# Decoding from many neurons: population codes

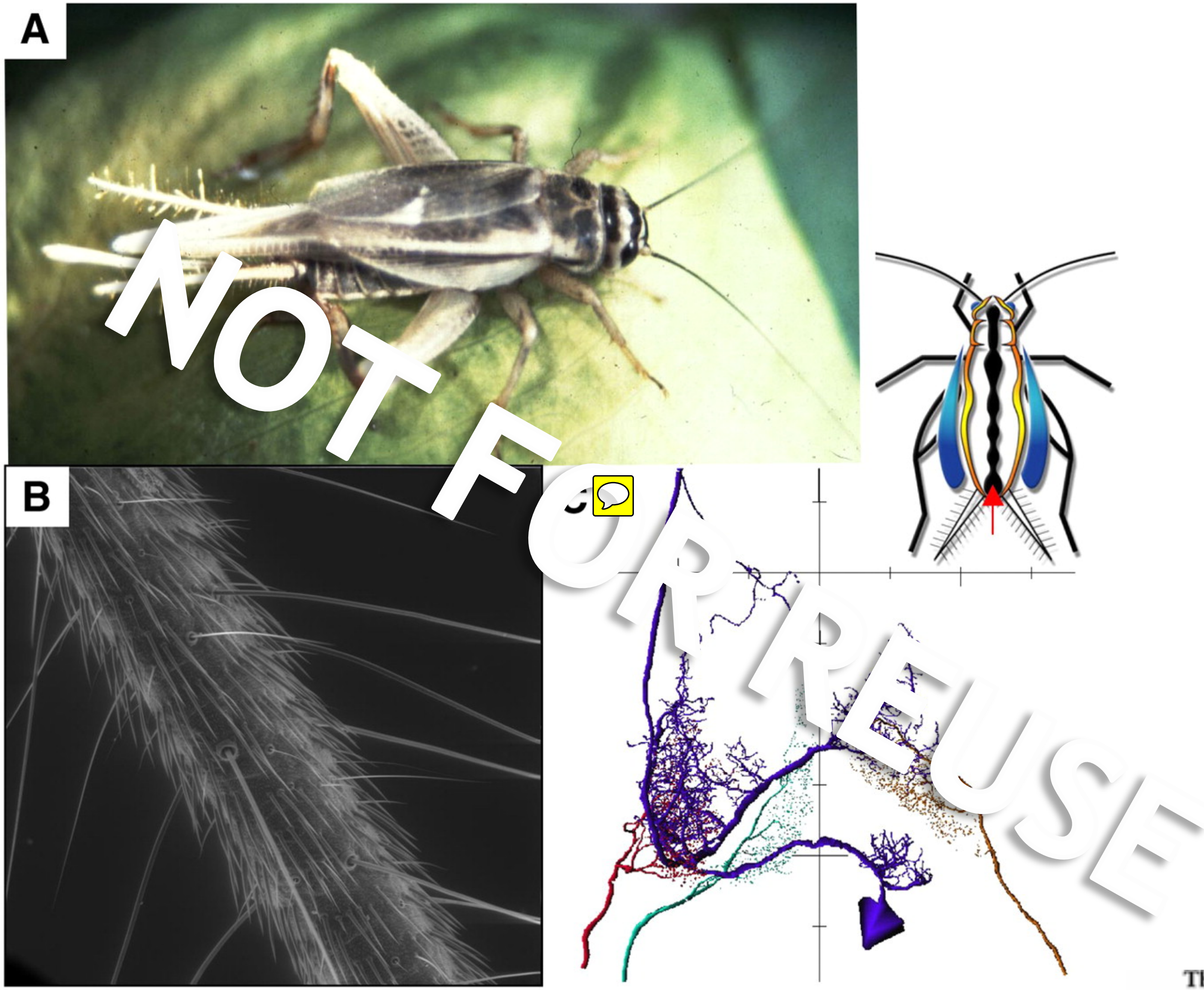


- Population code formulation

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

- Fisher information

# Cricket cercal cells

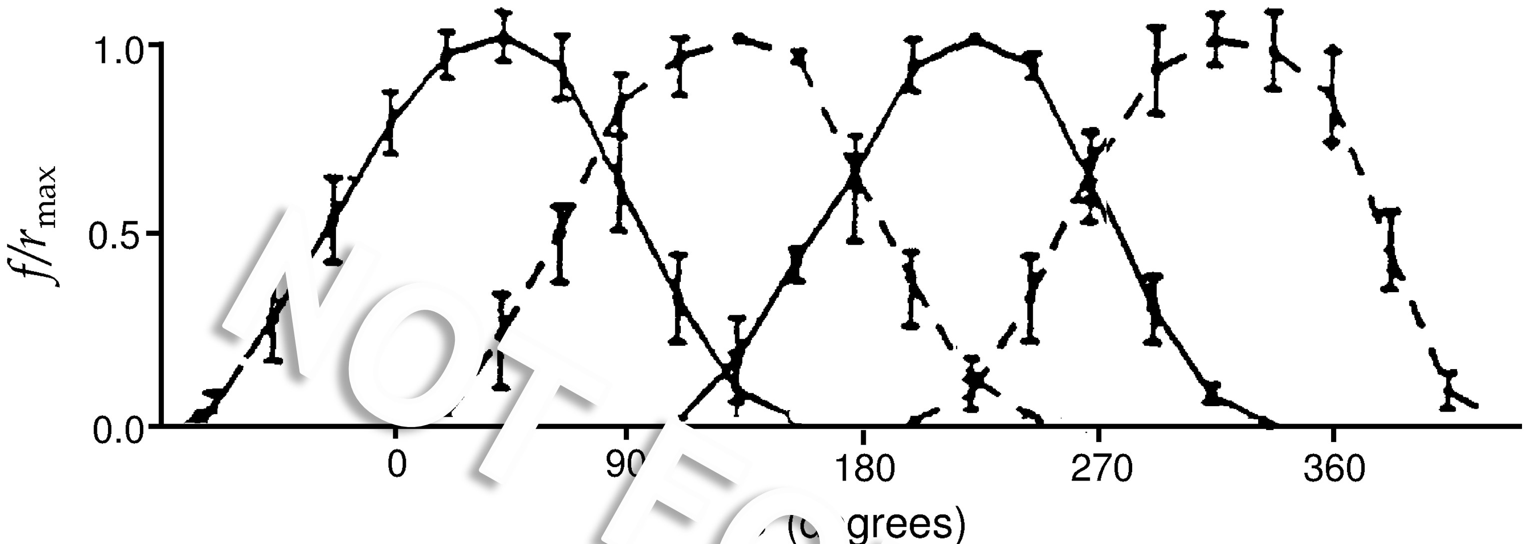


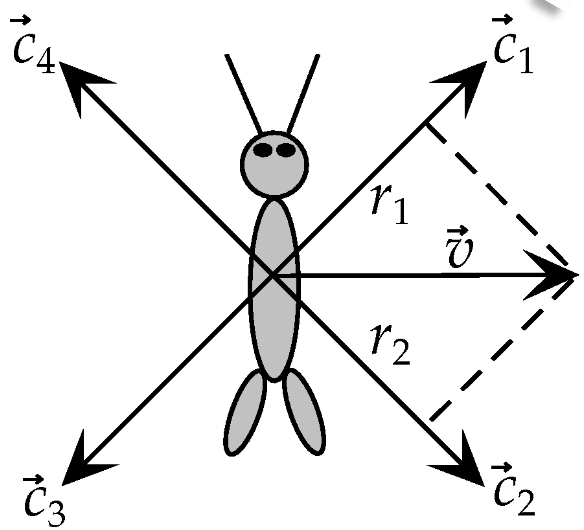



