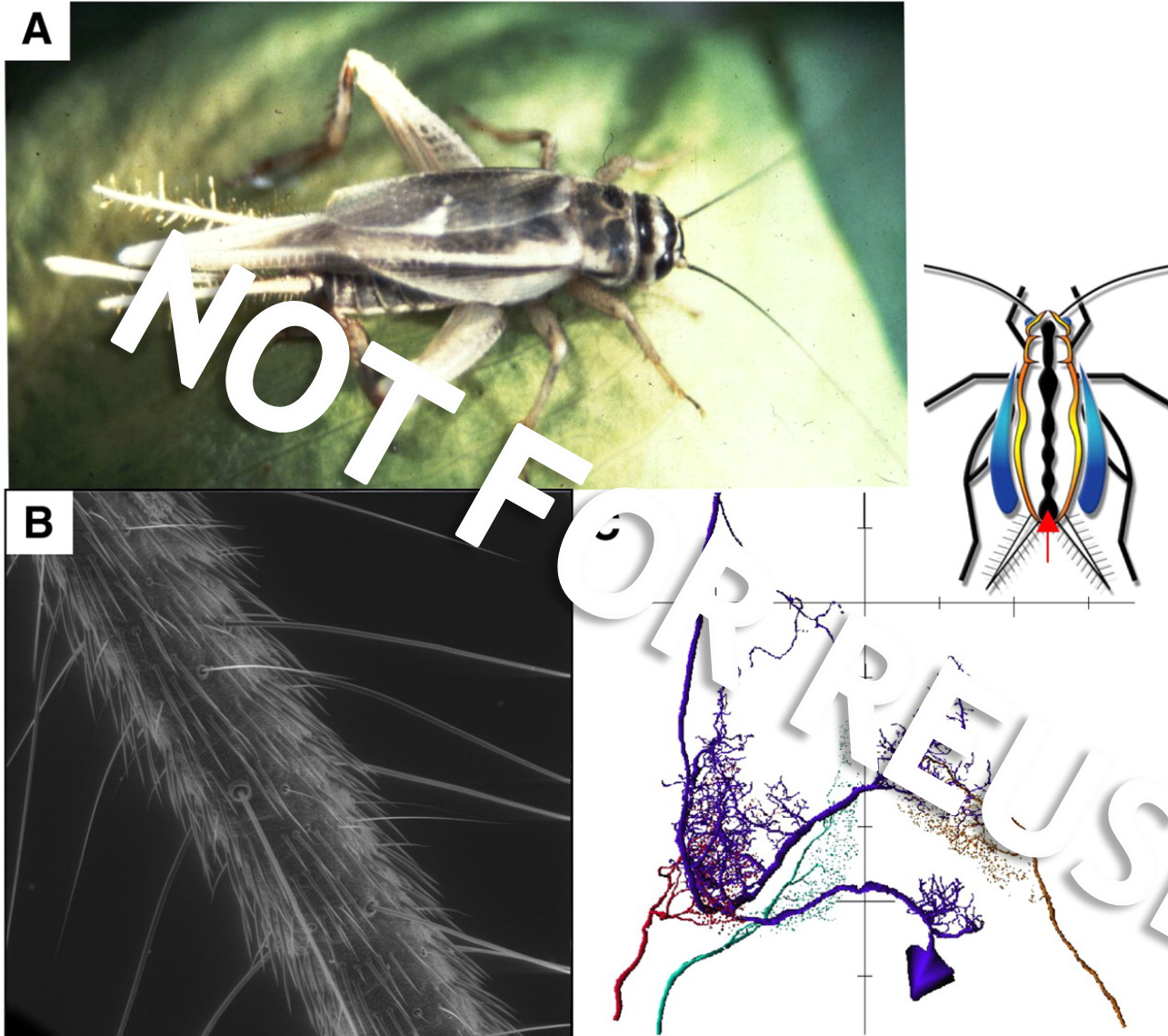


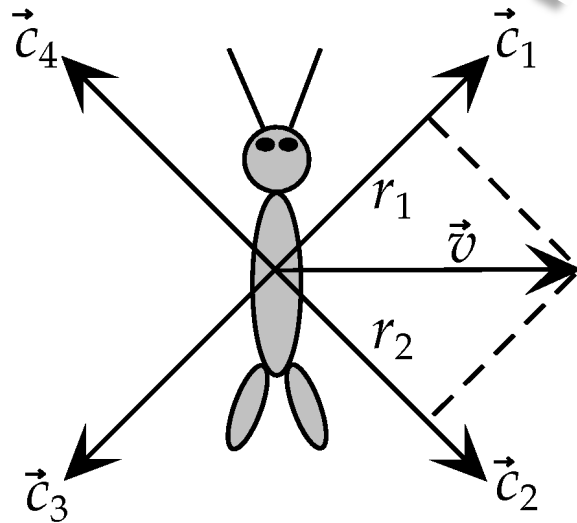
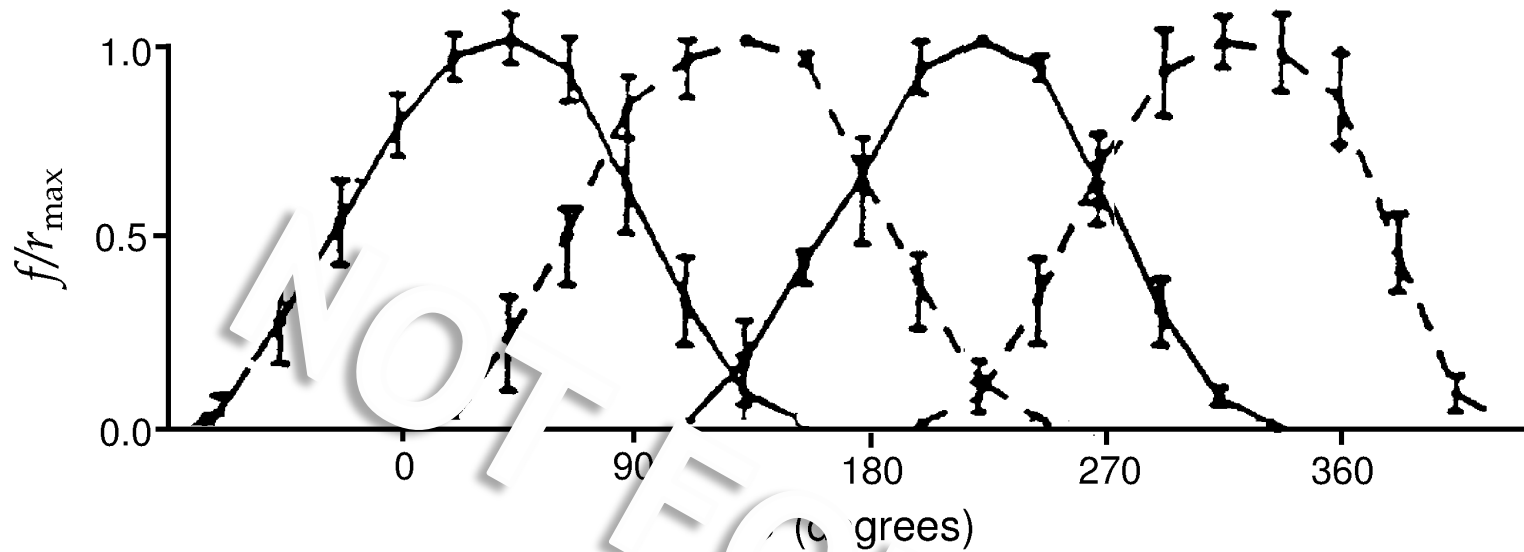
# Decoding from many neurons: population codes

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

