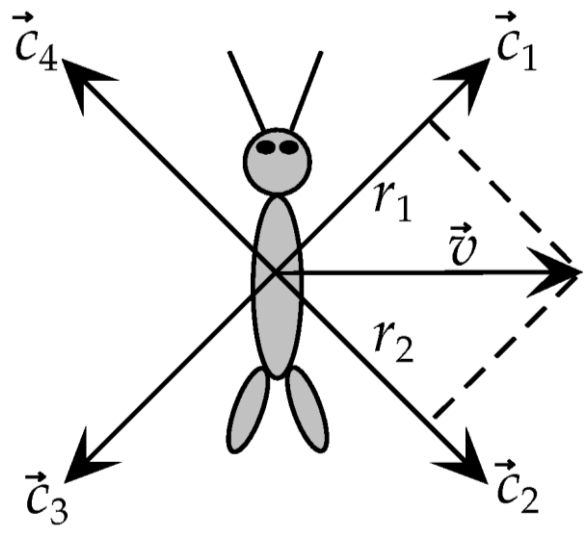
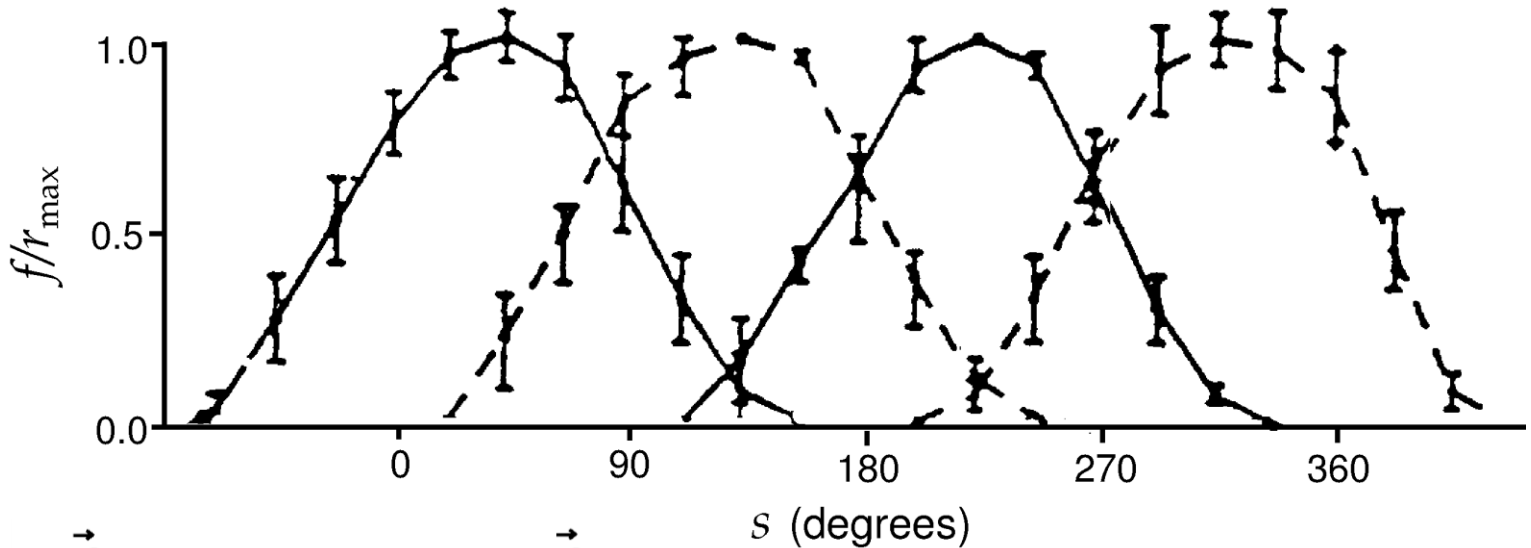
$P[-|r] = p[r|-]P[-]/p(r)$ ;

$\rightarrow l(r) = p[r|+]/p[r|-] > L_+ P[-] / L_- P[+]$  .

# Decoding from many neurons: population codes

- Population code formulation
- Methods for decoding:
  - population vector
  - Bayesian inference
  - maximum likelihood
  - maximum a posteriori
- Fisher information

# Cricket cercal cells

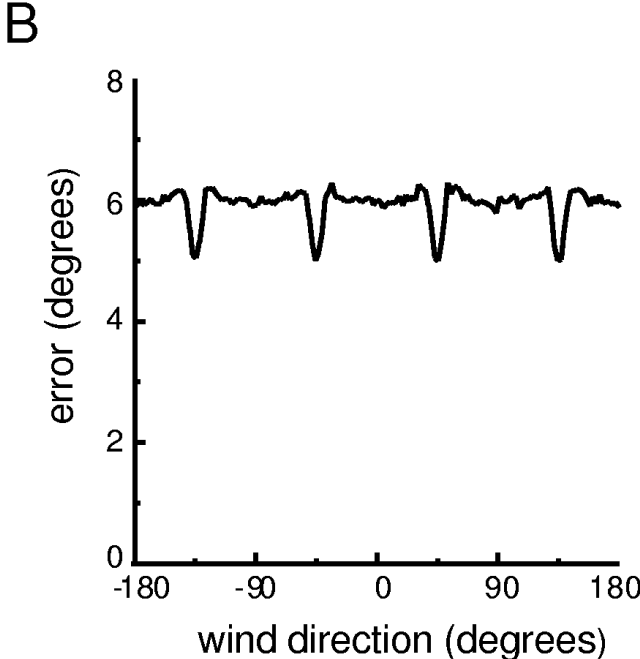
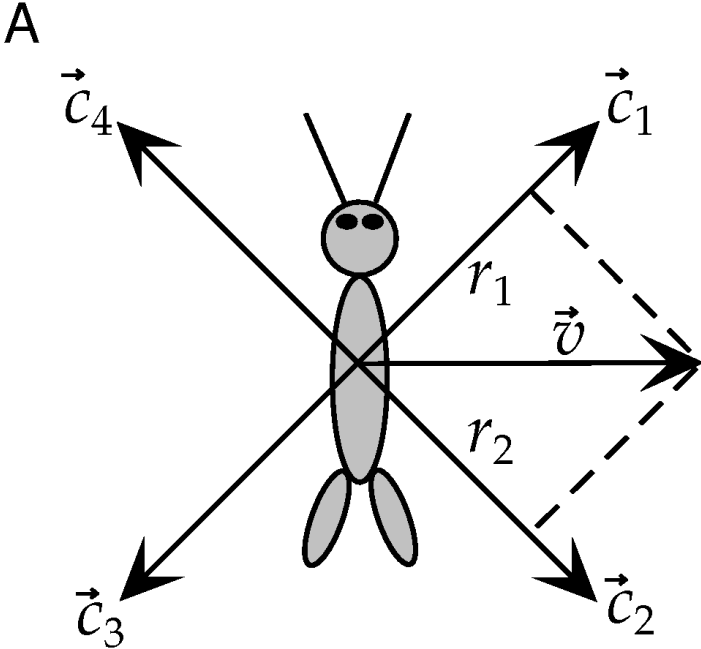