**Jacobs G A et al. J Exp Biol 2008;211:1819-1828**

The Journal of Experimental Biology

# Cricket cercal cells



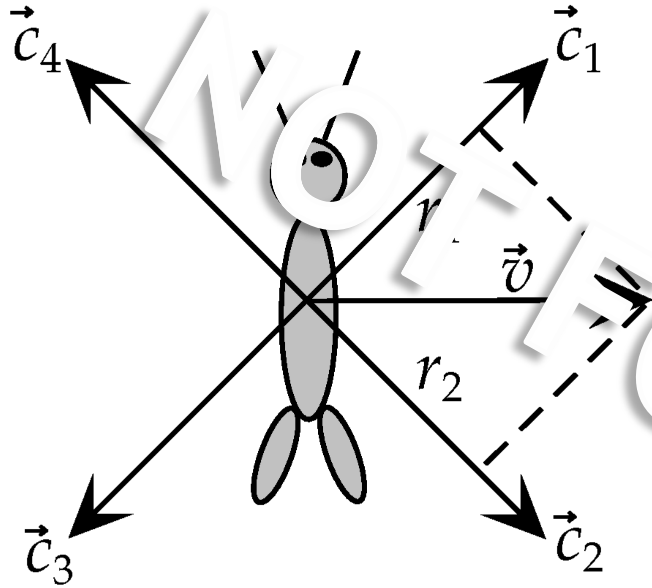

$$\left(\frac{f(s)}{r_{max}}\right)_a = [\cos(s - s_a)]_+$$

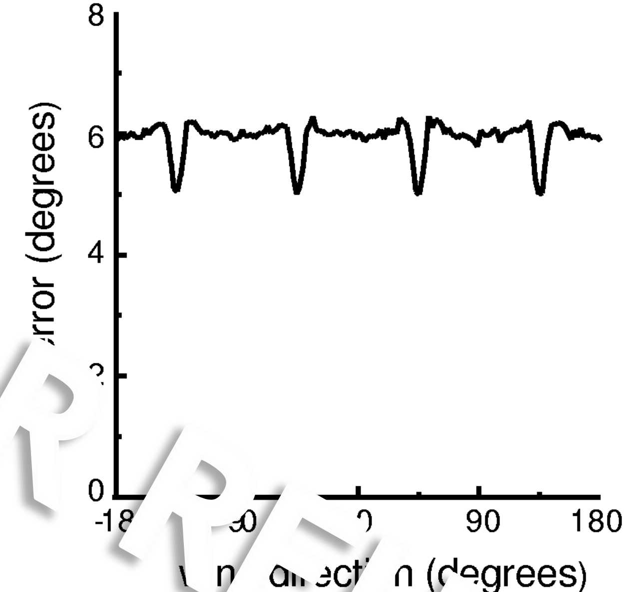
$$\left(\frac{f(s)}{r_{max}}\right)_a = [\vec{v} \cdot \vec{c}_a]_+$$

