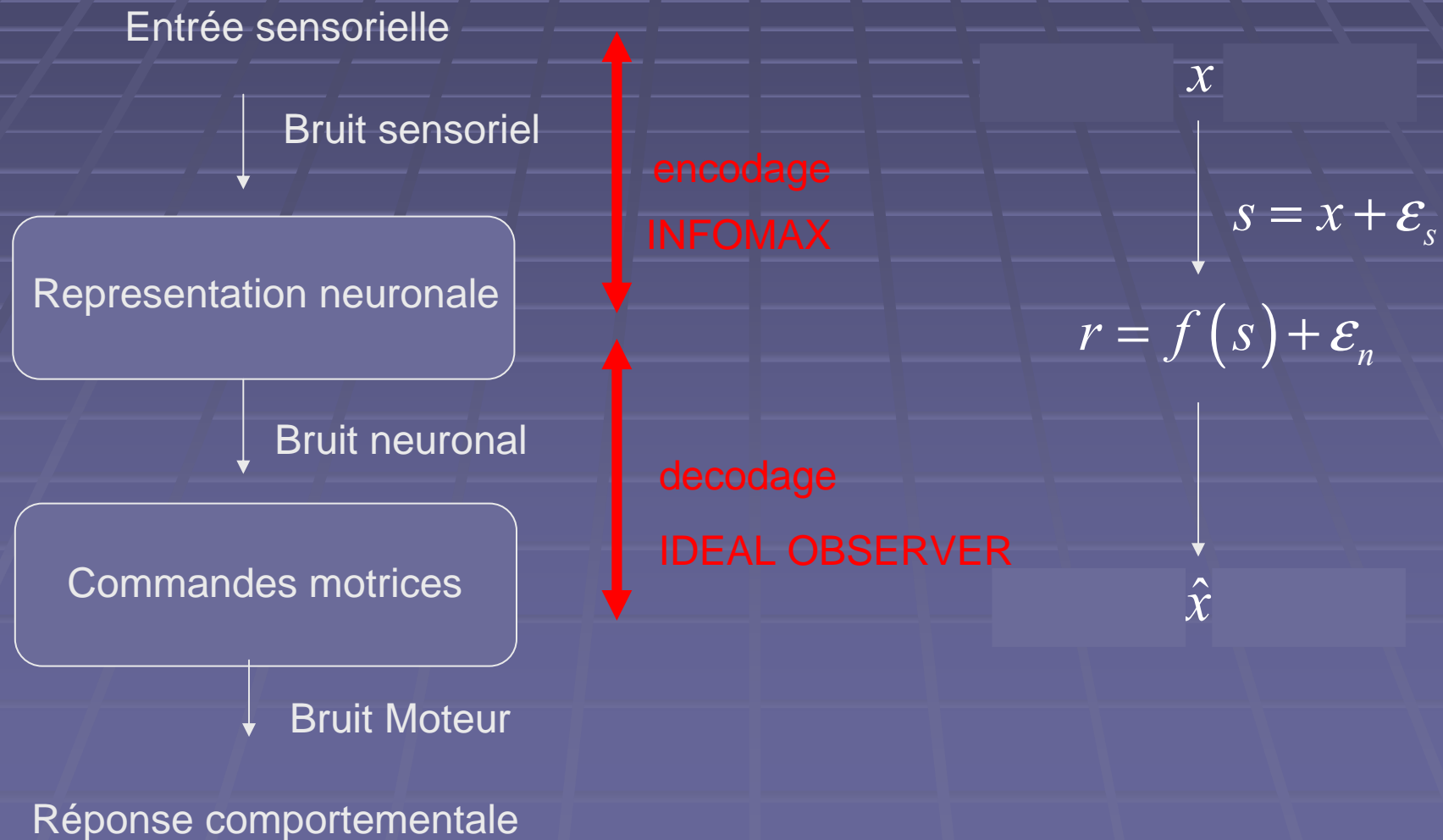


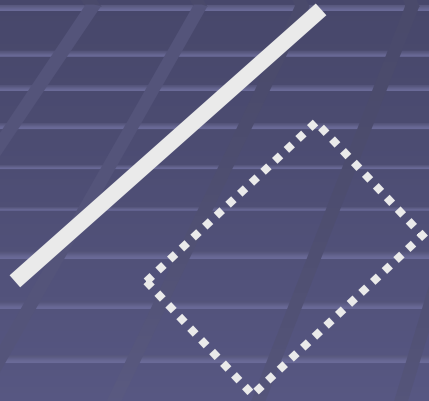
Population coding and decoding

Sophie Deneve
Group for Neural Theory
Ecole Normale Supérieure
Paris, France.

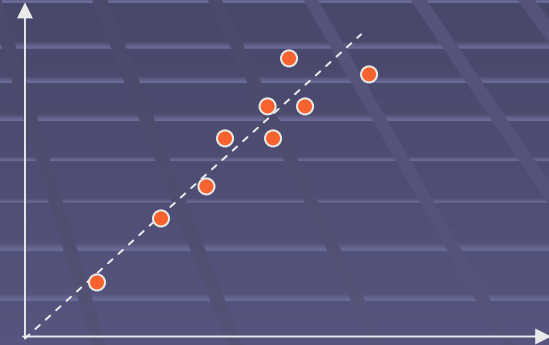
Le traitement du signal appliqué au cerveau