$$\left(\frac{f(s)}{r_{\max}}\right)_a = [\cos(s - s_a)]_+$$

$$\left(\frac{f(s)}{r_{\max}}\right)_a = [\vec{v} \cdot \vec{c}_a]_+$$

# Population vector

$$\vec{v}_{\text{pop}} = \sum_{a=1}^4 \left( \frac{r}{r_{\text{max}}} \right)_a \vec{c}_a$$



RMS error in estimate

Theunissen & Miller, 1991

# Population coding in M1

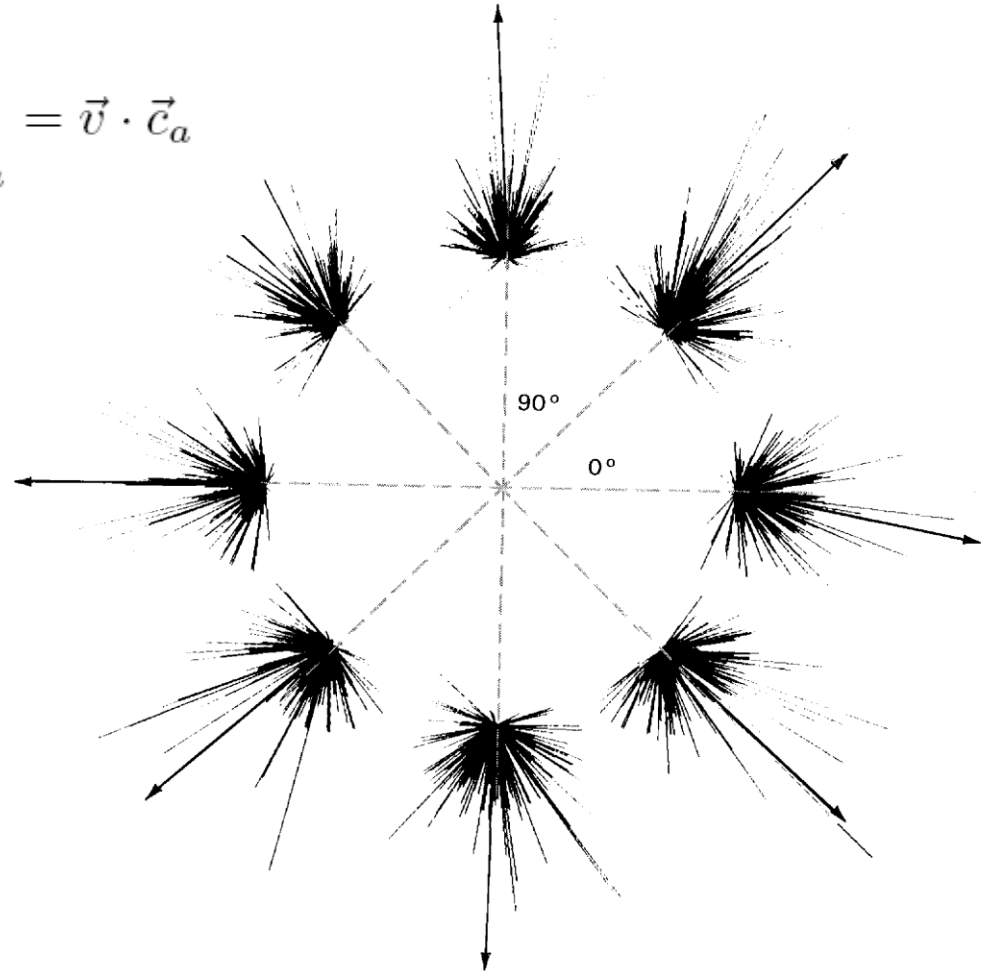
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Cosine tuning:

$$\left( \frac{\langle r \rangle - r_0}{r_{\max}} \right)_a = \left( \frac{f(s) - r_0}{r_{\max}} \right)_a = \vec{v} \cdot \vec{c}_a$$

Pop. vector:

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



# Is this the best one can do?

---

The population vector is neither general nor optimal.

“Optimal”:

make use of all information in the stimulus/response distributions



# Bayesian inference

---

Bayes' law:

The diagram illustrates Bayes' law with the following components and labels:

- conditional distribution**:  $p[\mathbf{r}|s]$  (green text, points to the likelihood function in the numerator)
- likelihood function**:  $p[\mathbf{r}|s]$  (green text, points to the likelihood function in the numerator)
- prior distribution**:  $p[s]$  (purple text, points to the prior distribution in the numerator)
- marginal distribution**:  $p[\mathbf{r}]$  (blue text, points to the denominator)
- a posteriori* distribution**:  $p[s|\mathbf{r}]$  (red text, points to the entire fraction)

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

# Bayesian estimation

---

Want an estimator  $s_{\text{Bayes}}$

Introduce a cost function,  $L(s, s_{\text{Bayes}})$ ; minimize mean cost.

$$\int ds L(s, s_{\text{Bayes}}) p[s|\mathbf{r}]$$

For least squares cost,  $L(s, s_{\text{Bayes}}) = (s - s_{\text{Bayes}})^2$  .  
Let's calculate the solution..