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

# Population vector

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



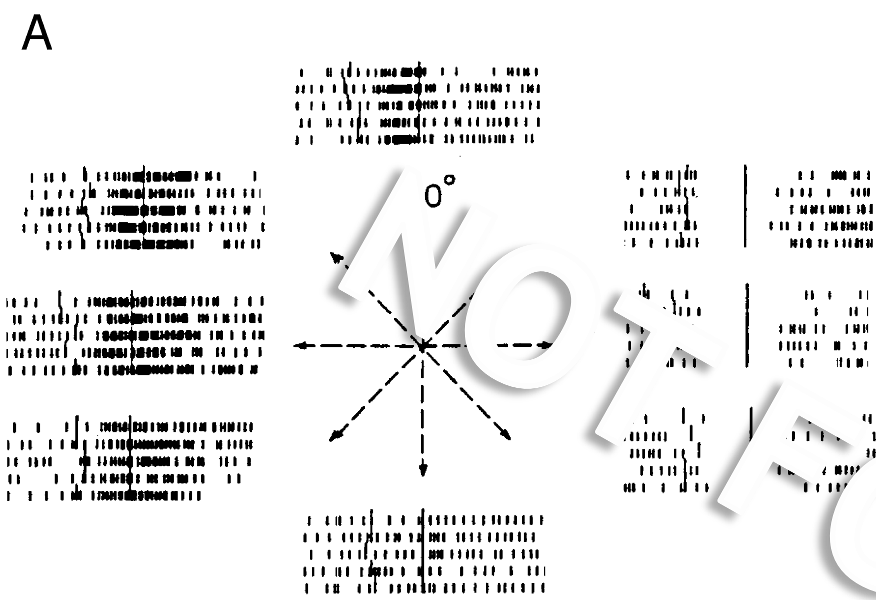




RMS error in estimate

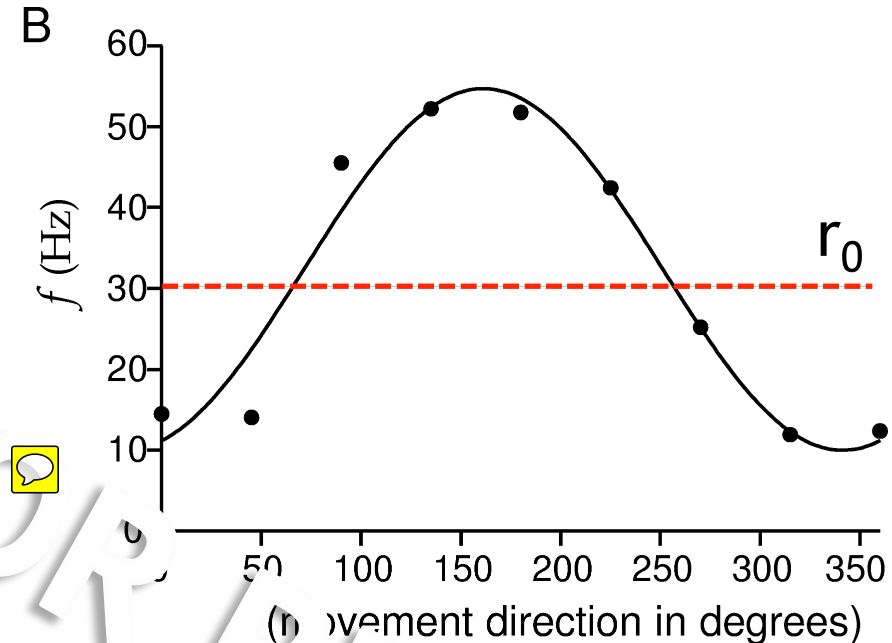


Theunissen & Miller, 1991; in Dayan and Abbott, *Theoretical Neuroscience*

# Population coding in M1




Hand reaching direction




Cosine tuning curve of a motor cortical neuron

# Population coding in M1

Cosine tuning:

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

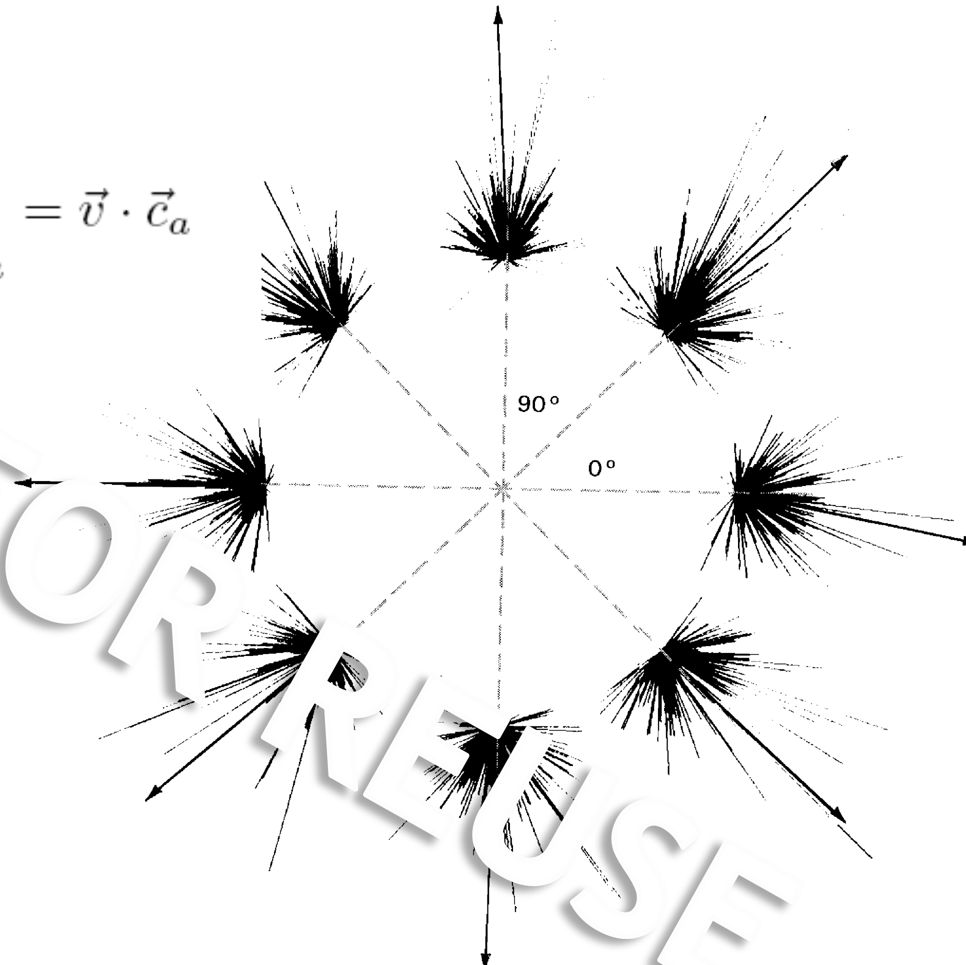
Pop. vector:

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

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

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

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

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

*a posteriori* distribution

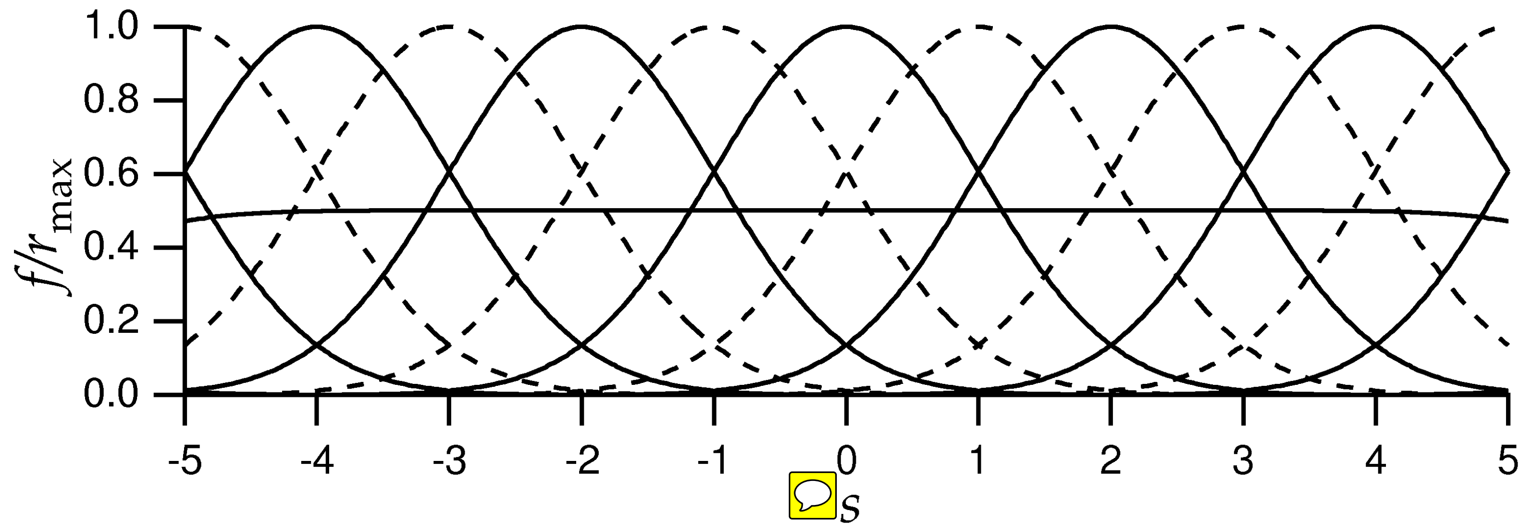
Maximum *a posteriori*:
s* which maximizes p[s|r]

# Decoding an arbitrary continuous stimulus

Let’s take a particular case….