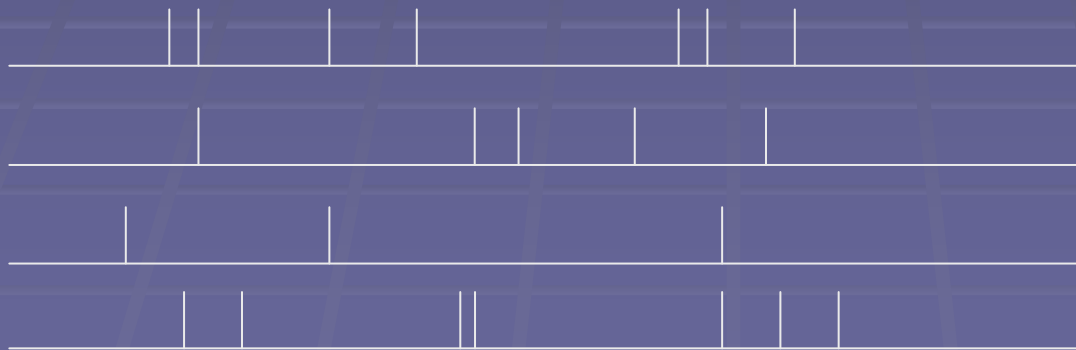
Poisson Variability in Cortex



Variance of Spike Count



Mean Spike Count



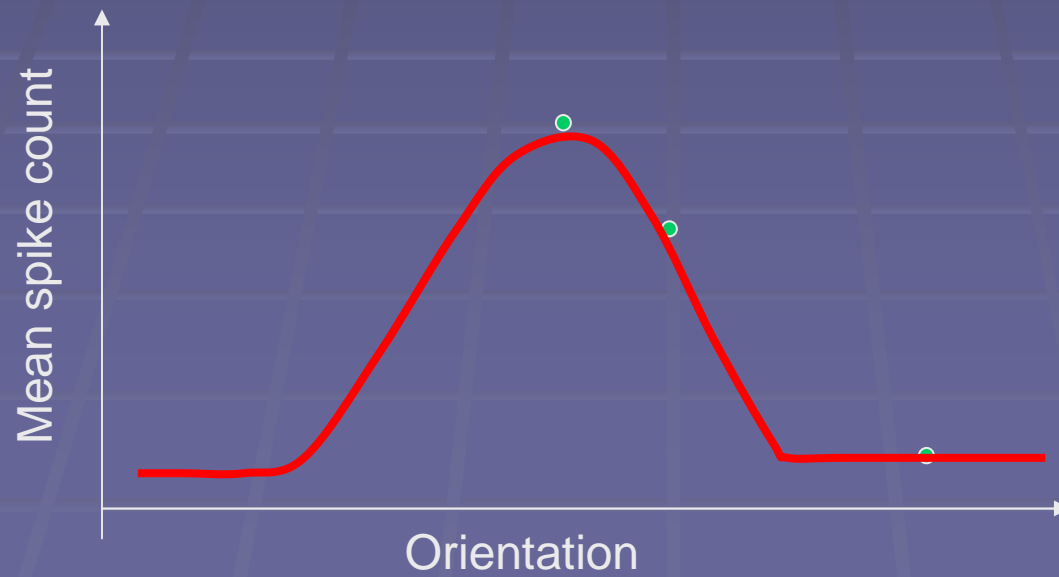
Trial 1

Trial 2

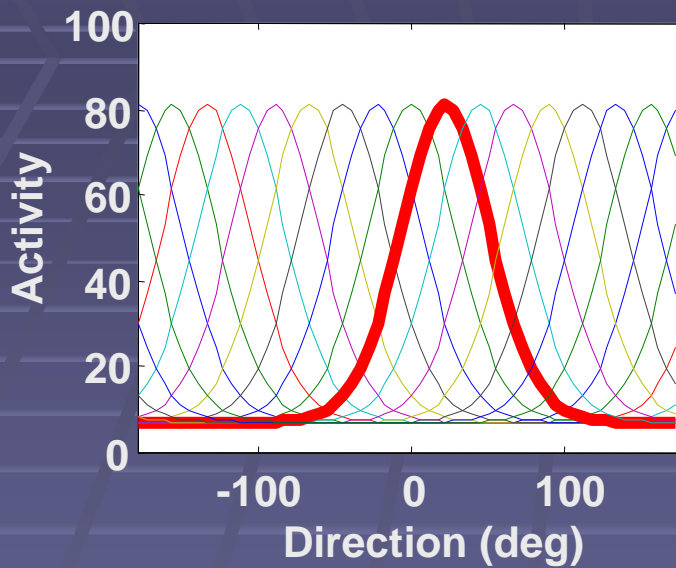
Trial 3

Trial 4

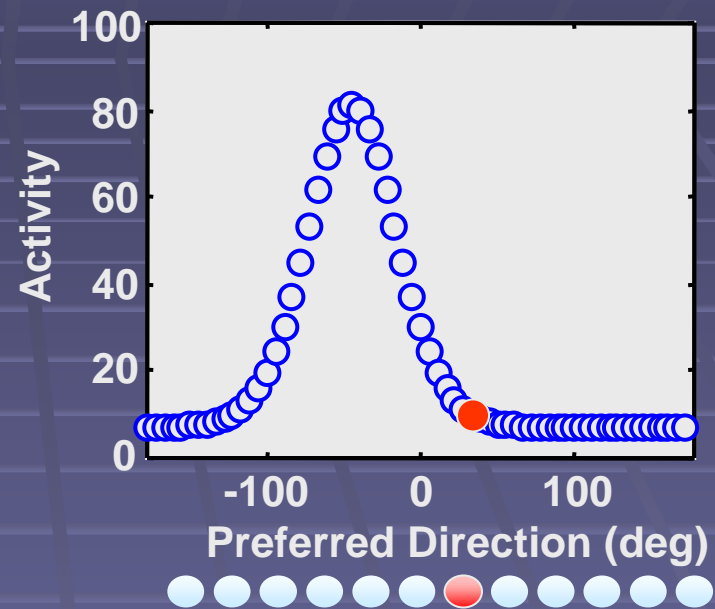
Tuning curves



Why “population coding”?