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

# Bayesian inference

---

By Bayes' law,

likelihood function

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

*a posteriori* distribution

# Maximum likelihood

---

Find maximum of  $p[r|s]$  over  $s$

More generally, probability of the data given the “model”

“Model” = stimulus

assume parametric form for tuning curve

# Bayesian inference

---

By Bayes' law,

likelihood function

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

*a posteriori* distribution

# MAP and ML

---

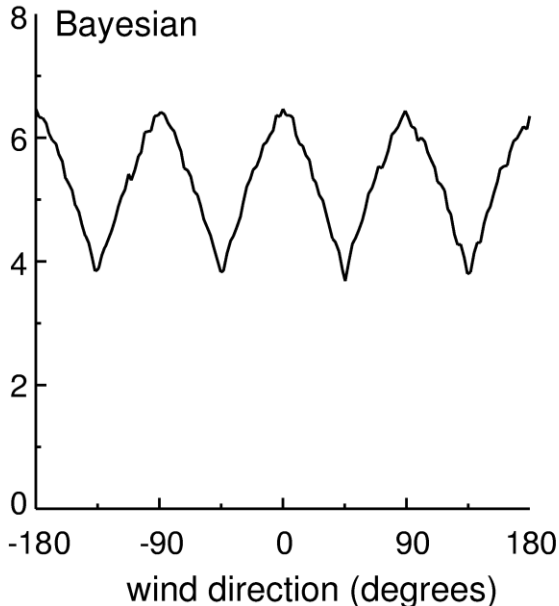
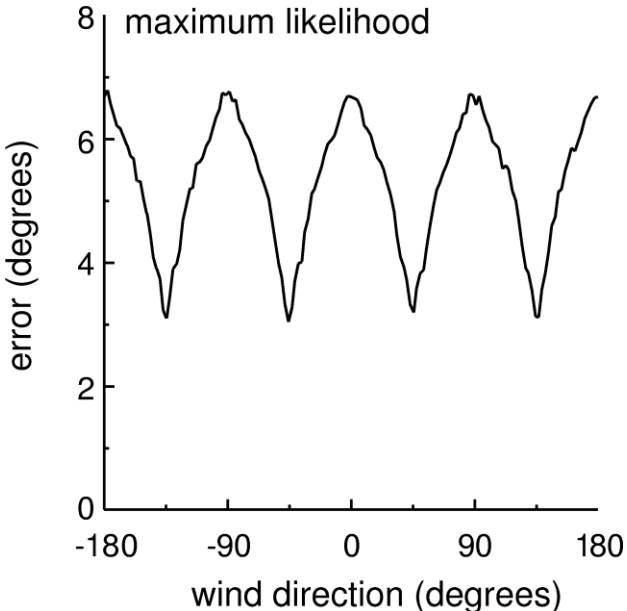
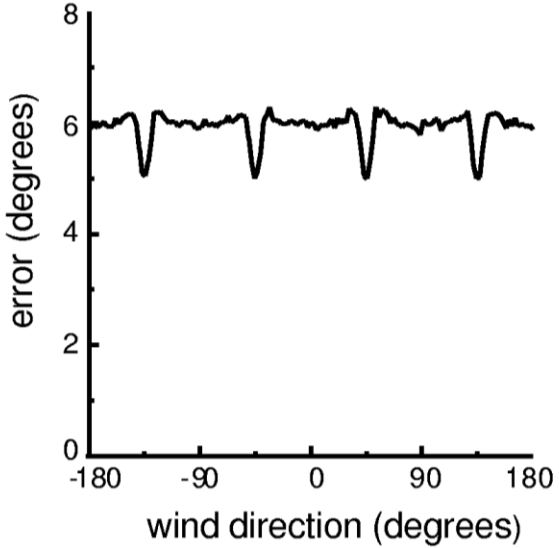
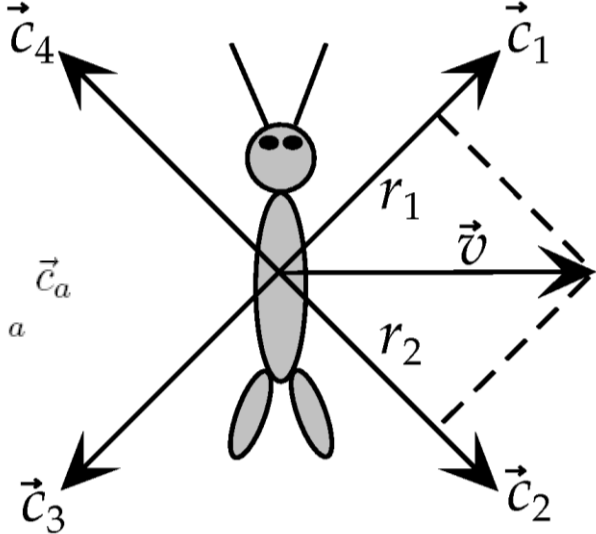
ML:  $s^*$  which maximizes  $p[r|s]$

MAP:  $s^*$  which maximizes  $p[s|r]$

Difference is the role of the prior: differ by factor  $p[s]/p[r]$

# Comparison with population vector

$$\vec{v}_{\text{pop}} = \sum_{a=1}^4 \left( \frac{r}{r_{\text{max}}} \right)_a \vec{c}_a$$



# Decoding an arbitrary continuous stimulus

---

Many neurons “voting” for an outcome.