- assume independence
- assume Poisson firing

# Decoding an arbitrary continuous stimulus

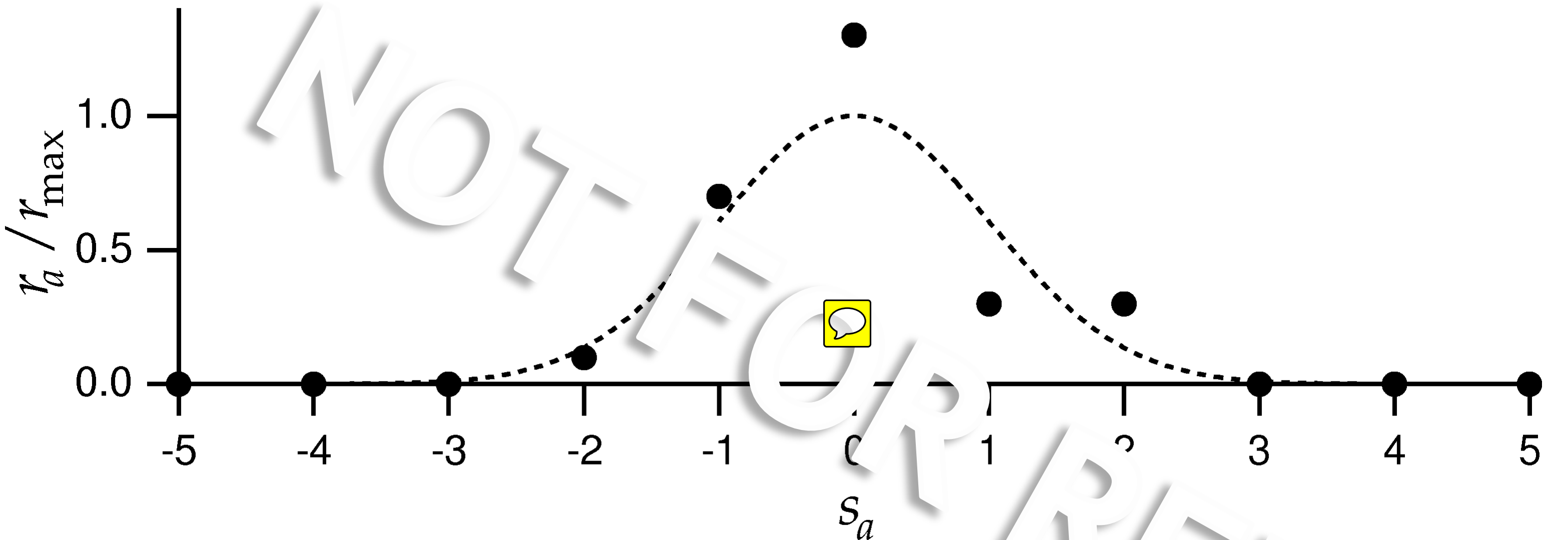



Let's take an example: Gaussian tuning curves

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

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]

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

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

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 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,

