Decoding from many neurons: population codes

- Population code formulation

- Methods for decoding:
  → population vector
  → Bayesian inference
  → maximum likelihood
  → maximum a posteriori

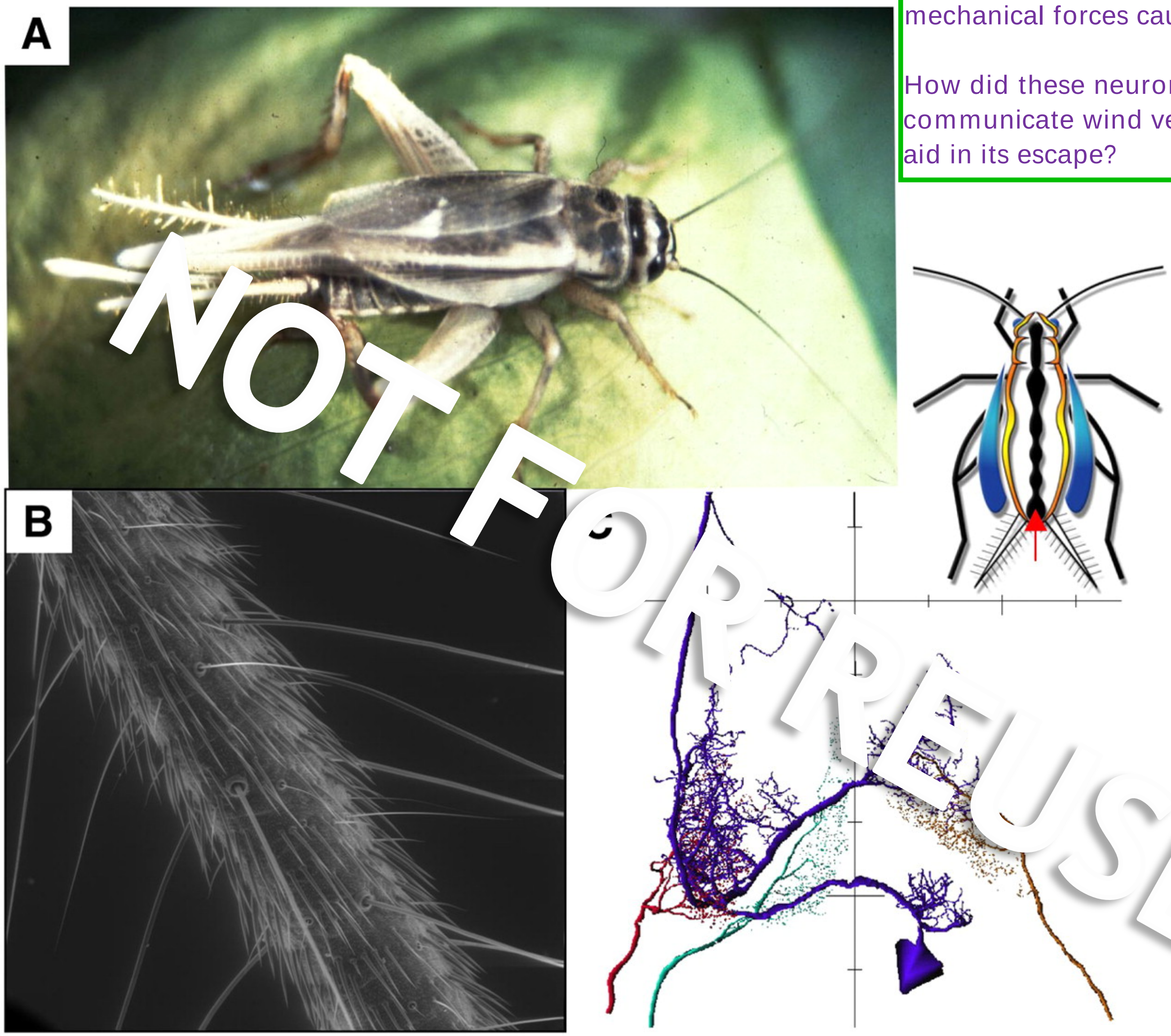
ML
MAP

- Fisher information

Cricket cercal cells

The wind velocity is transduced into an electrical signal by the movements of these hairs. They're innovated at their base by neurons that are able to sense the mechanical forces caused by their motion.

How did these neurons as a group communicate wind velocity to the animal, to aid in its escape?