Work through a specific example

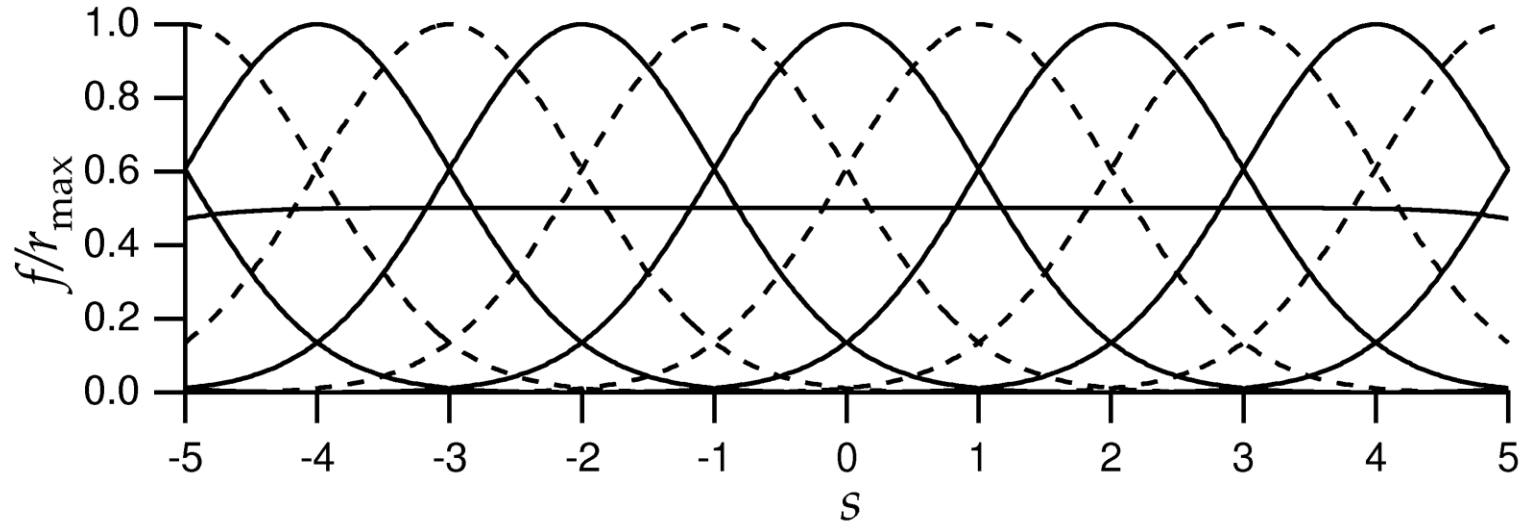
- assume independence
- assume Poisson firing

Noise model: Poisson distribution

$$P_T[k] = (\lambda T)^k \exp(-\lambda T) / k!$$



# Decoding an arbitrary continuous stimulus



E.g. Gaussian tuning curves

$$f_a(s) = r_{\max} \exp\left(-\frac{1}{2} \left[\frac{(s - s_a)}{\sigma_a}\right]^2\right)$$

$$\sum_{a=1}^N f_a(s) \text{ const.}$$

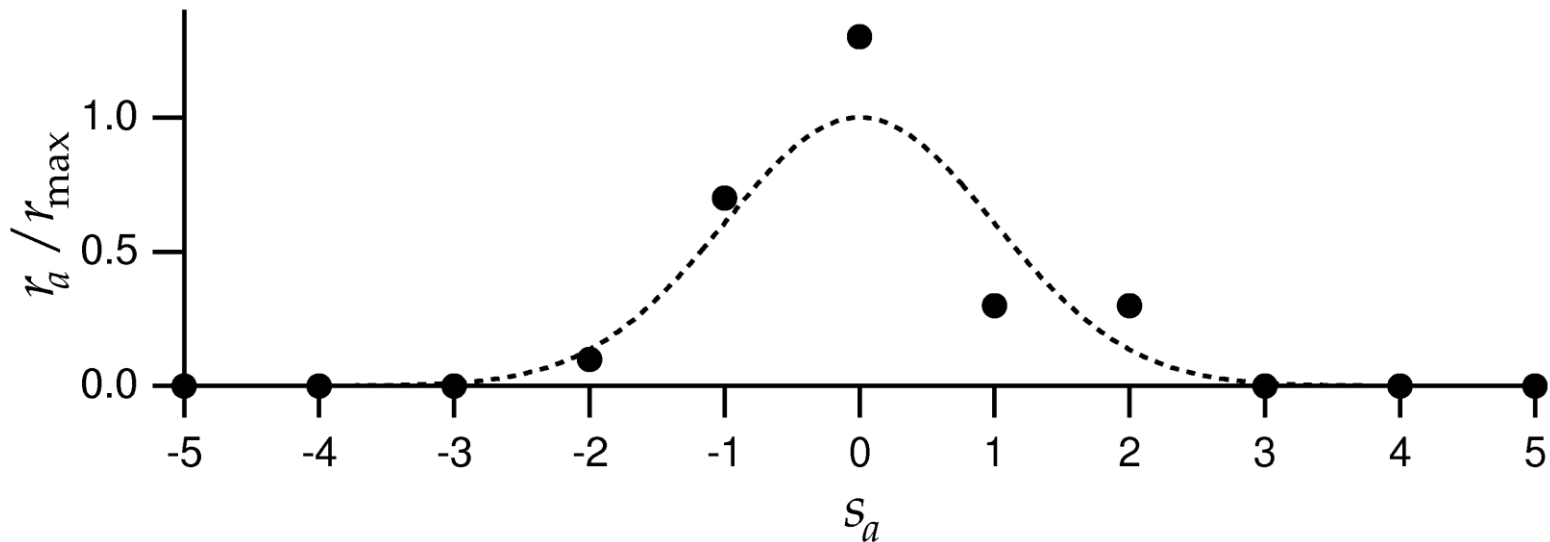
.. what is  $P(r_a|s)$ ?