# Cricket cercal cells



# Cricket cercal cells



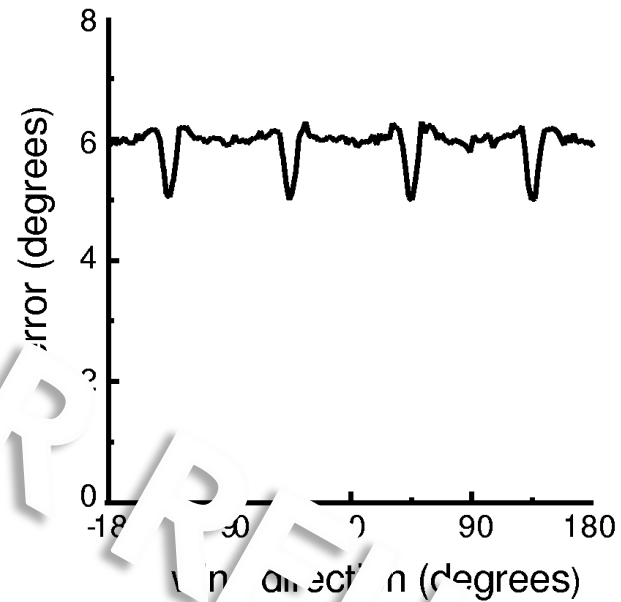
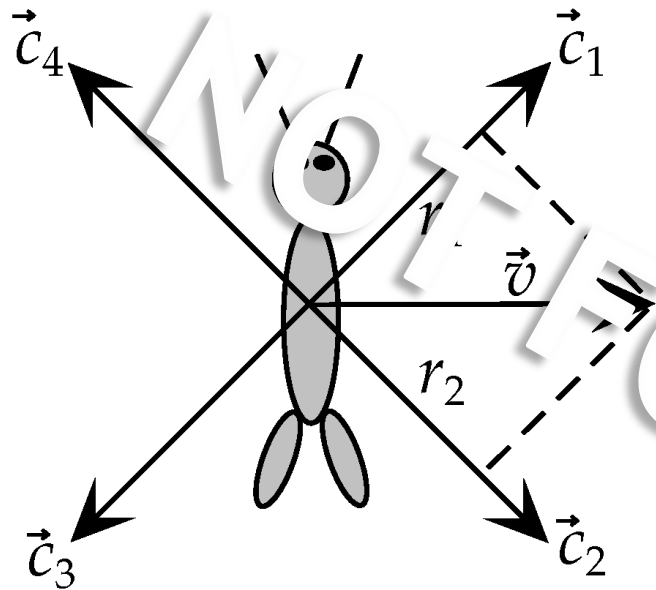
$$\left( \frac{f(s)}{r_{\max}} \right)_a = [\cos(s - s_a)]_+$$