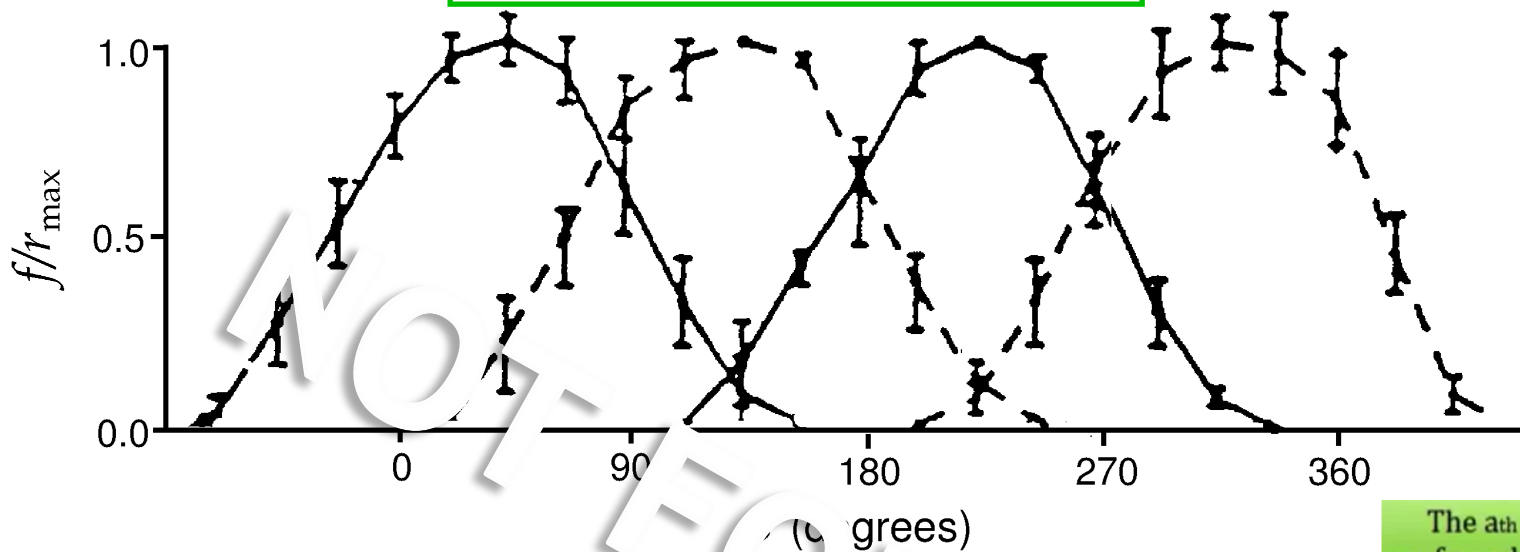


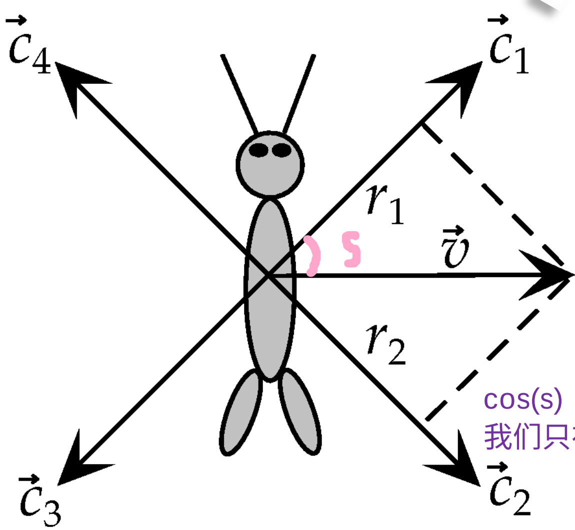
Jacobs G A et al. J Exp Biol 2008;211:1819-1828

The Journal of Experimental Biology

Cricket cercal cells

Firing rate response codes for different neurons
4 tuning curves.





The ath neuron has a preferred direction where response is maximum, denoted by *angle* s_a or vector $\mathbf{c}_a$

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

cos(s) = r/|v|
我们只在意方向，不在意大小

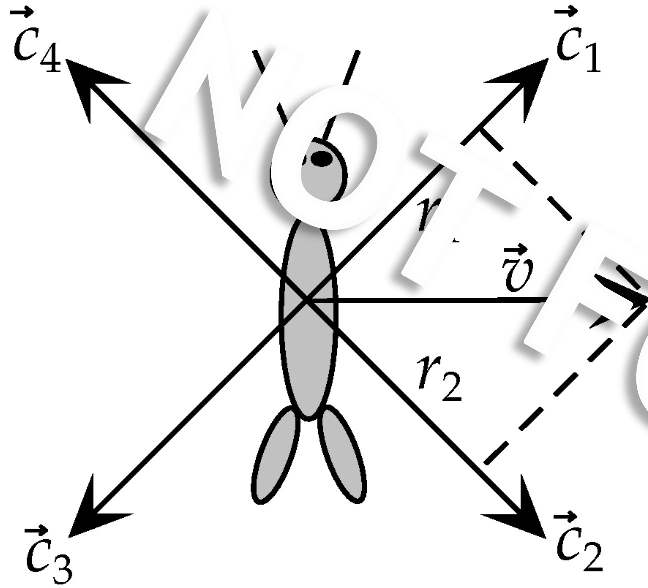
$$\left(\frac{f(s)}{r_{\max}}\right)_a = [\vec{v} \cdot \vec{c}_a]_+$$

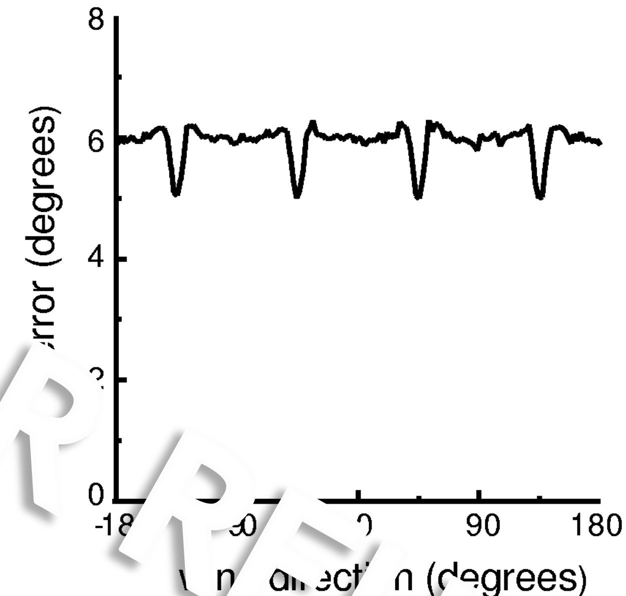
Theunissen & Miller, 1991; in Dayan and Abbott, *Theoretical Neuroscience*