# Need to know full $P[\mathbf{r}|s]$

---

Assume Poisson: 
$$P[r_a|s] = \frac{(f_a(s)T)^{r_a} \exp(-f_a(s)T)}{(r_a T)!}$$

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



Population response of 11 cells with Gaussian tuning curves

# ML

---

Apply ML: maximize  $\ln P[\mathbf{r}|s]$  with respect to  $s$

$$\ln P[\mathbf{r}|s] = T \sum_{a=1}^N r_a \ln(f_a(s)) + \dots$$

Set derivative to zero, use sum = constant

$$\sum_{a=1}^N r_a \frac{f'(s^*)}{f(s^*)} = 0$$

From Gaussianity of tuning curves,

$$s^* = \frac{\sum r_a s_a / \sigma_a^2}{\sum r_a / \sigma_a^2}$$

If all  $\sigma$  same

$$s^* = \frac{\sum r_a s_a}{\sum r_a}$$

# MAP

---

Apply MAP: maximise  $\ln p[s|\mathbf{r}]$  with respect to  $s$

$$\ln p[s|\mathbf{r}] = \ln P[\mathbf{r}|s] + \ln p[s] - \ln P[\mathbf{r}]$$

$$\ln p[s|\mathbf{r}] = T \sum_{a=1}^N r_a \ln(f_a(s)) + \ln p[s] + \dots$$

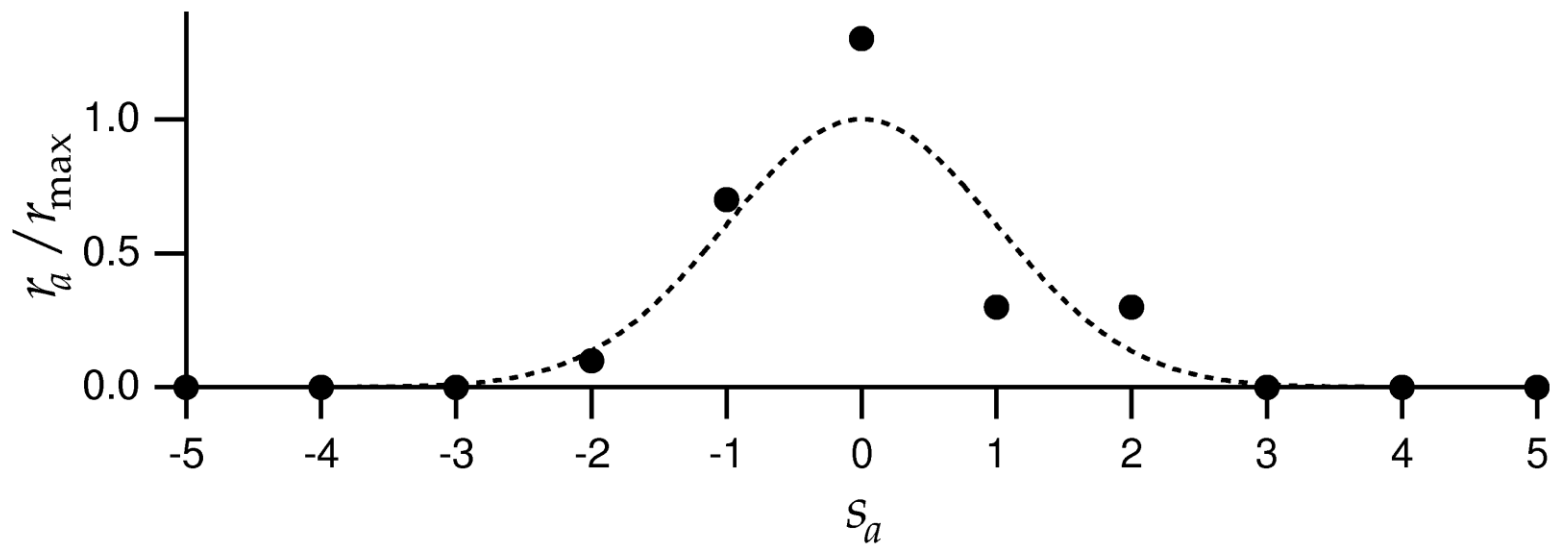
Set derivative to zero, use sum = constant