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

Theunissen & Miller, 1991; in Dayan and Abbott, *Theoretical Neuroscience*

# Population vector

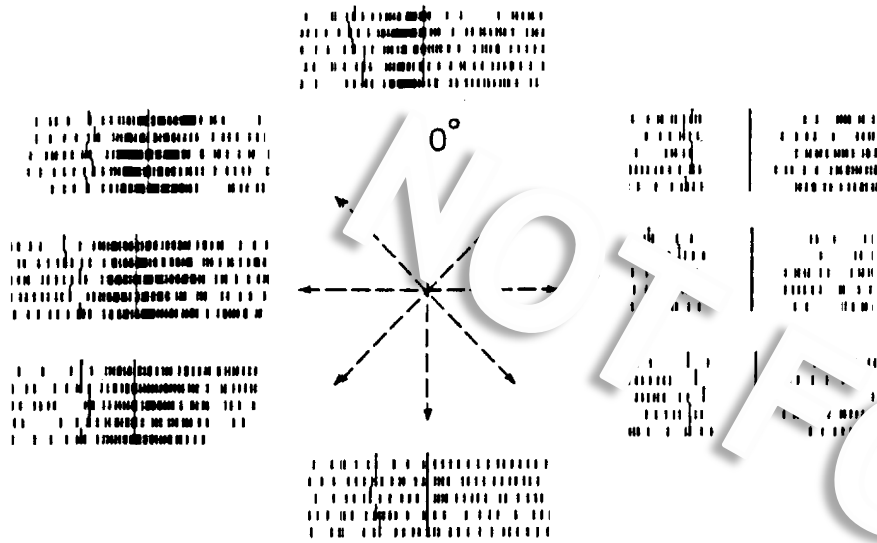
$$\vec{v}_{\text{pop}} = \sum_{a=1}^4 \left( \frac{r}{r_{\text{max}}} \right)_a \vec{c}_a$$



RMS error in estimation

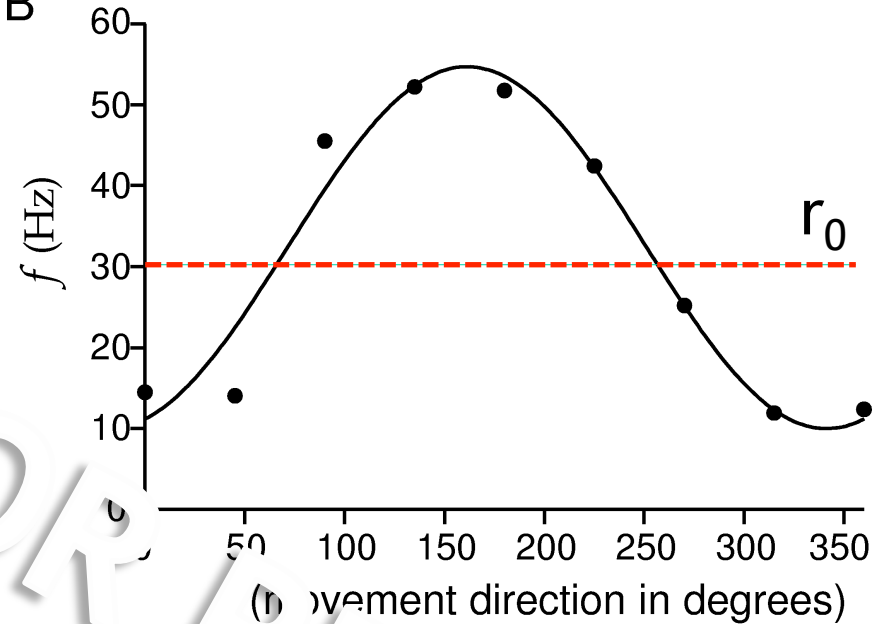
# Population coding in M1

A



Hand reaching direction

B



Cosine tuning curve of a motor cortical neuron

# Population coding in M1

Cosine tuning:

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

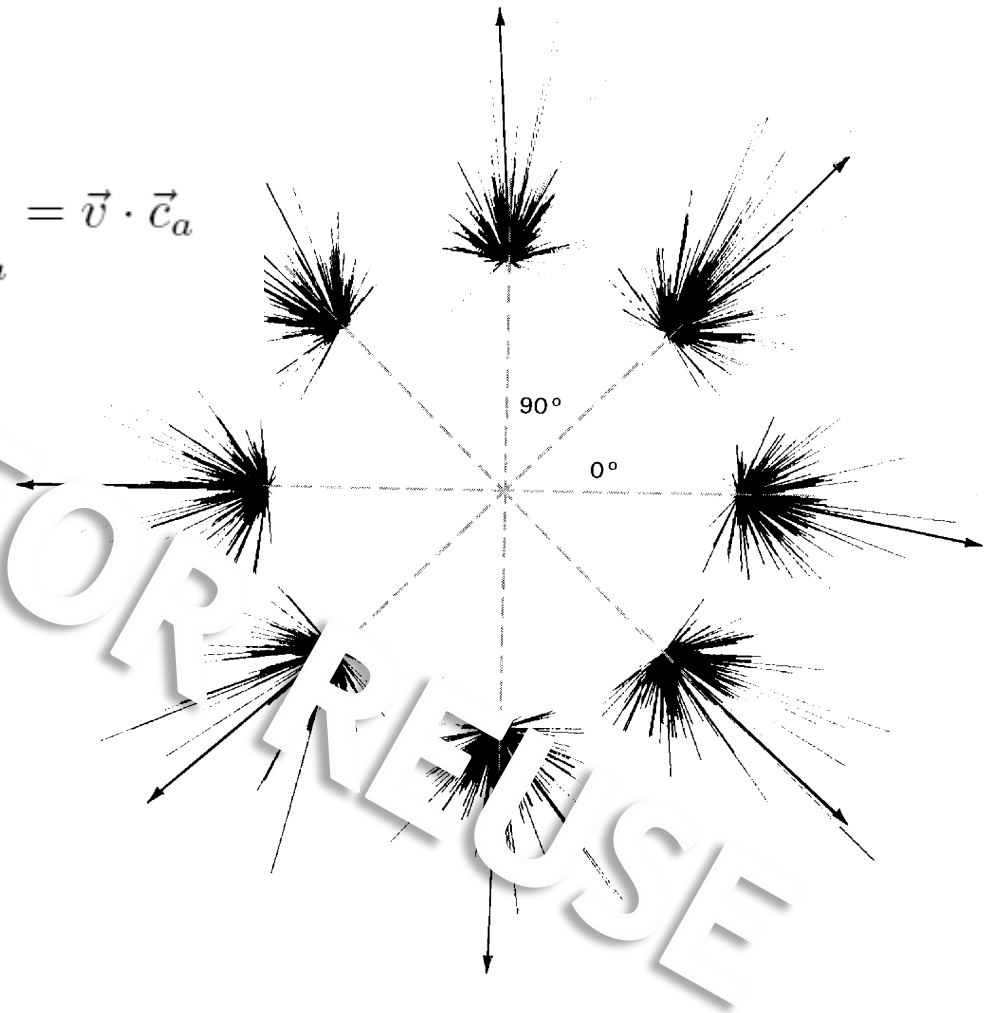
Pop. vector:

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

For sufficiently large N,

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

is parallel to the direction of arm movement



# Is this the best one can do?

The population vector is neither general nor optimal.

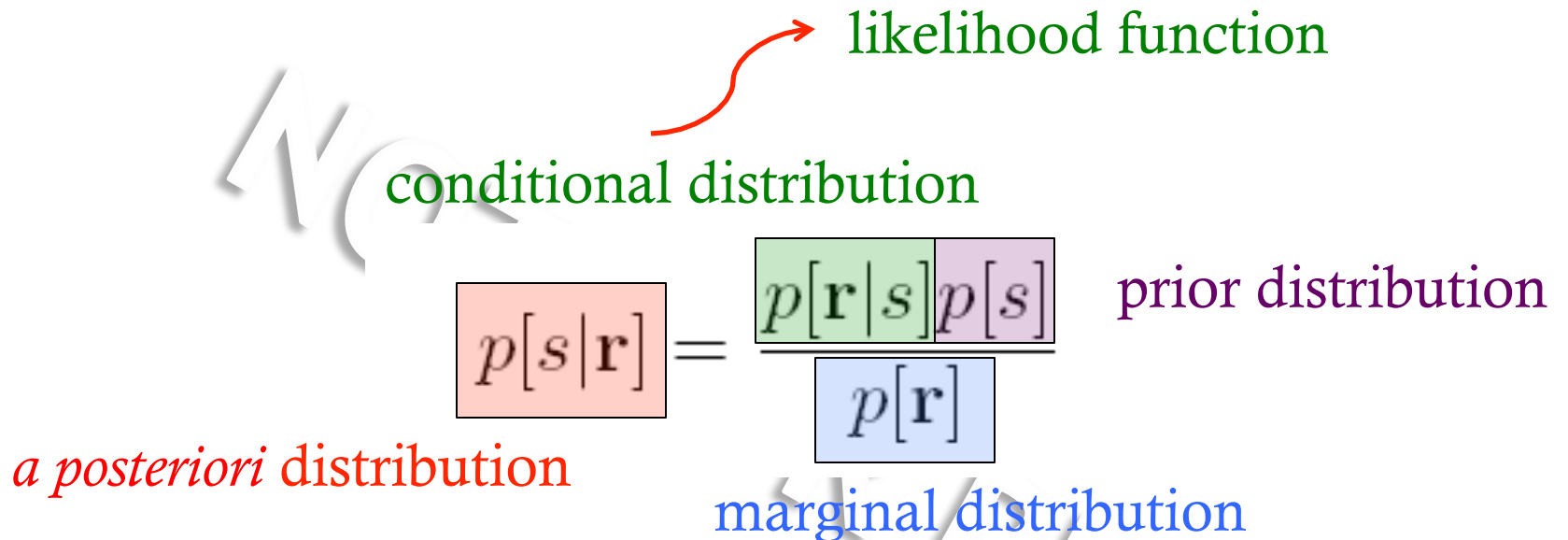
“Optimal”:

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**: A green label pointing to the term  $p[\mathbf{r}|s]$  in the numerator.
- likelihood function**: A green label with a red arrow pointing to the term  $p[s]$  in the numerator.
- prior distribution**: A purple label pointing to the term  $p[s]$  in the numerator.
- marginal distribution**: A blue label pointing to the term  $p[\mathbf{r}]$  in the denominator.
- a posteriori* distribution**: A red label pointing to the term  $p[s|\mathbf{r}]$  in the numerator.