Population vector

all neurons

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



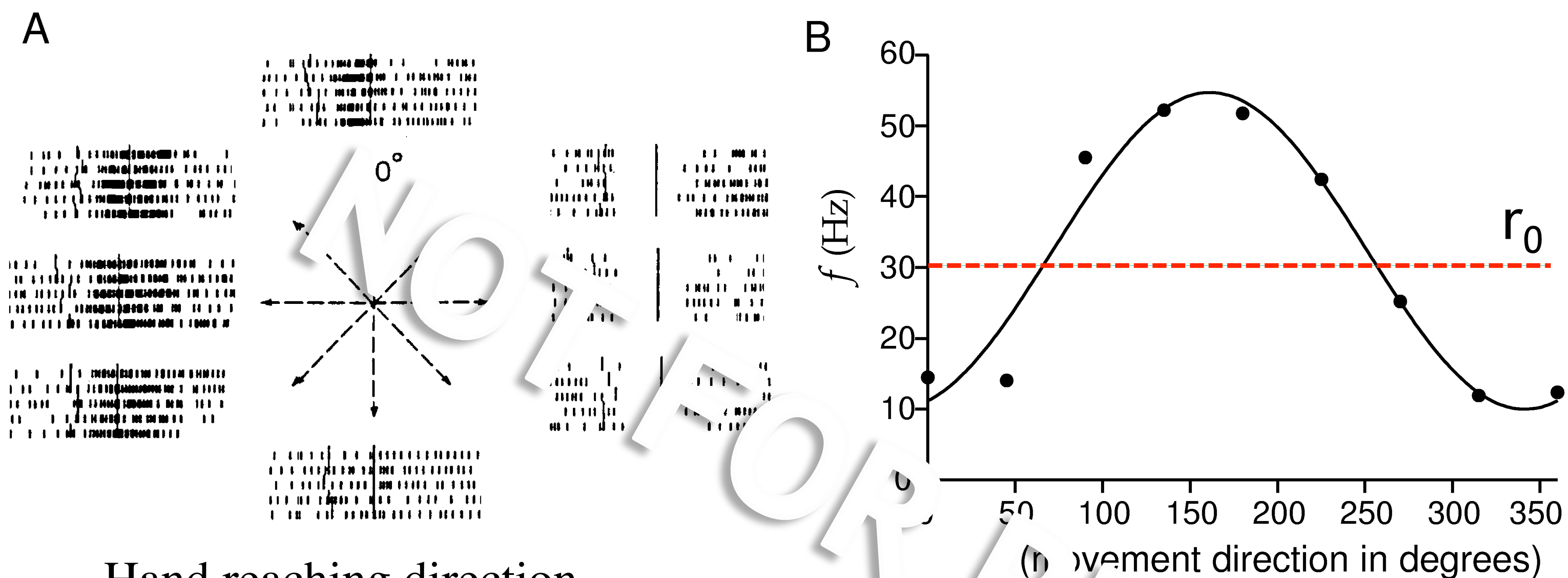


RMS error in estimate

只需要2个basis就能够表达二维空间的方向，但是这里有4个basis
why？
因为没有负的firing rate来coding负方向

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

Population coding in M1



Hand reaching direction

Cosine tuning curve of a motor cortical neuron

Population coding in M1

Cosine tuning:

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

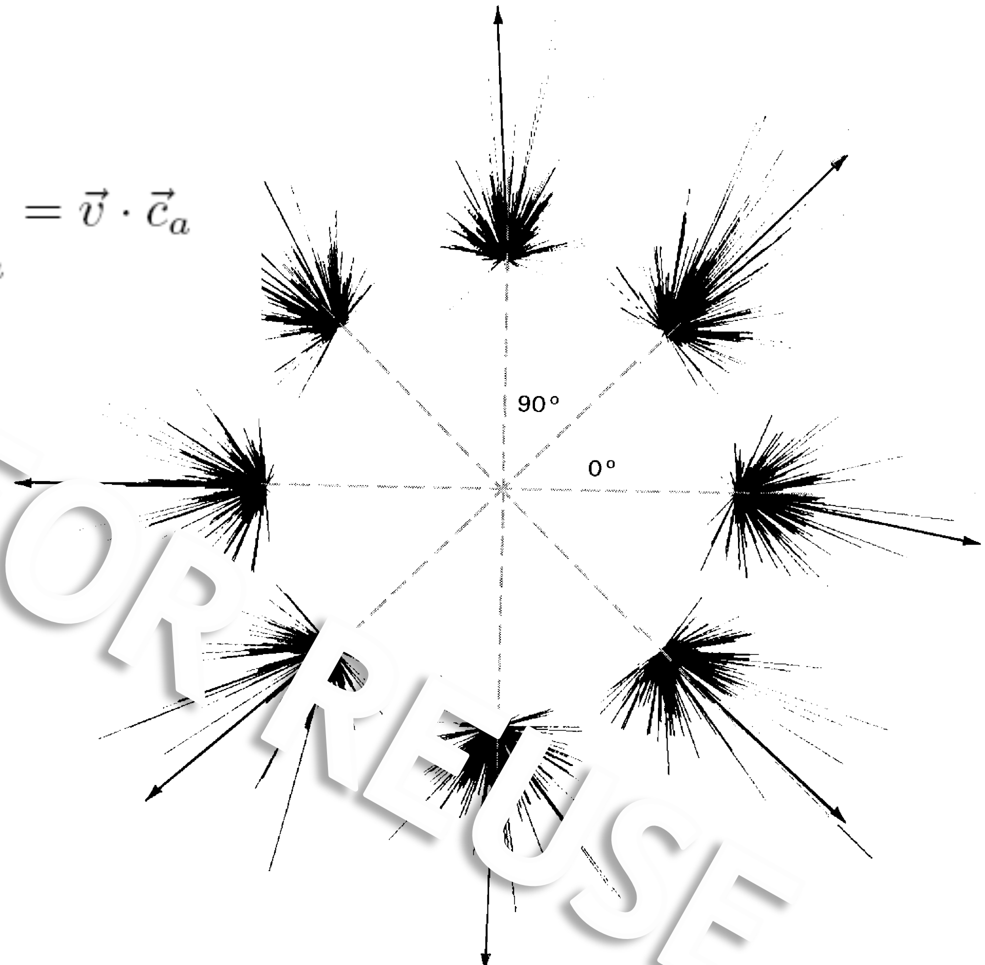
Pop. vector:

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

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:

likelihood function

conditional distribution

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

prior distribution

a posteriori distribution

marginal distribution

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

In general, these are going to differ because of the role of the prior, that's what makes the two sides differ.

That means in maximizing the a posteriori distribution, we're biasing our choice for what we know about the stimulus in advance.

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

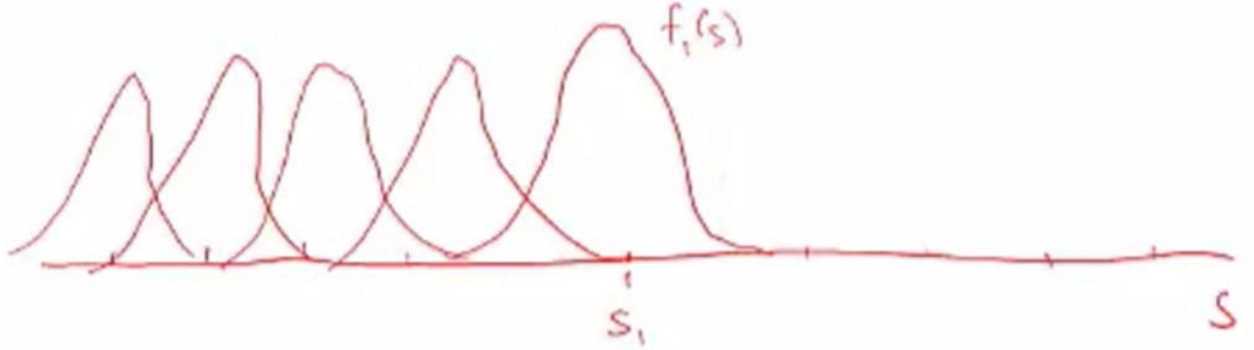
a posteriori distribution

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

Decoding an arbitrary continuous stimulus

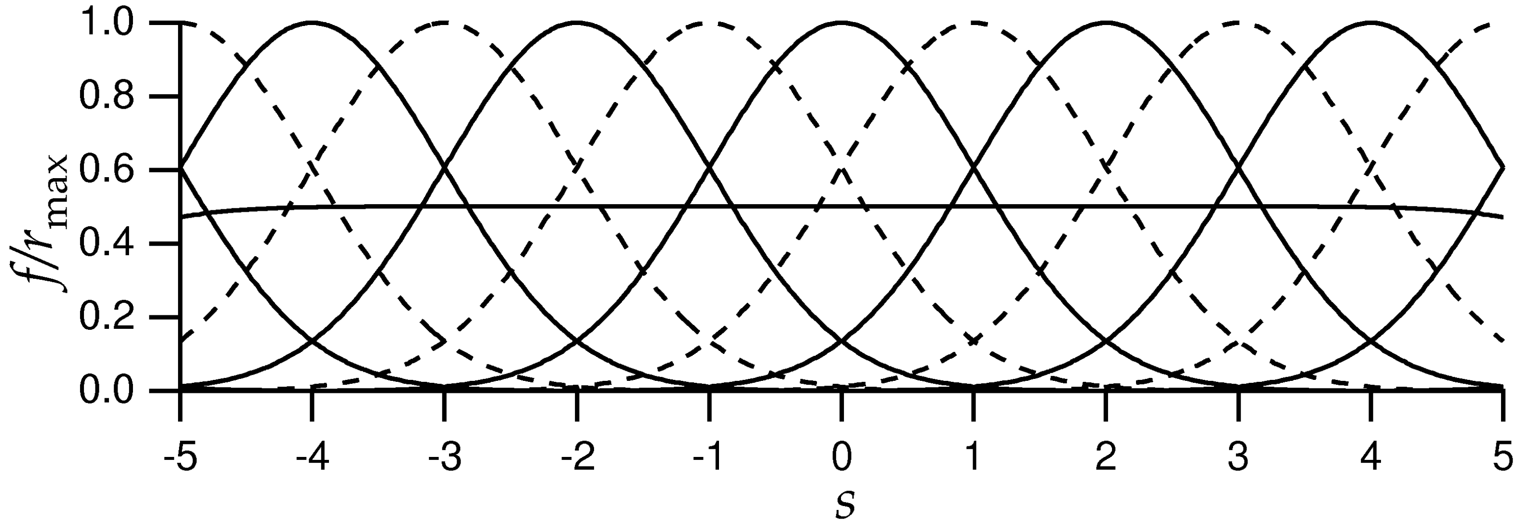
Let's take a particular case….