$$\sum_{a=1}^N r_a \frac{f'(s^*)}{f(s^*)} + \frac{p'[s]}{p[s]} = 0$$

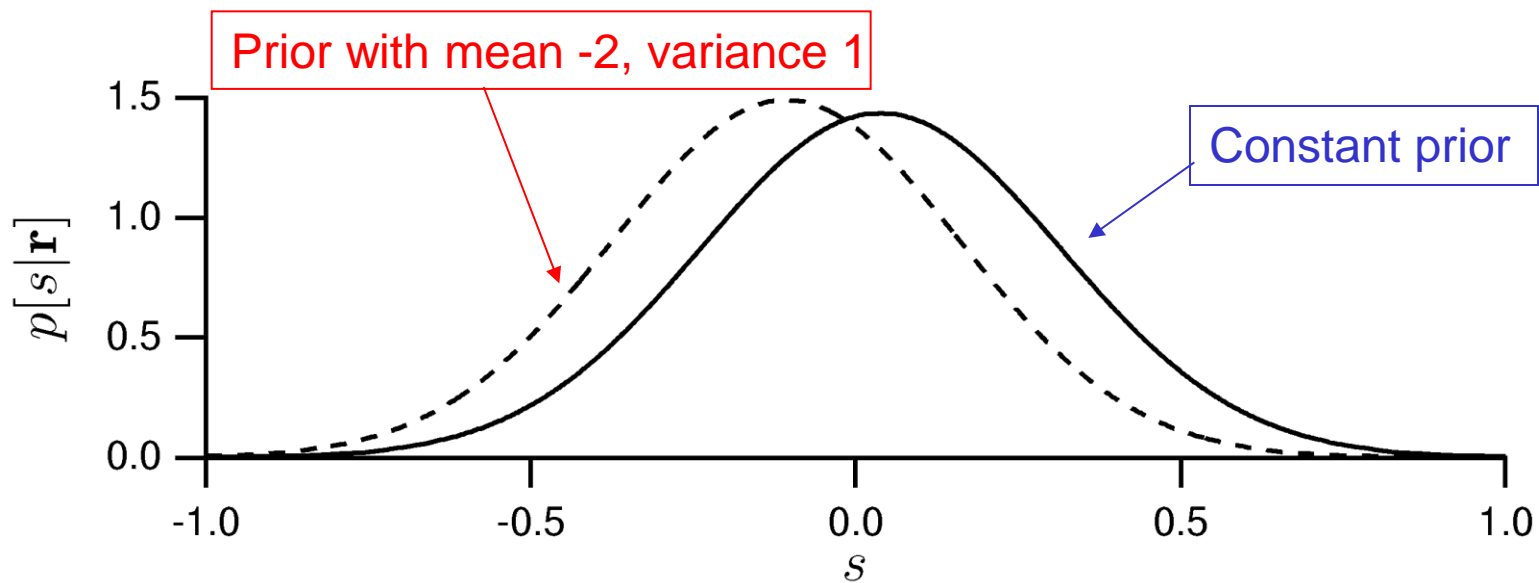
From Gaussianity of tuning curves,

$$s^* = \frac{T \sum r_a s_a / \sigma_a^2 + s_{\text{prior}} / \sigma_{\text{prior}}^2}{T \sum r_a / \sigma_a^2 + 1 / \sigma_{\text{prior}}^2}$$

Given this data:



MAP:



# How good is our estimate?

---

For stimulus  $s$ , have estimated  $s_{\text{est}}$

Bias:  $b_{\text{est}}(s) = \langle s_{\text{est}} - s \rangle$

Variance:  $\sigma_{\text{est}}^2(s) = \langle (s_{\text{est}} - \langle s_{\text{est}} \rangle)^2 \rangle$

Mean square error:

$$\langle (s_{\text{est}} - s)^2 \rangle = \langle (s_{\text{est}} - \langle s_{\text{est}} \rangle + b_{\text{est}}(s))^2 \rangle = \sigma_{\text{est}}^2(s) + b_{\text{est}}^2(s).$$

Cramer-Rao bound:  $\sigma_{\text{est}}^2 \geq \frac{(1 + b'_{\text{est}})^2}{I_{\text{F}}(s)}$

Fisher information

(ML is unbiased:  $b = b' = 0$ )

# Fisher information

---

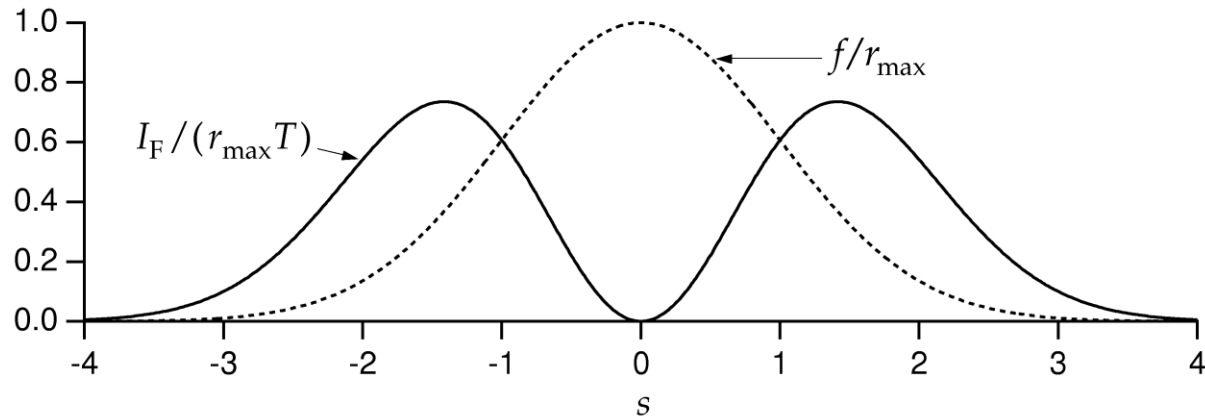
$$I_{\text{F}}(s) = \left\langle -\frac{\partial^2 \ln p[\mathbf{r}|s]}{\partial s^2} \right\rangle = \int d\mathbf{r} p[\mathbf{r}|s] \left( -\frac{\partial^2 \ln p[\mathbf{r}|s]}{\partial s^2} \right)$$

Alternatively:

$$I_{\text{F}}(s) = \left\langle \left( \frac{\partial \ln p[\mathbf{r}|s]}{\partial s} \right)^2 \right\rangle = \int d\mathbf{r} p[\mathbf{r}|s] \left( \frac{\partial \ln p[\mathbf{r}|s]}{\partial s} \right)^2$$

Quantifies local stimulus discriminability

# Fisher information for Gaussian tuning curves



For the Gaussian tuning curves w/Poisson statistics:

$$I_F(s) = \left\langle \left( \frac{d^2 \ln P[\mathbf{r}|s]}{ds^2} \right) \right\rangle = T \sum_{a=1}^N \langle r_a \rangle \left( \left( \frac{f'_a(s)}{f_a(s)} \right)^2 - \frac{f''_a(s)}{f_a(s)} \right)$$



# Are narrow or broad tuning curves better?

---

$$I_F = T \sum_{a=1}^N \frac{r_{\max}(s - s_a)^2}{\sigma_r^4} \exp\left(-\frac{1}{2} \left(\frac{s - s_a}{\sigma_r}\right)^2\right)$$

Approximate: 
$$I_F \sim \frac{\sqrt{2\pi} \rho_s \sigma_r r_{\max} T}{\sigma_r^2}.$$

Thus,  $I_F \sim 1/\sigma_r$  → Narrow tuning curves are better

But not in higher dimensions!

$$I_F \sim (2\pi)^{D/2} D \rho_s \sigma_r^{D-2} r_{\max} T$$

..what happens in 2D?