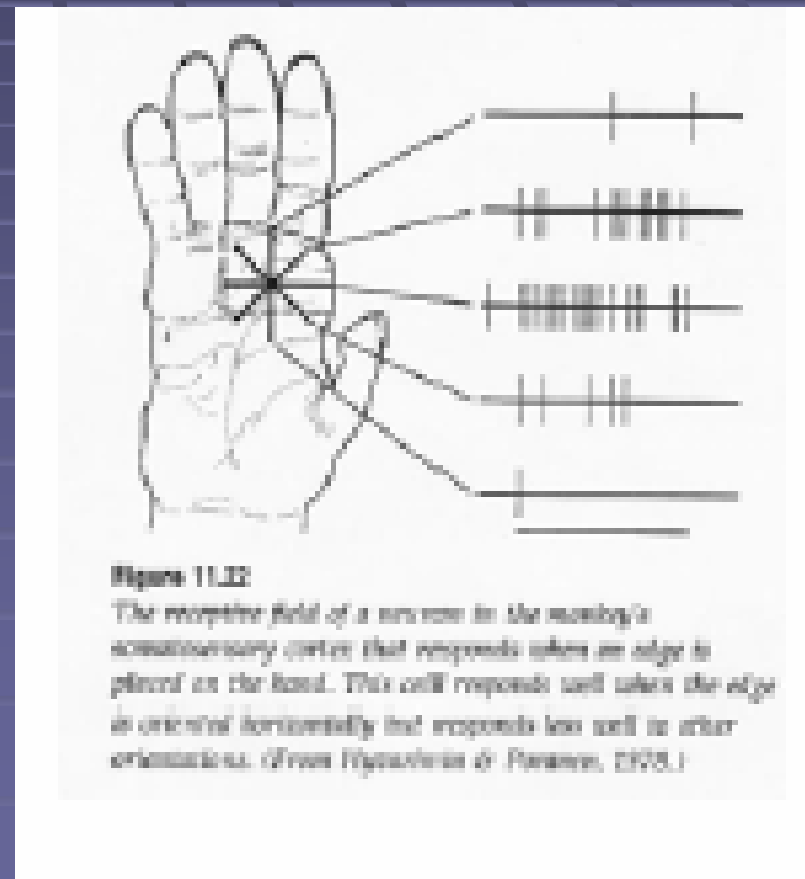
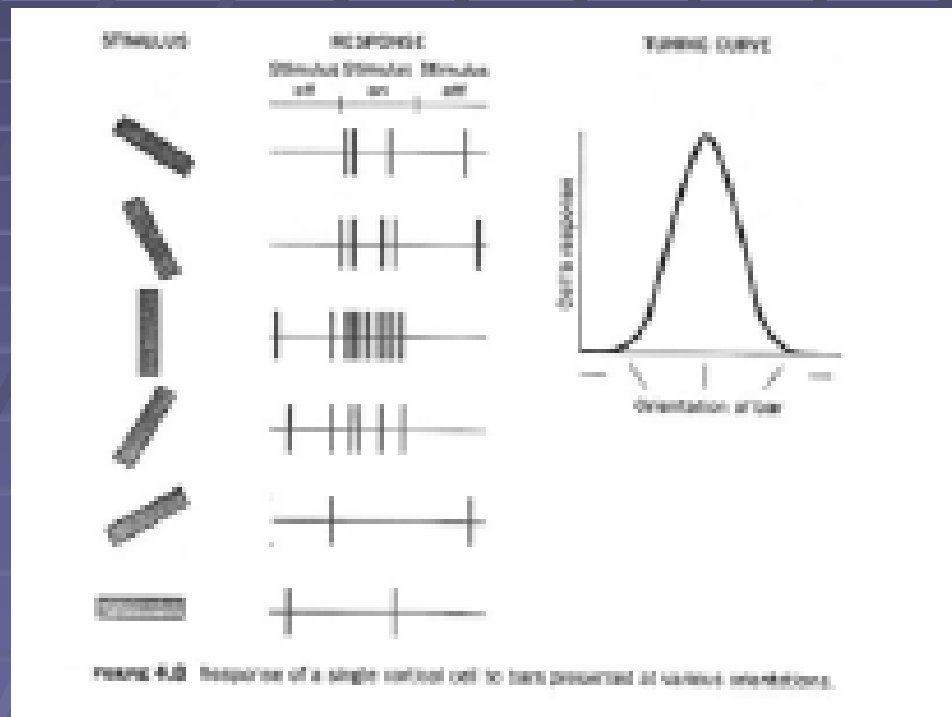
Tuning Curves