不同神经元和不同的tuning function



- assume independence
- assume Poisson firing

Decoding an arbitrary continuous stimulus

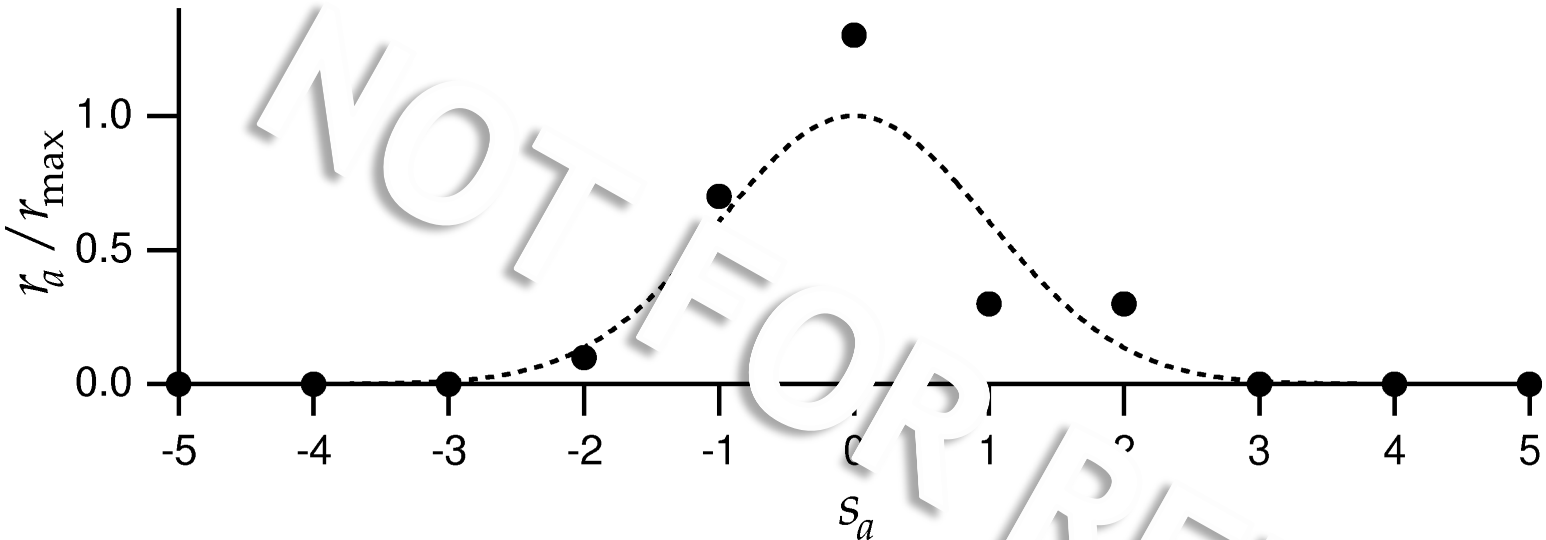


Let's take an example: Gaussian tuning curves

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

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

Need to know full P[**r**|s]



Population response of 11 cells with Gaussian tuning curves

Need to know full P[**r**|s]

T个neuron

这里都是对likelihood function的假设

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[**r**|s] with respect to s

Maximum likelihood

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

$$\ln P(r|s) = \sum_{a=1}^{N} \Big\{ r_a T \ln(f_a(s)T) - \underline{f_a(s)T} - \underline{\ln((r_a T)!)} \Big\}$$

const

Maximize ln P[**r**|s] with respect to s

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

$$\frac{\partial}{\partial s} \ln P(r|s) = T \sum_{a=1}^{N} r_a \frac{f_a'(s)T}{f_a(s)}$$