# Fisher information and discrimination

---

Recall  $d' = \text{mean difference} / \text{standard deviation}$

Can also decode and discriminate using decoded values.

Trying to discriminate  $s$  and  $s + \Delta s$ :

Difference in ML estimate is  $\Delta s$  (unbiased)  
variance in estimate is  $1/I_F(s)$ .

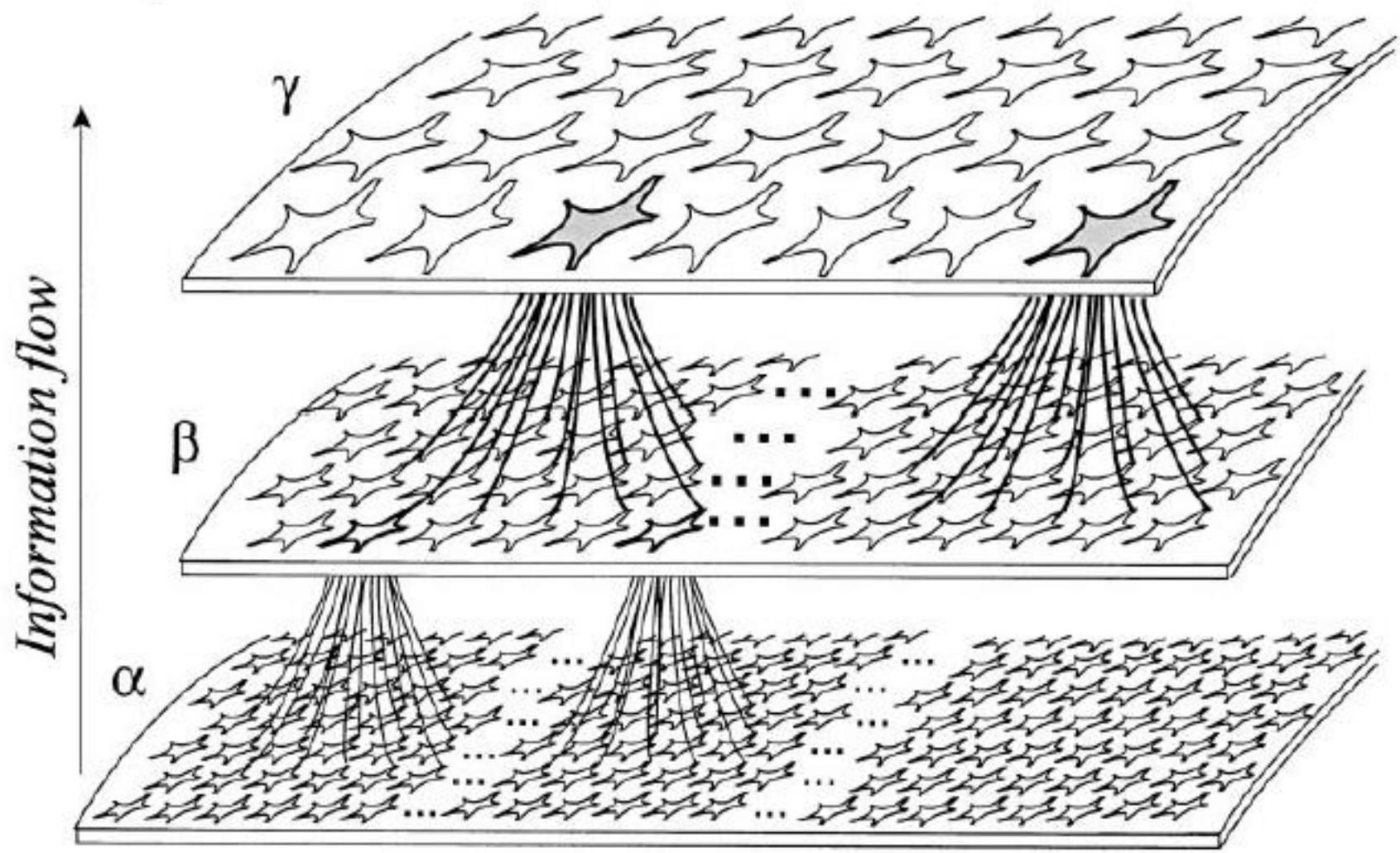
$$\rightarrow d' = \Delta s \sqrt{I_F(s)}$$