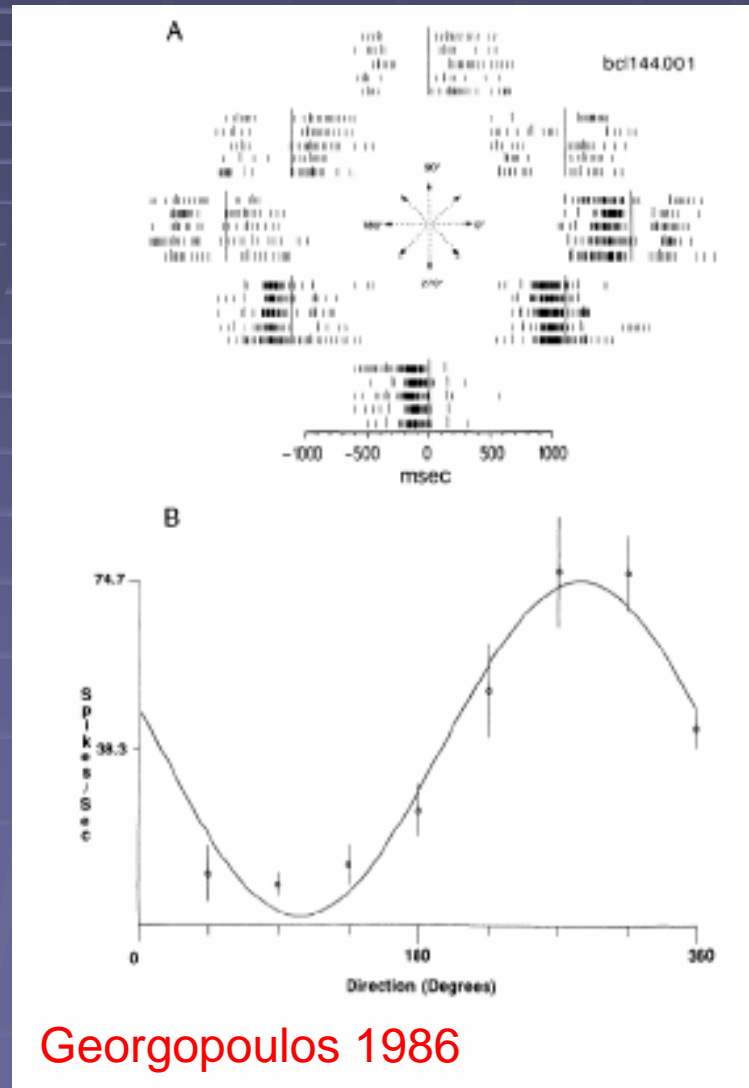
Average pattern of activity

$$\langle r_i \rangle = f(x - x_i) = f_i(x)$$

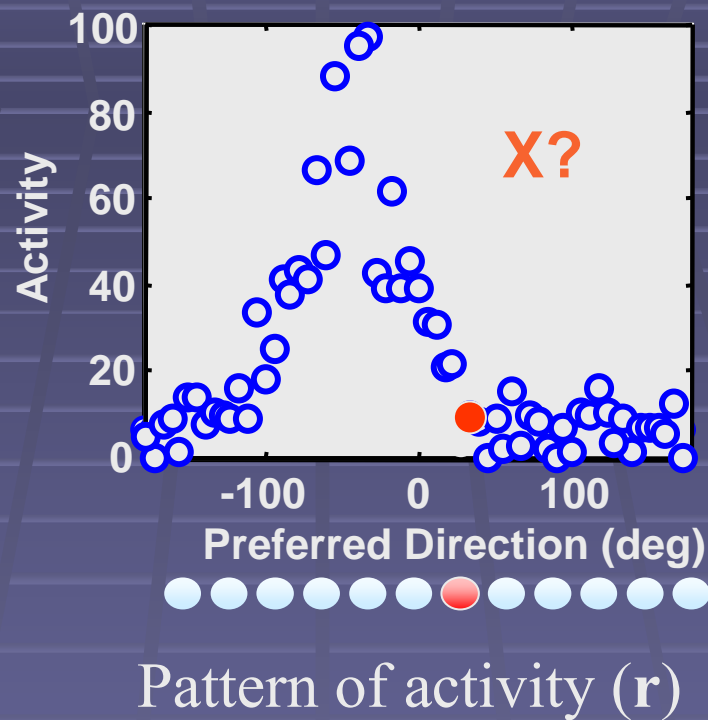
Examples of Population codes



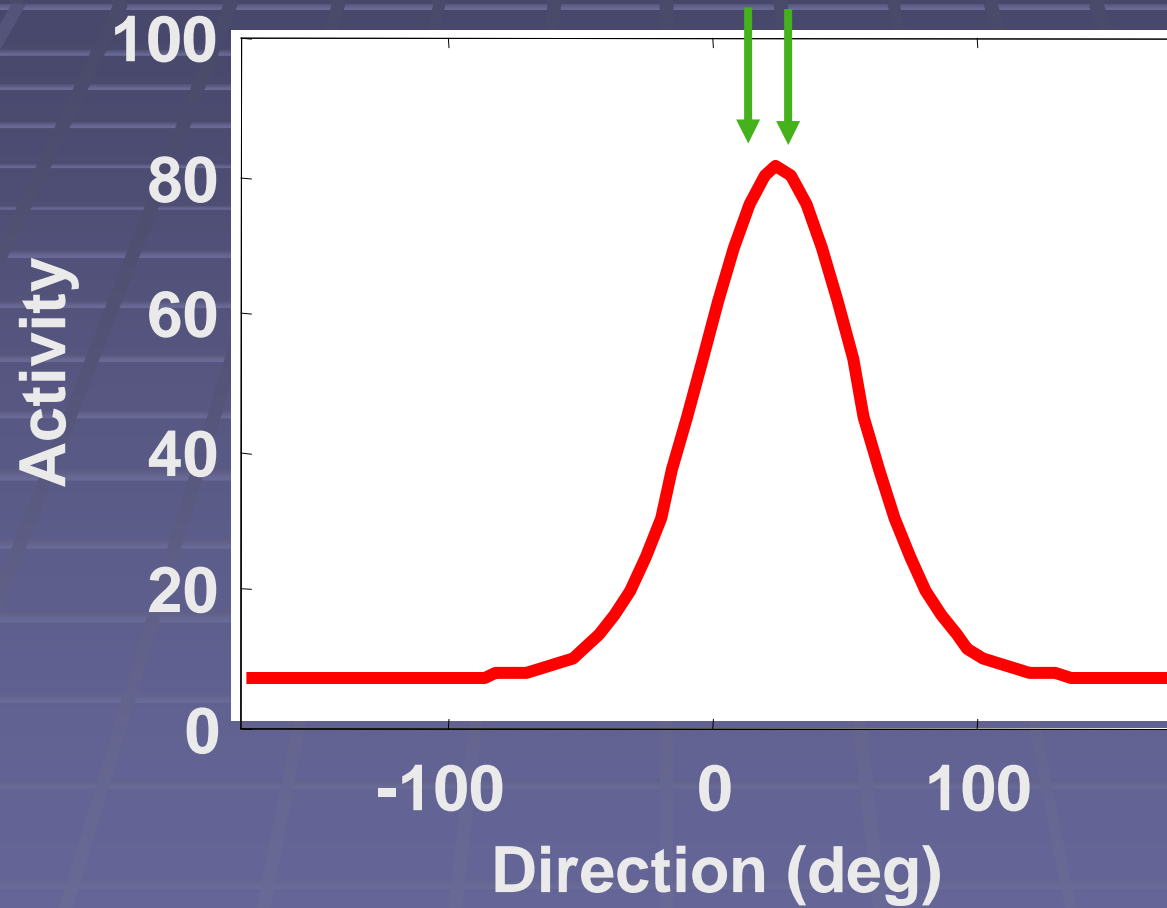
Examples of Population codes