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



# Bayesian inference

---

Bayes' law:

likelihood function

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

*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

---

Bayes' law:

likelihood function

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

*a posteriori* distribution

# Decoding strategies

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

likelihood function

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

*a posteriori* distribution

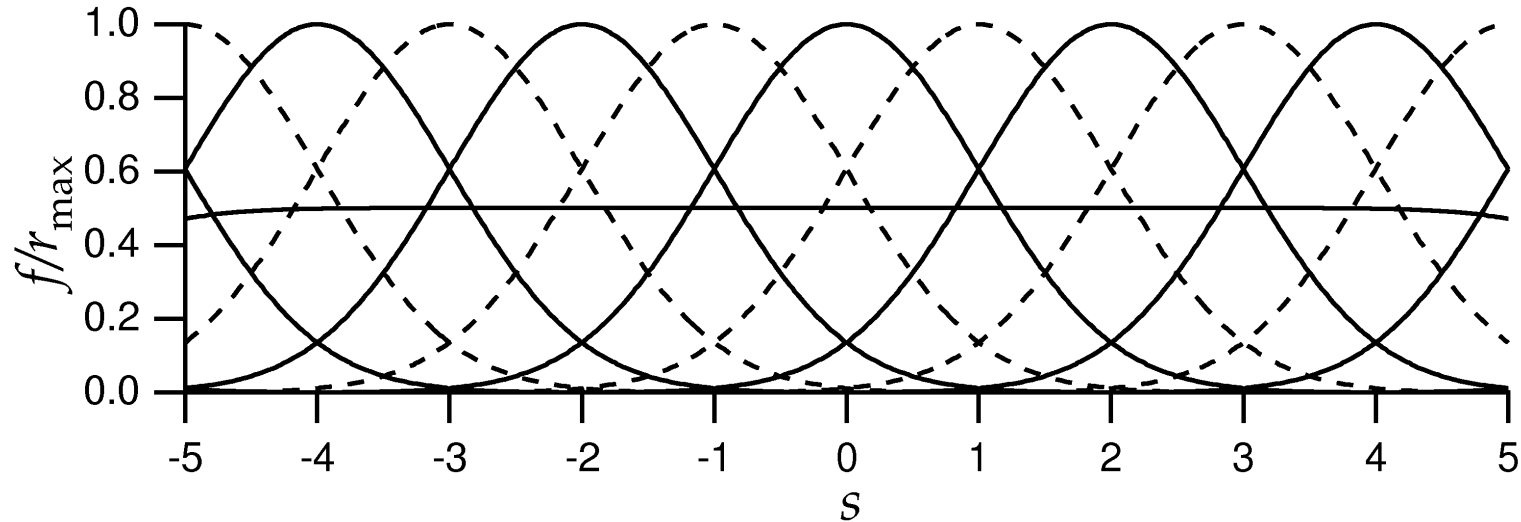
Maximum *a posteriori*:  
 $s^*$  which maximizes  $p[s|r]$

# Decoding an arbitrary continuous stimulus

Let's take a particular case....