$$= T \sum_a r_a \frac{f'(s)}{f(s)} = 0$$

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

Set derivative to zero, use sum = constant

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

Maximum likelihood

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

对f(s)的假设

From Gaussianity of tuning curves,

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

所有neuron的tuning curves的sigma

If all σ same

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

Maximum *a posteriori*

Maximize ln p[s|**r**] with respect to s

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

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

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,

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

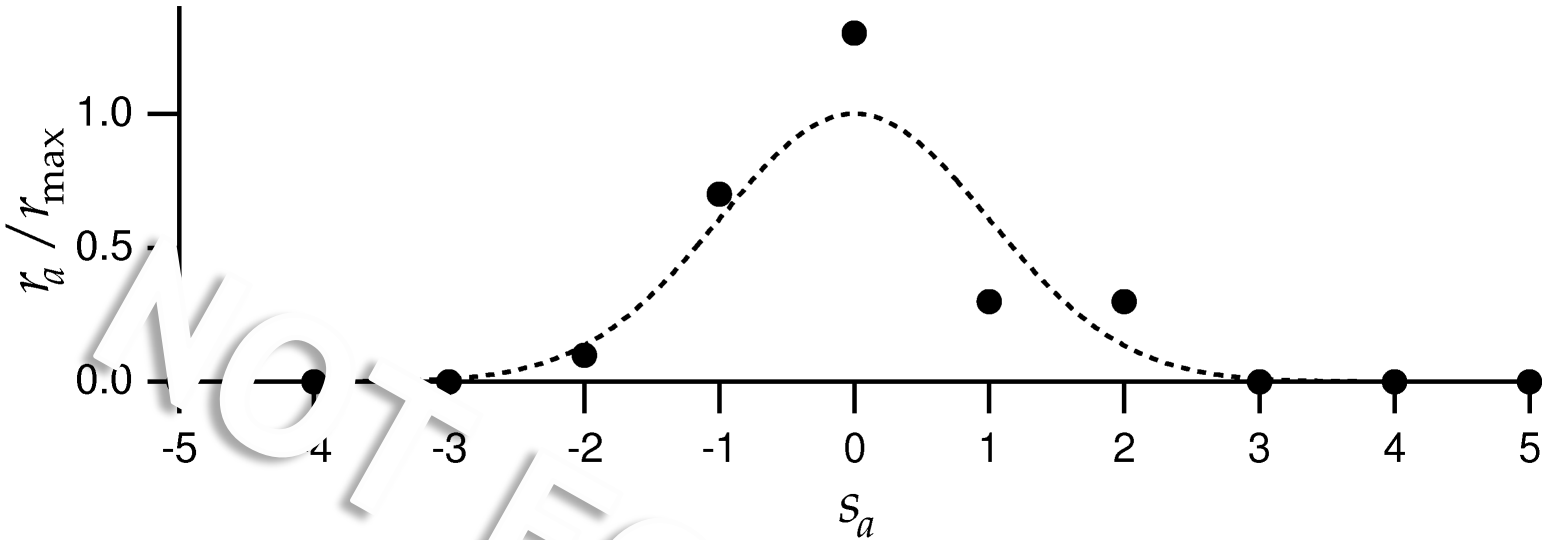
Maximum *a posteriori*

Maximize ln p[s|**r**] with respect to s

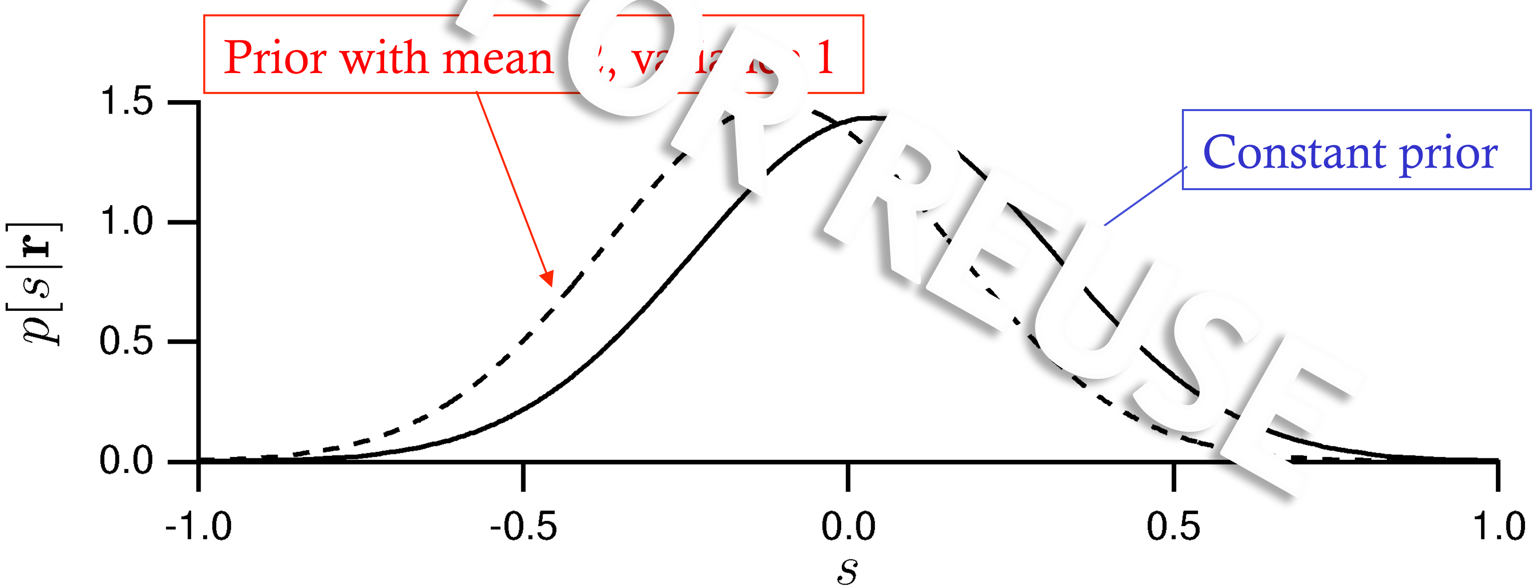
$$\ln p[s|\mathbf{r}] = \ln P[\mathbf{r}|s] + \ln p[s] - \ln P[\mathbf{r}]$$

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

Given this data:



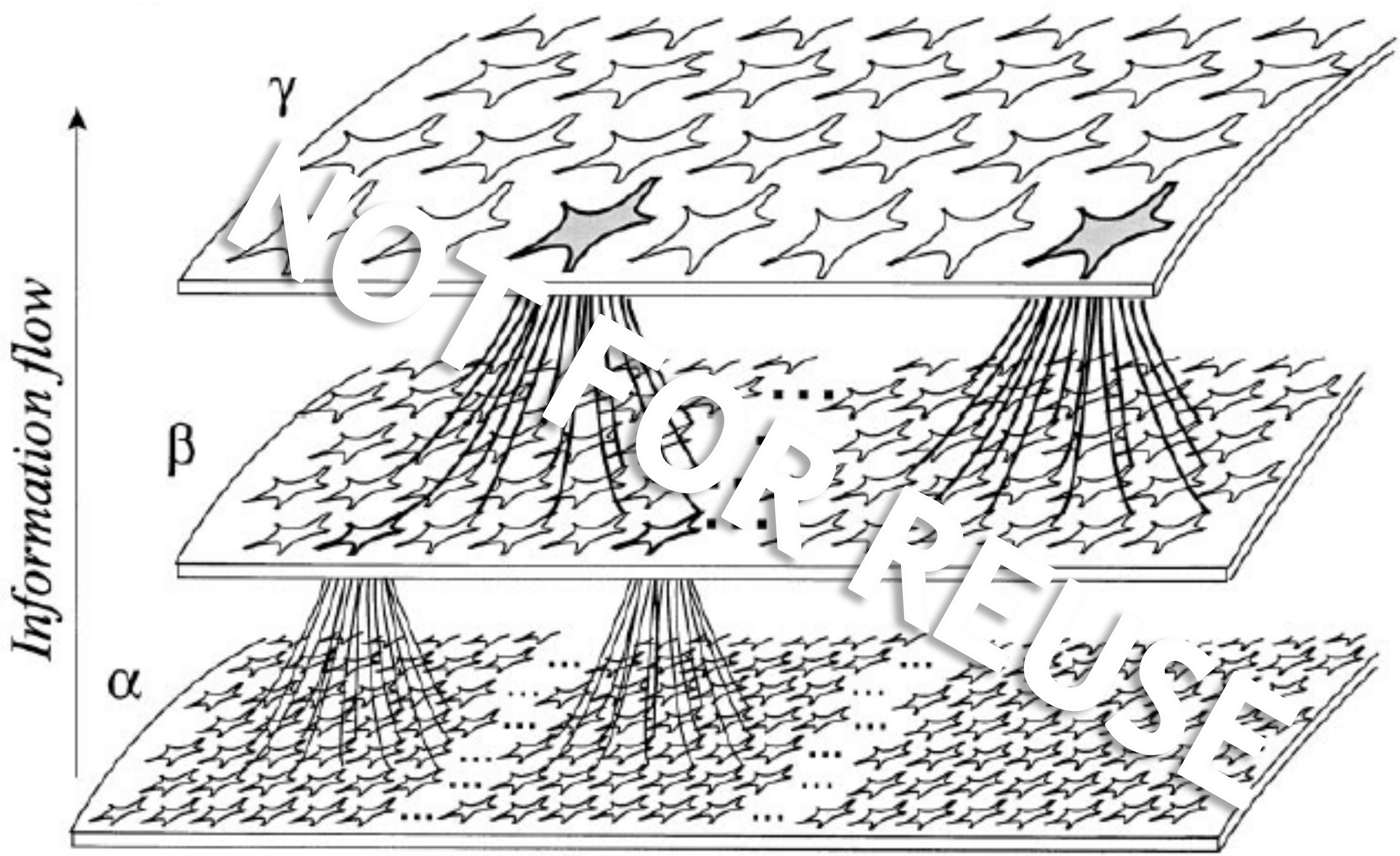
MAP:



Limitations of these approaches

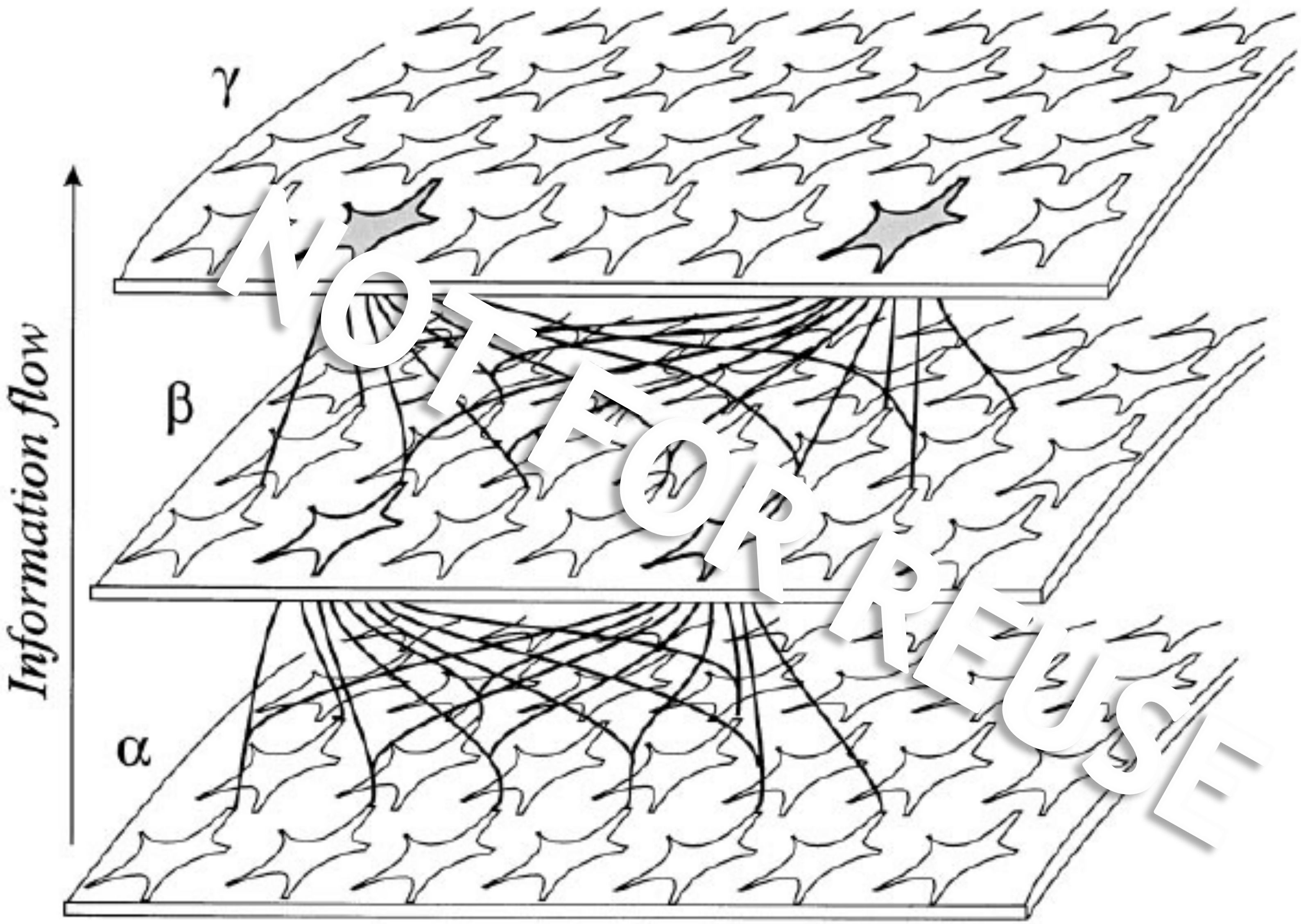
- Tuning curve/mean firing rate 没有考虑到快速的时间变异
- Correlations in the population 这一点很重要