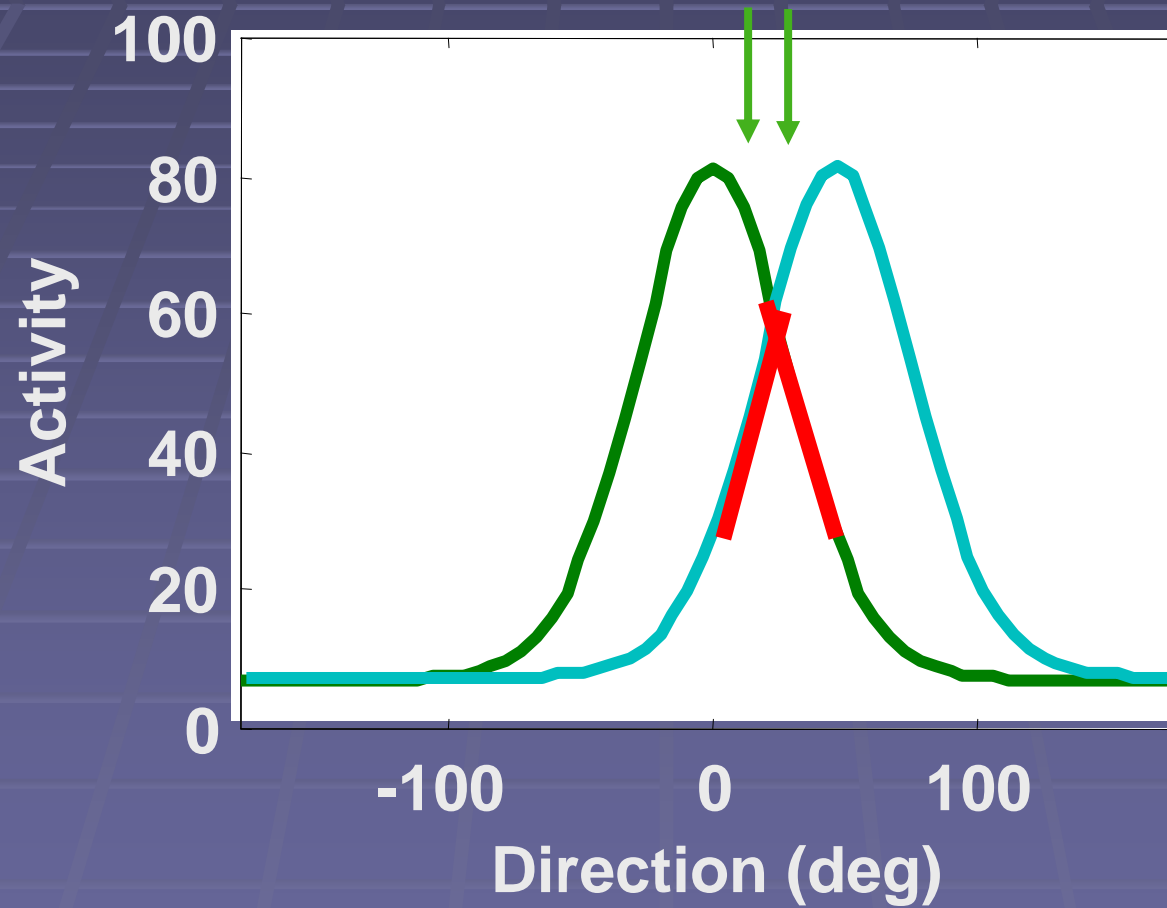
On a single trial: noisy population Code



How precisely can we read a noisy population code?

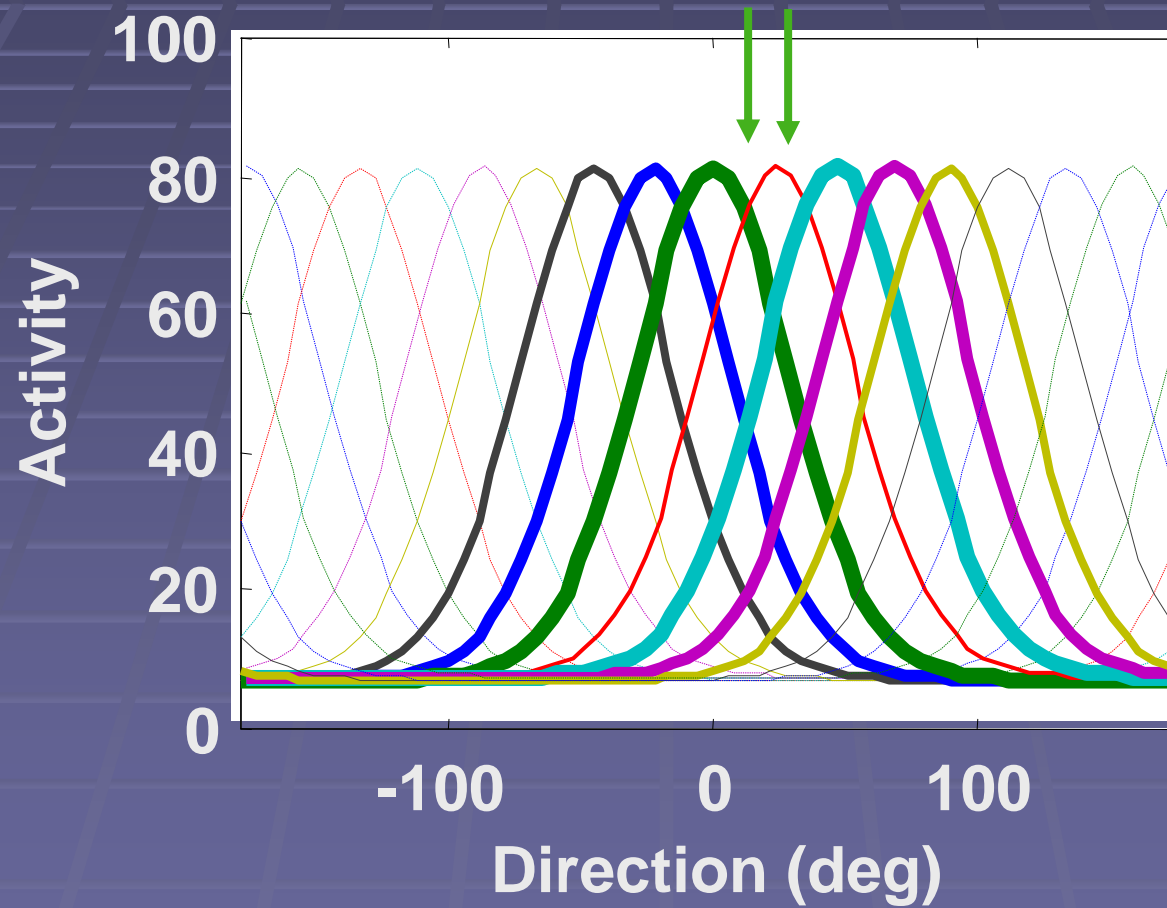


How precisely can we read a noisy population code?