- assume independence
- assume Poisson firing

# Decoding an arbitrary continuous stimulus

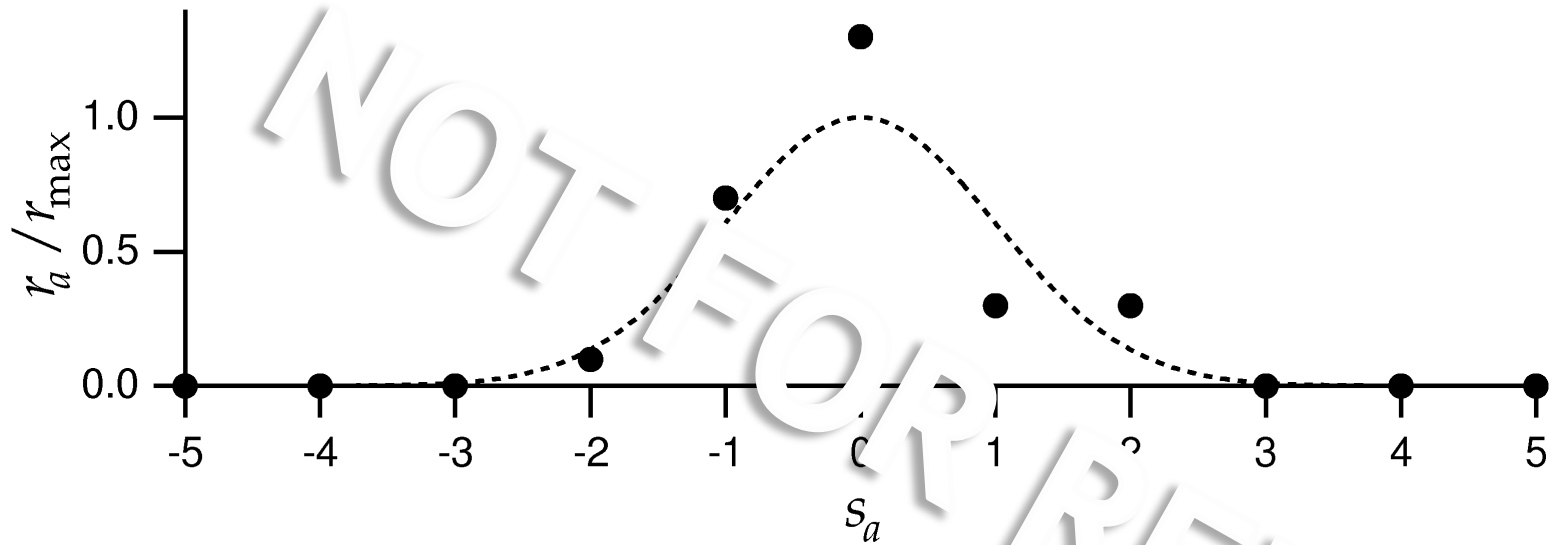


Let's take an example: Gaussian tuning curves

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

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

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



Population response of 11 cells with Gaussian tuning curves

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

1. Assume Poisson:  $P_T[k] = (rT)^k \exp(-rT)/k!$

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

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



# Maximum likelihood

---

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

Maximize  $\ln P[\mathbf{r}|s]$  with respect to  $s$

# Maximum likelihood

---

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

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

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

# Maximum likelihood

---

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

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

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

# Maximum *a posteriori*

---

Maximize  $\ln p[s|\mathbf{r}]$  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,

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

# Maximum *a posteriori*

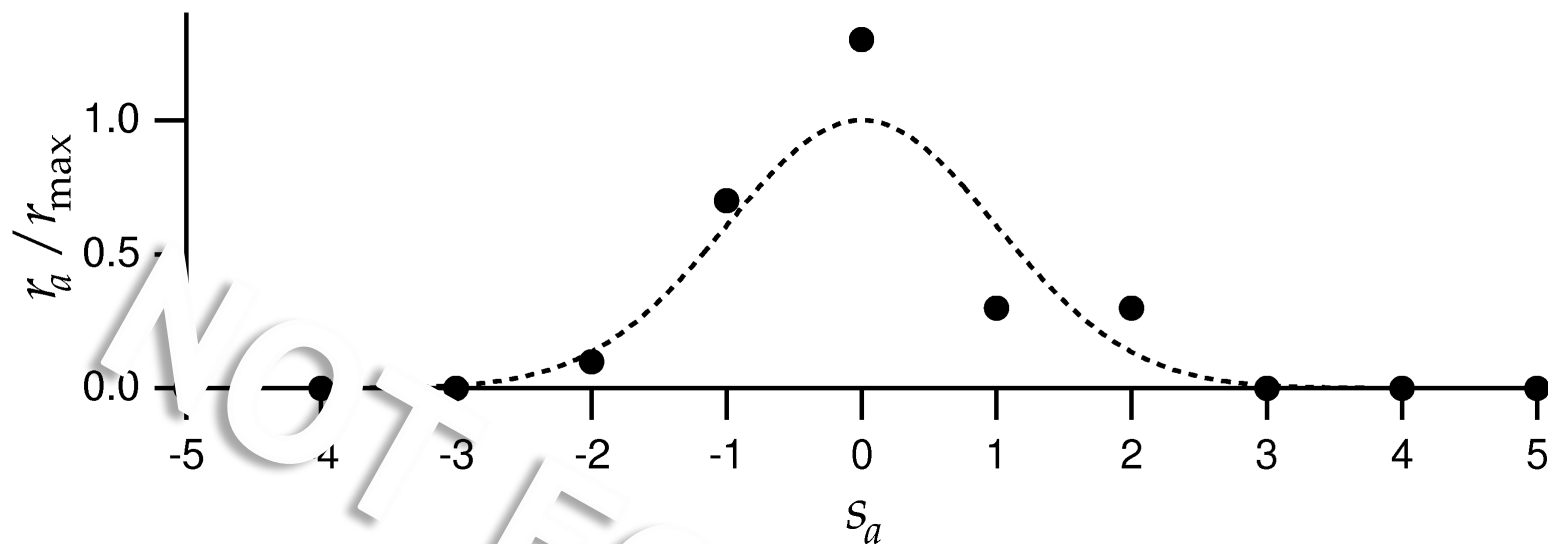
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Maximize  $\ln p[s|\mathbf{r}]$  with respect to  $s$