The importance of correlation



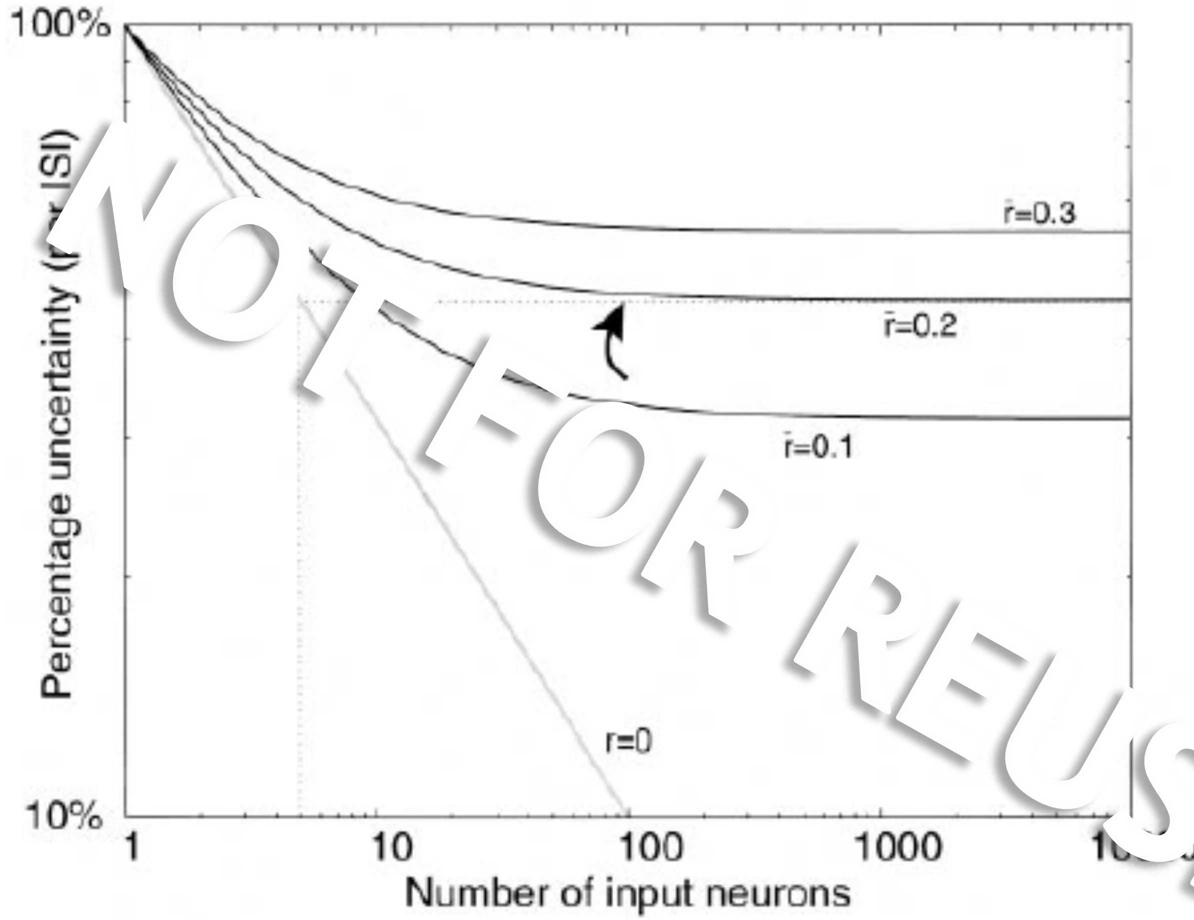
Shadlen and Newsome, '98

The importance of correlation



Shadlen and Newsome, '98

The importance of correlation



Shadlen and Newsome, '98