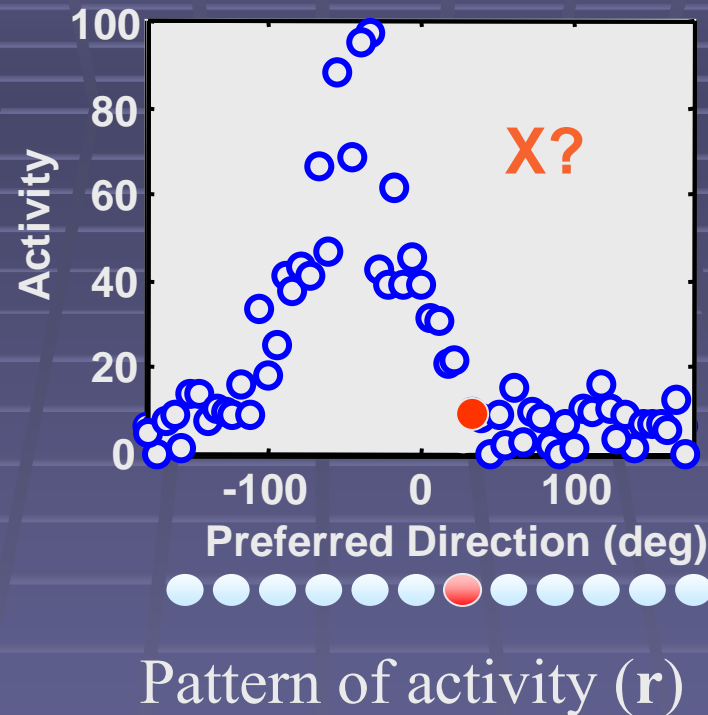
The higher the slope, the better

How precisely can we read a noisy population code?



The more neuron, the better

Fisher information quantifies the performance of the best possible estimator (ideal observer)



$$\sigma^2 = \left\langle (x - \hat{x})^2 \right\rangle = \frac{1}{I(x)}$$

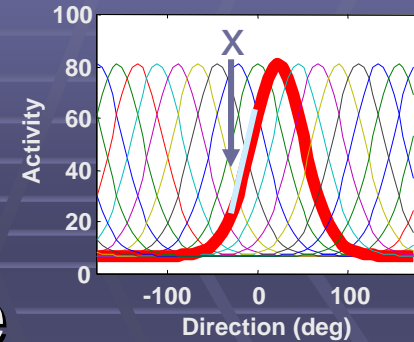
Fisher Information

- For one neuron with Poisson noise

$$I_i(x) = \frac{f'_i(x)^2}{f_i(x)}$$

Derivative of the tuning curve

Tuning curve (mean activity)



- For n independent neurons :

$$I(x) = \sum_i \frac{f'_i(x)^2}{f_i(x)}$$

Large slope is good!

The more neurons, the better!

Small variance is good!

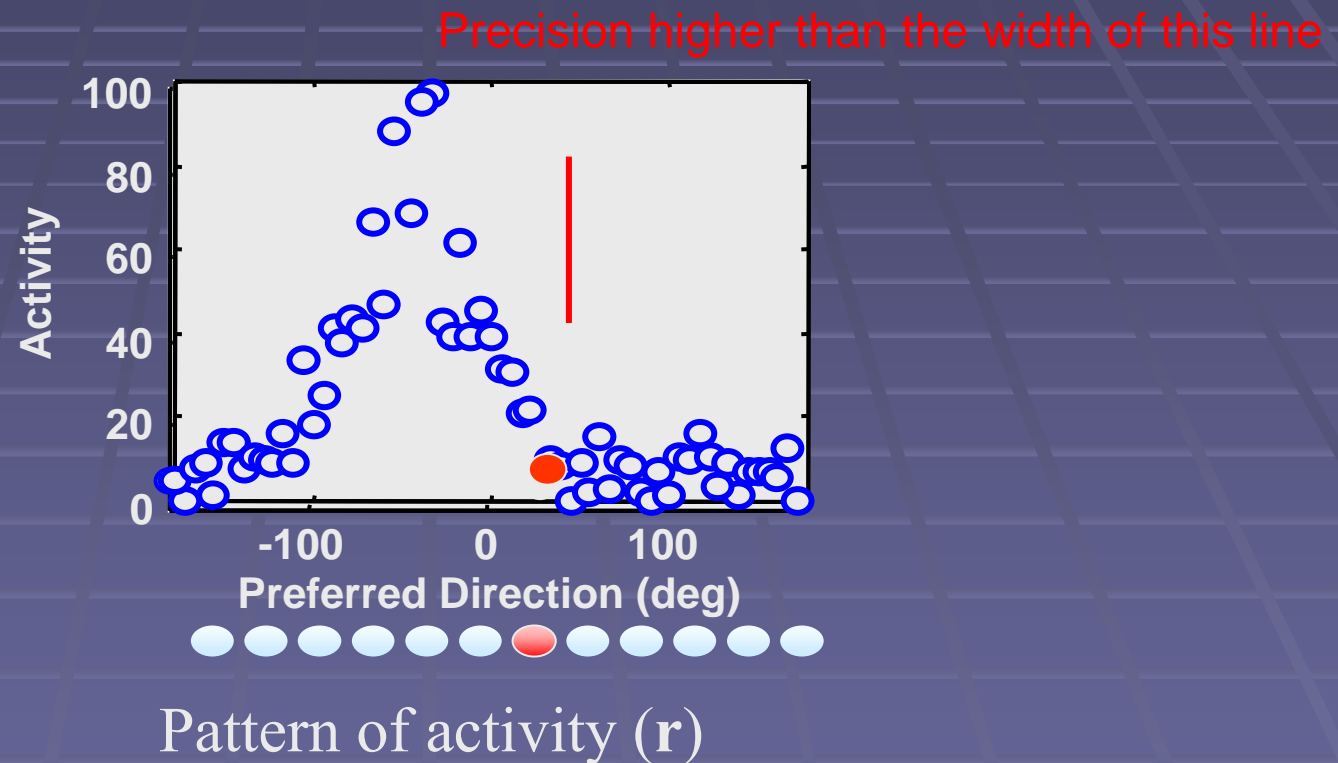
Variance of the best possible estimator (an ideal observer)

- Population of neuron with independent Poisson noise:

$$\sigma_{ML}^2 = \left\langle (x - \hat{x}_{ML})^2 \right\rangle = \frac{1}{\sum_i \frac{f_i'^2}{f_i}}$$