# Limitations of these approaches

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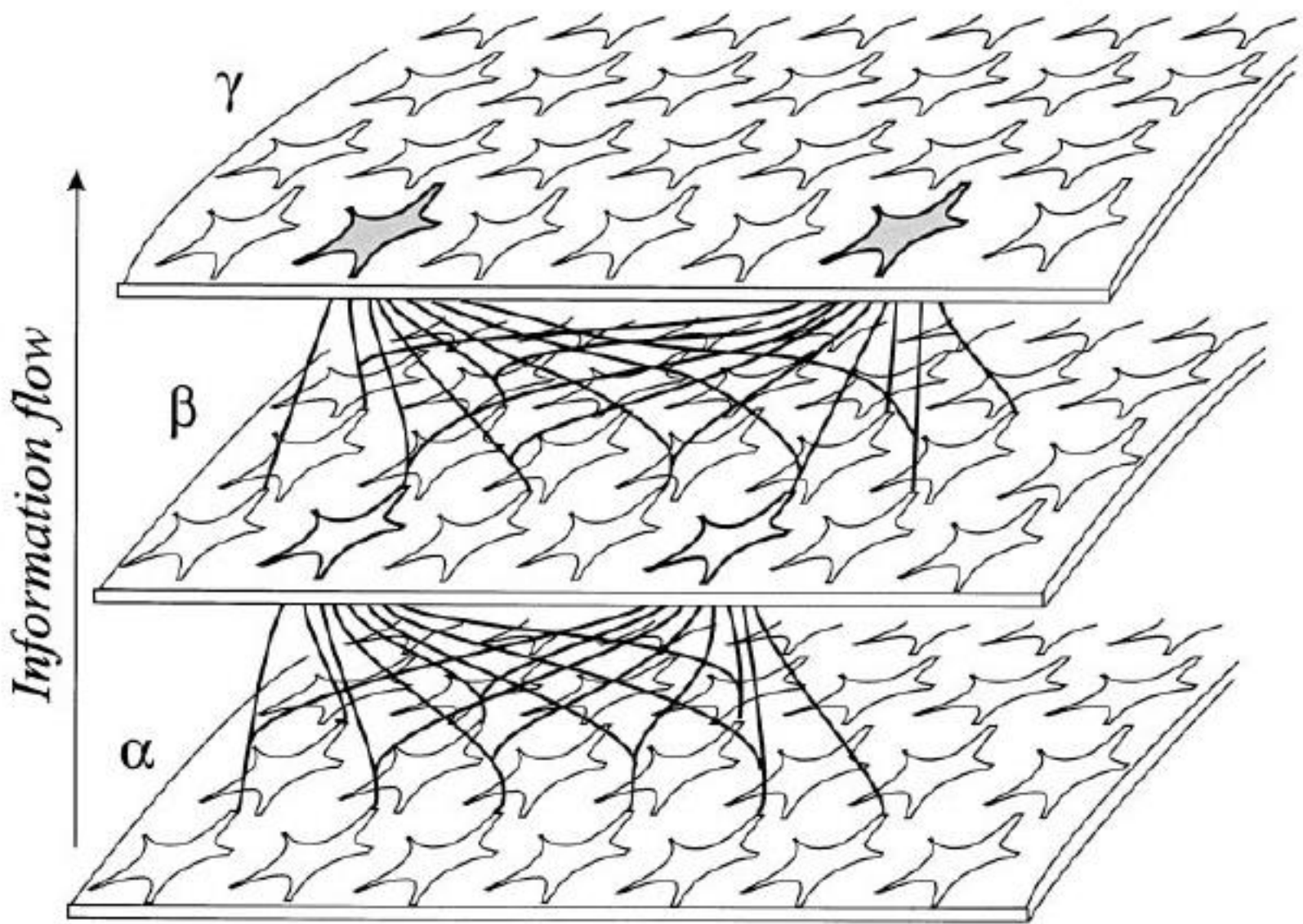
- Tuning curve/mean firing rate
- Correlations in the population

# The importance of correlation

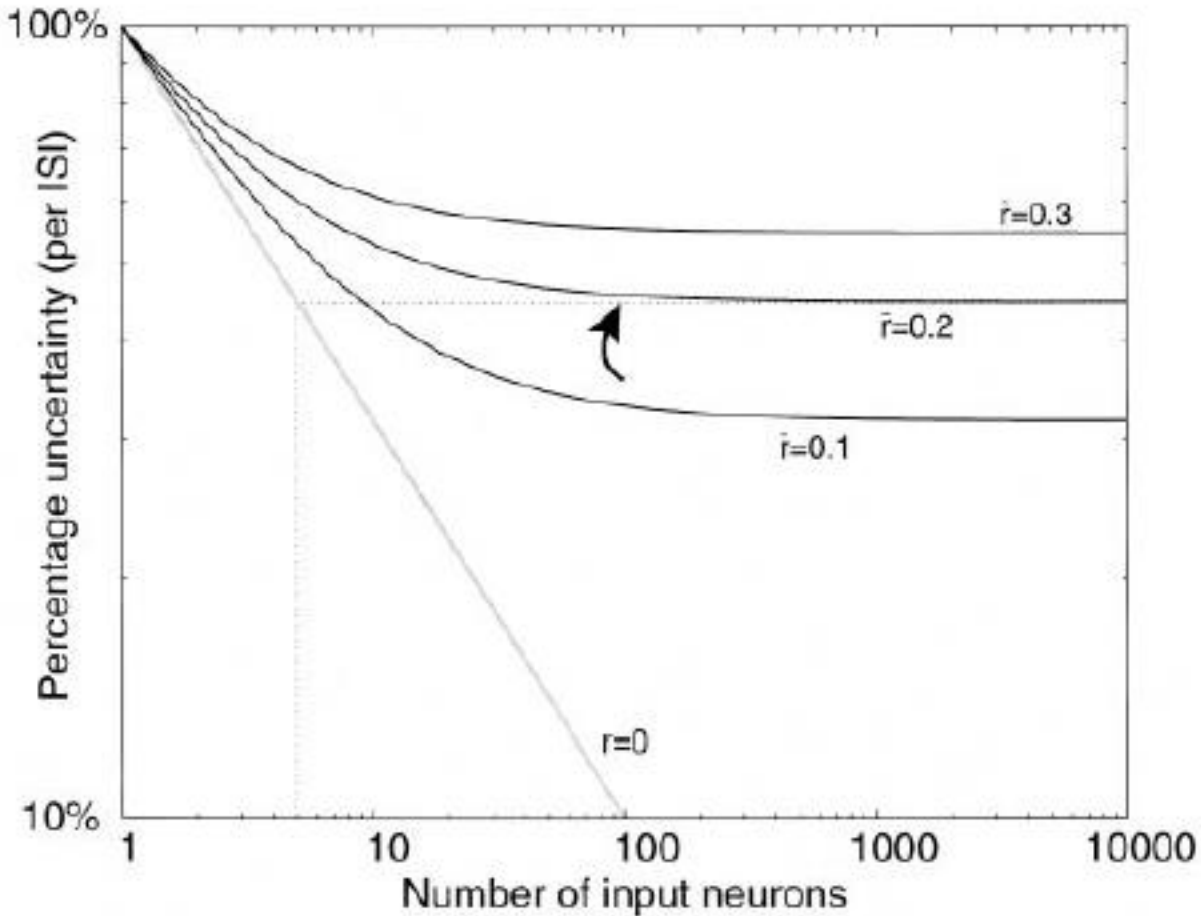


# The importance of correlation

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# The importance of correlation



# Entropy and Shannon information

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Model-based vs model free