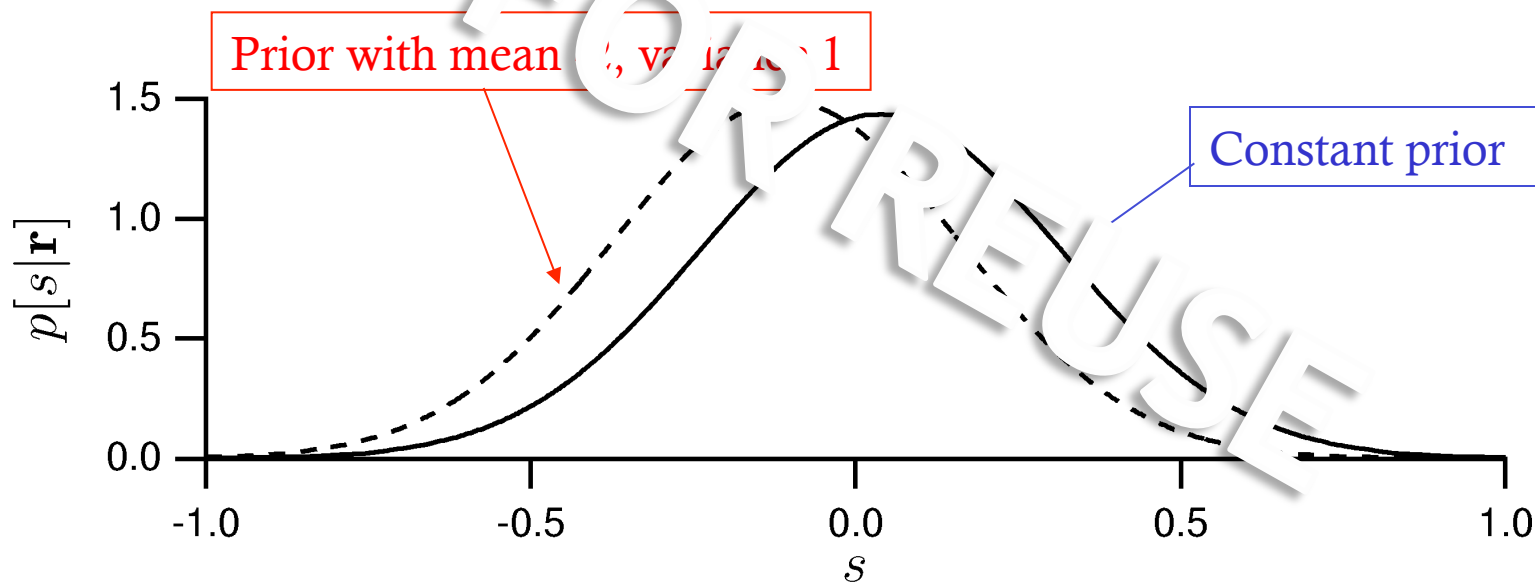
$$\ln p[s|\mathbf{r}] = \ln P[\mathbf{r}|s] + \ln p[s] - \ln P[\mathbf{r}]$$

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

Given this data:



MAP:

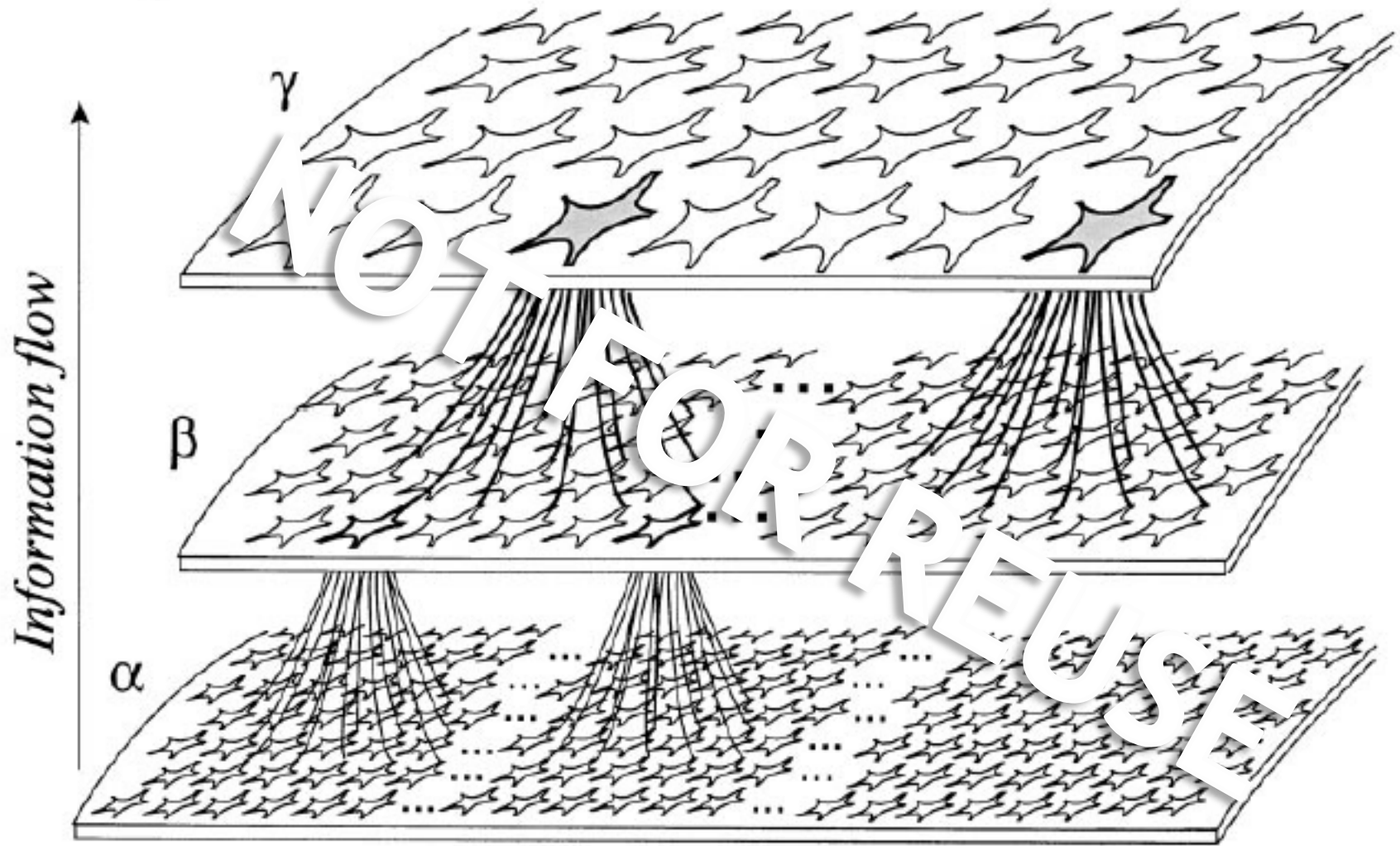


# Limitations of these approaches

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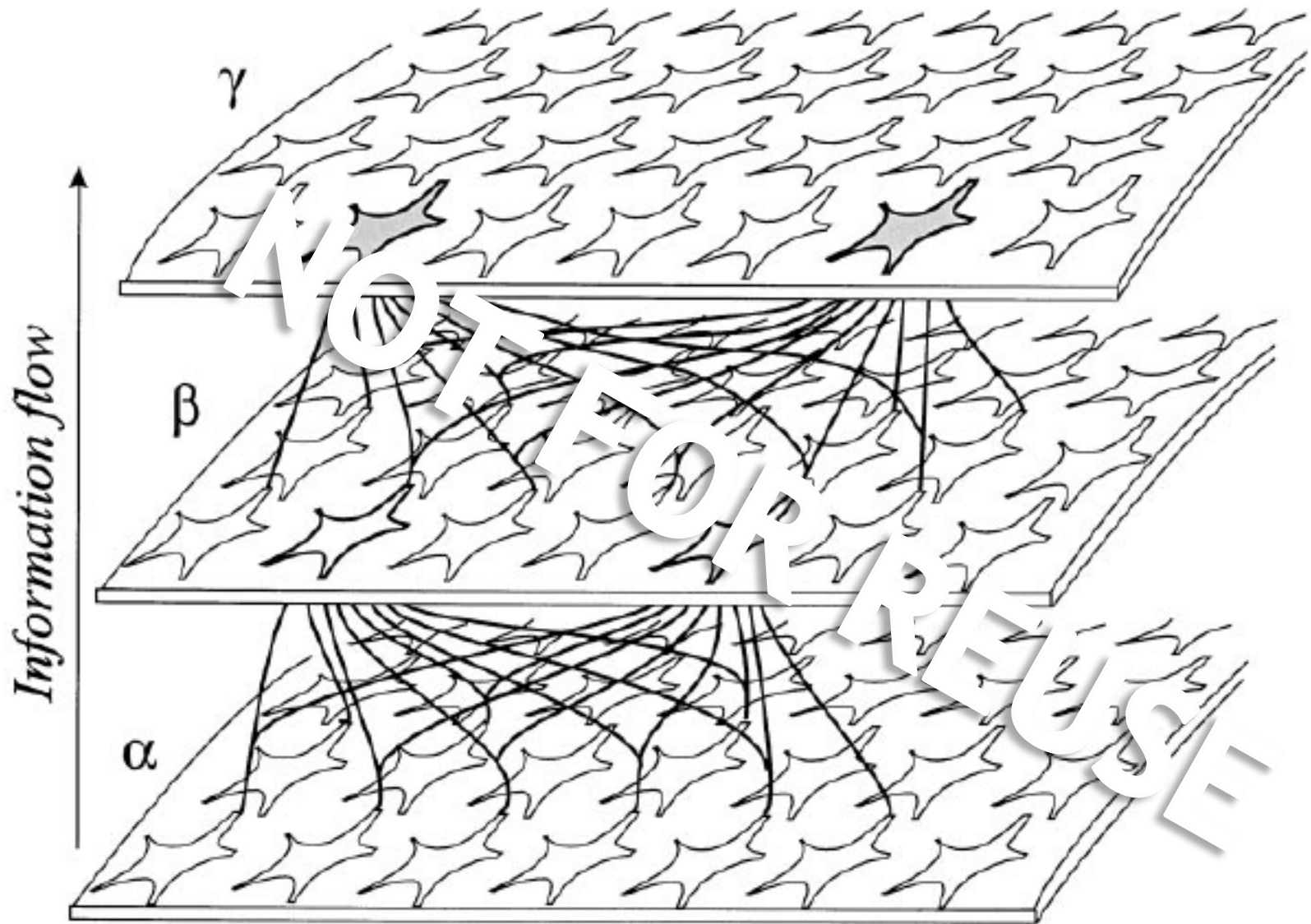
- Tuning curve/mean firing rate
- Correlations in the population

# The importance of correlation





# The importance of correlation



# The importance of correlation