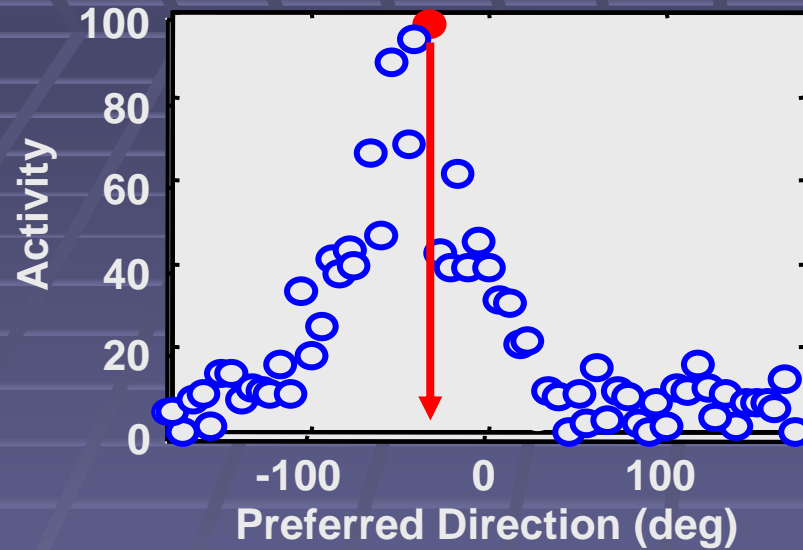
Can the brain reach such a level of performance?

Implication: very high precision with very noisy neurons

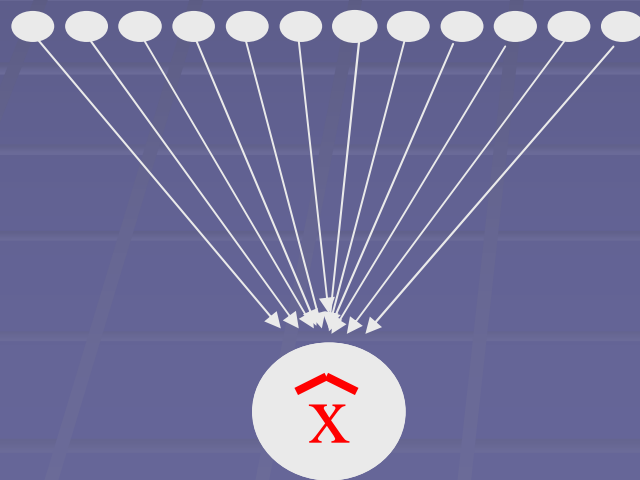


Hyper-acuity: usually the precision is much better than the distance between two adjacent neuron's preferred x

What estimator does the brain use?

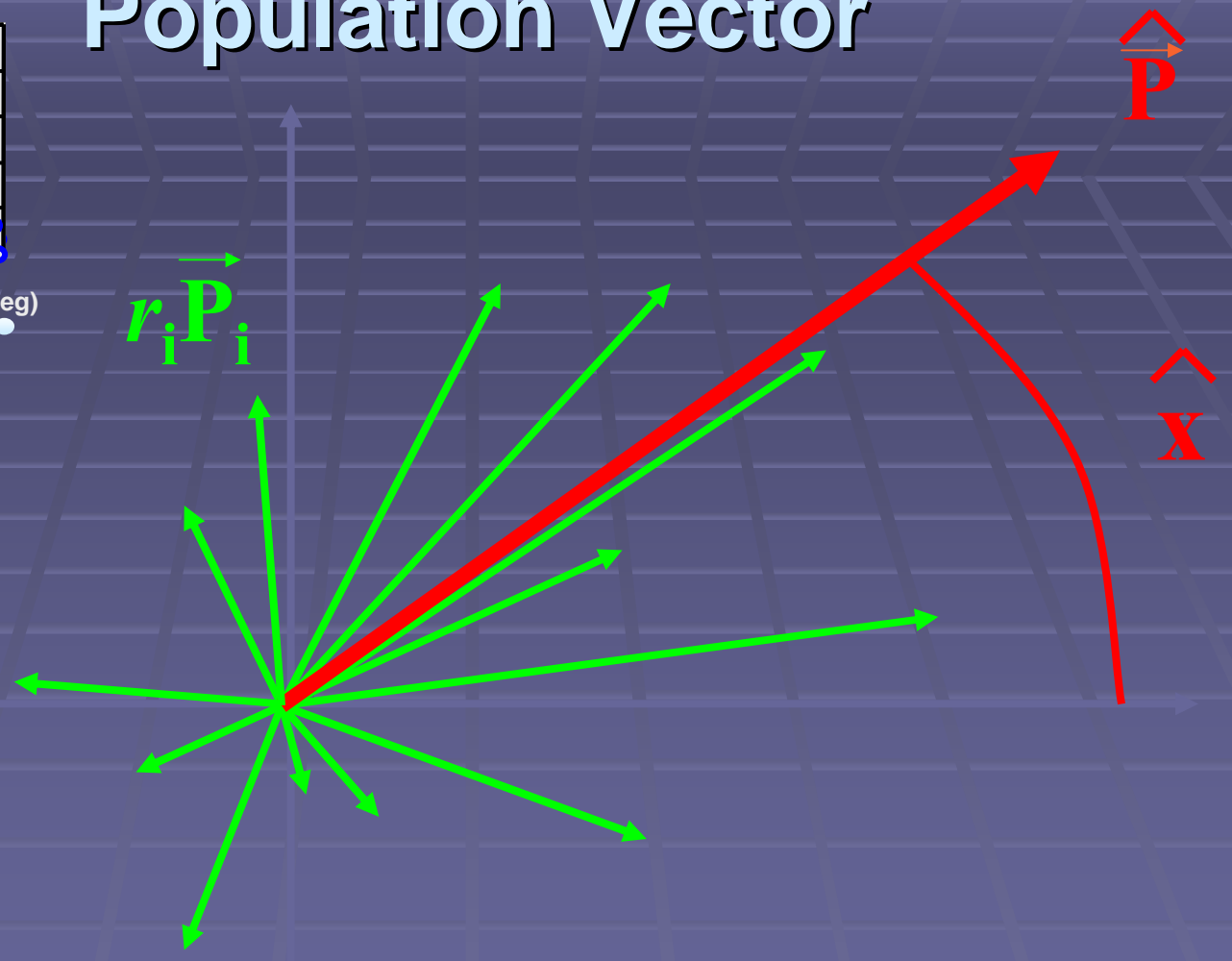
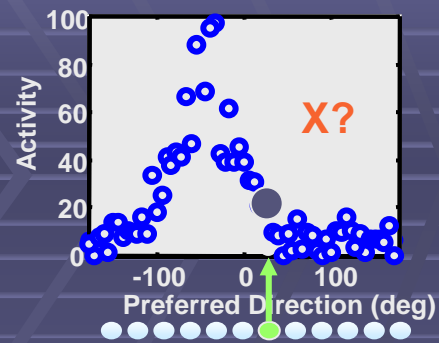


Maximally active unit: terrible!