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

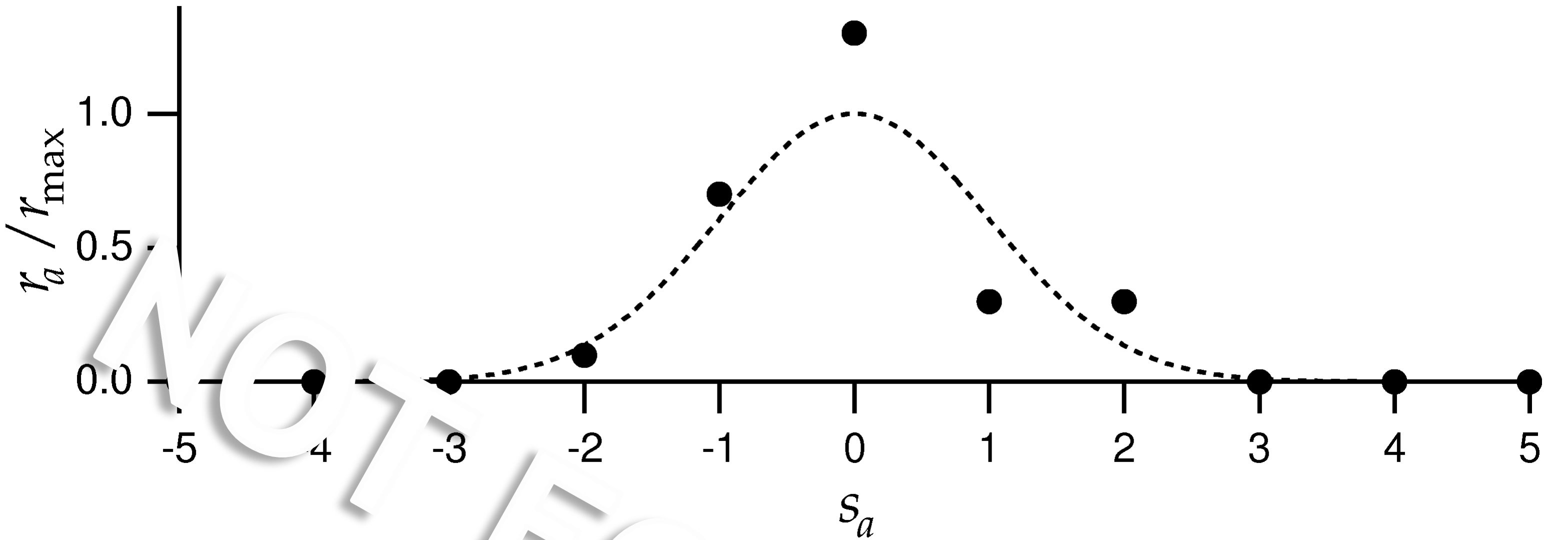
# Maximum *a posteriori*

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

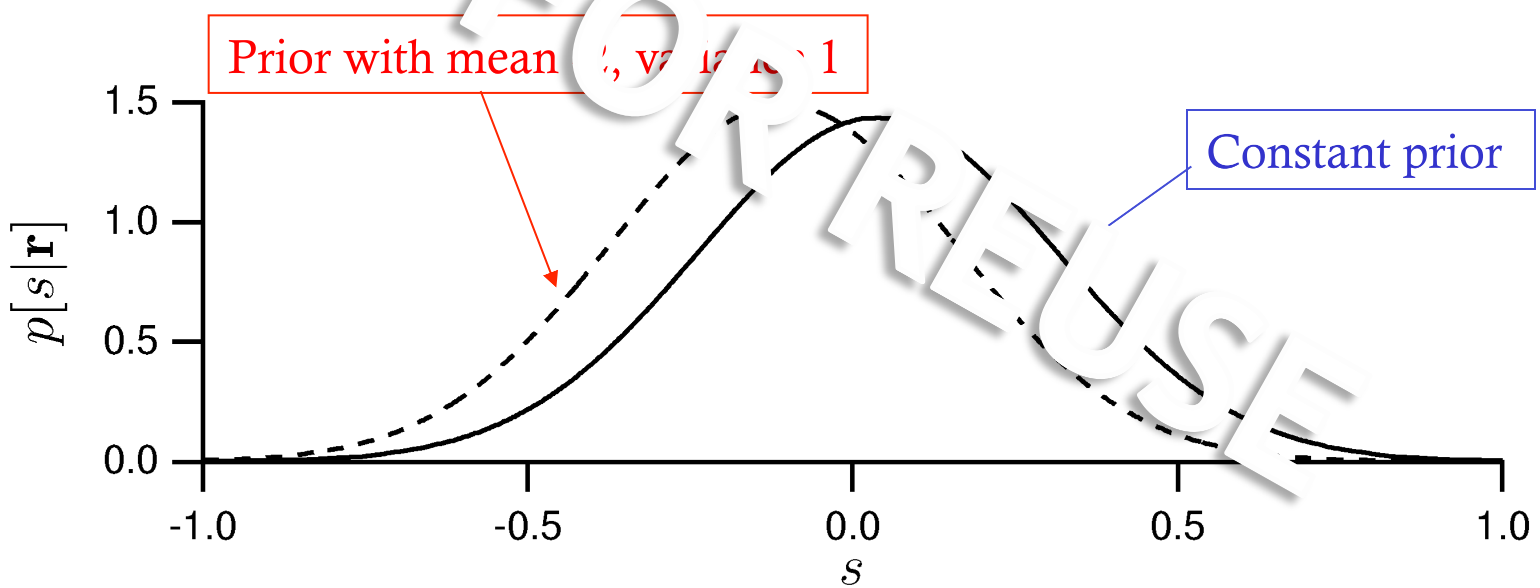
$$\ln p[s|\mathbf{r}] = \ln P[\mathbf{r}|s] + \ln p[s] - \ln P[\mathbf{r}]$$

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

Given this data:



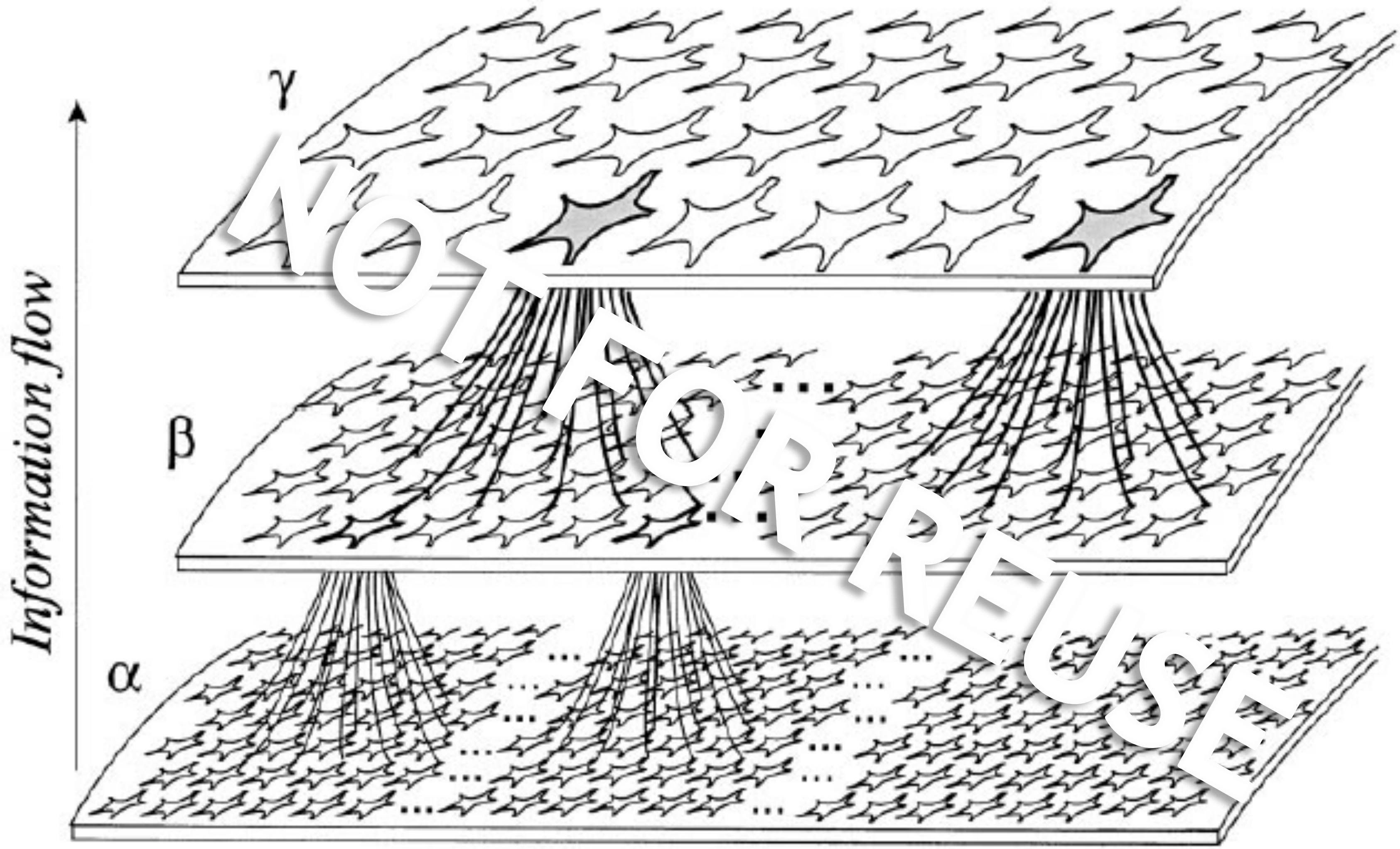

MAP:



# Limitations of these approaches

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

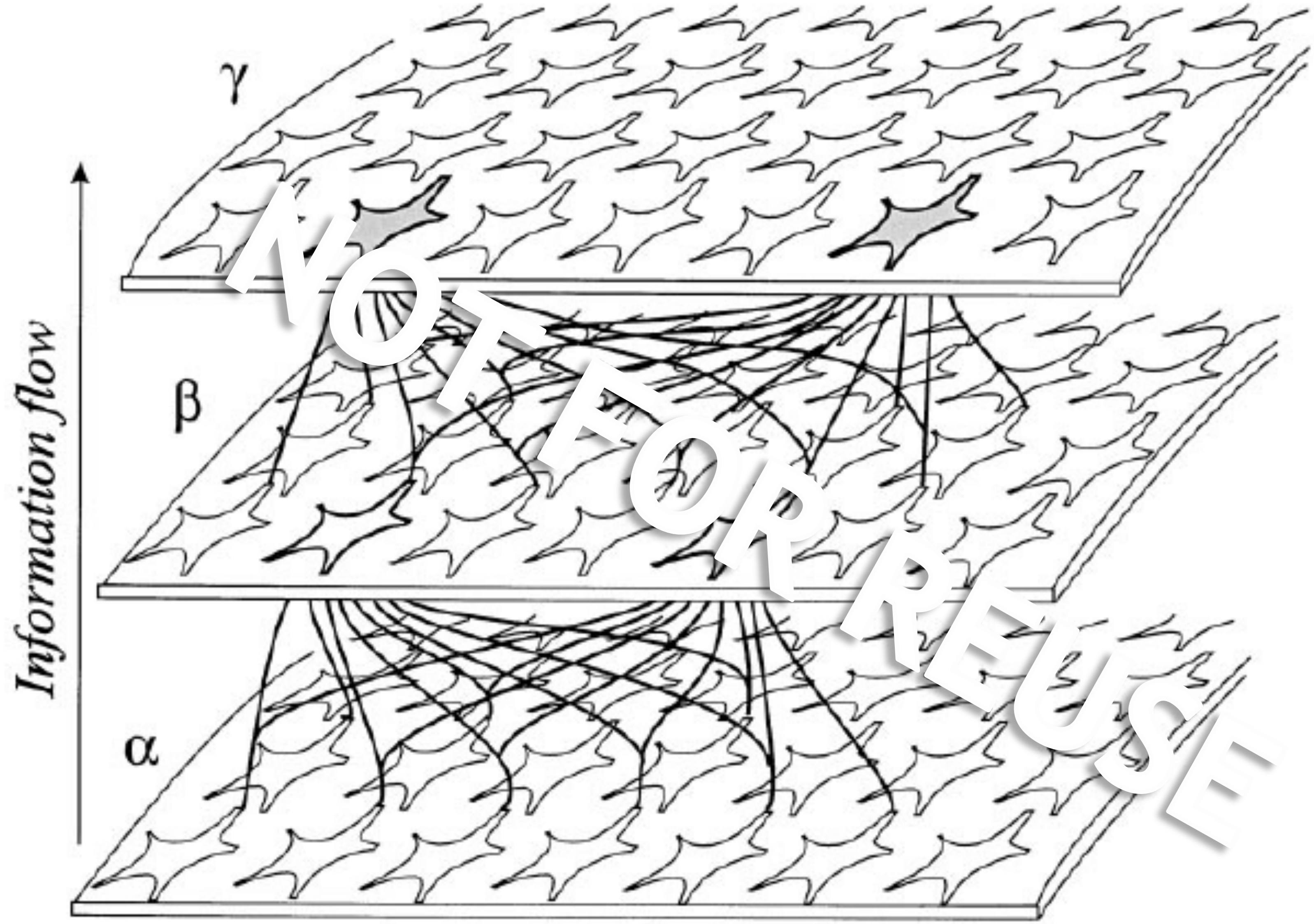
# The importance of correlation





Shadlen and Newsome, '98

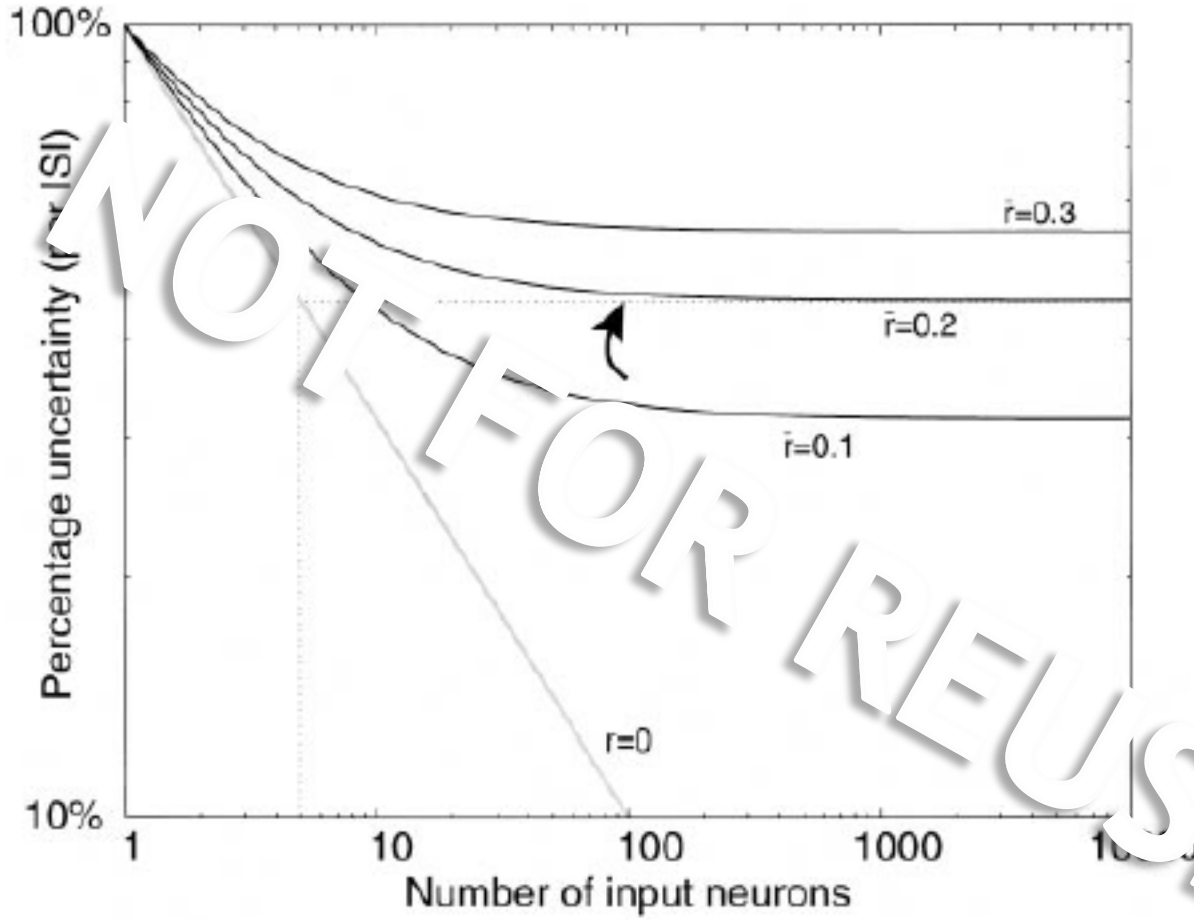
# The importance of correlation






Shadlen and Newsome, '98

# The importance of correlation





Shadlen and Newsome, '98