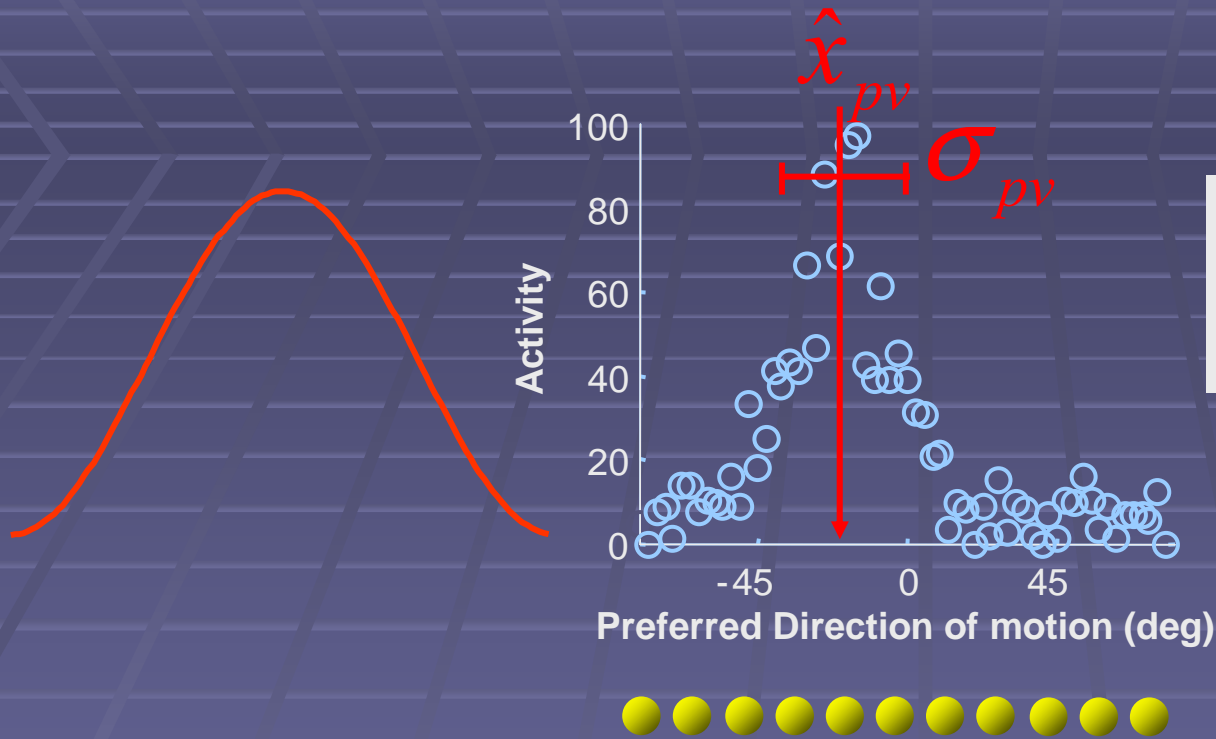
Linear estimator; not so good

Population Vector



Georgopoulos et al.

Maximum likelihood



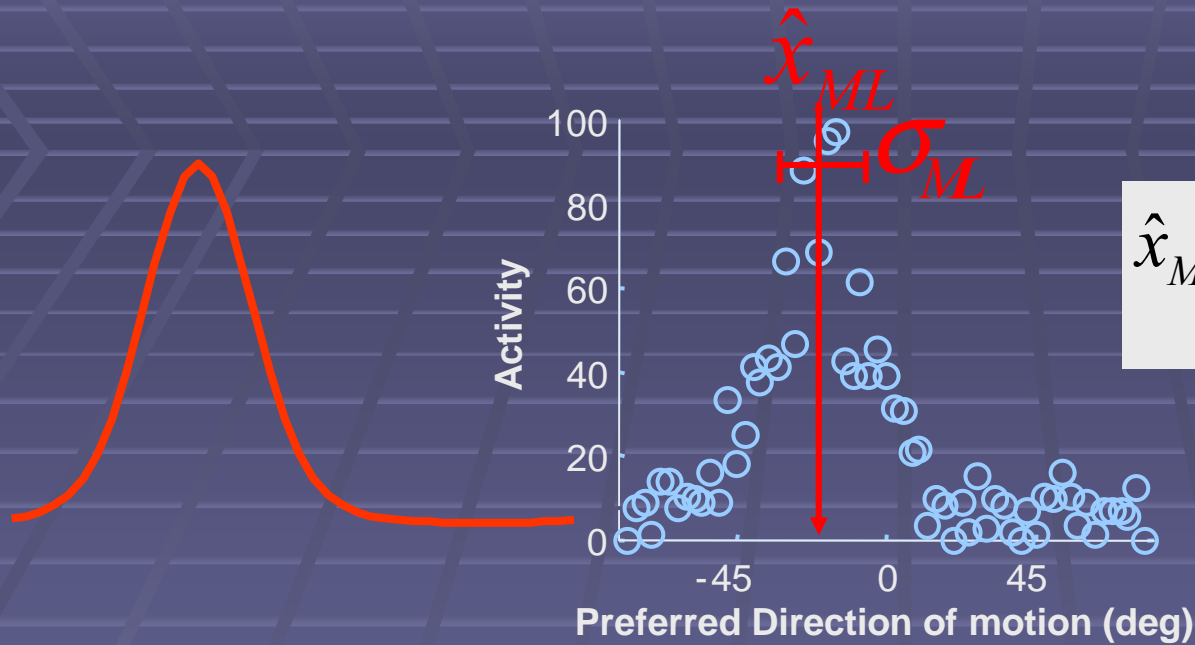
$$\hat{x}_{pv} = \text{angle} \left(\sum_i r_i \hat{P}_i \right)$$

$$\sigma_{pv}^2 = \left\langle \left(x - \hat{x}_{pv} \right)^2 \right\rangle = \frac{1}{I(x)}$$

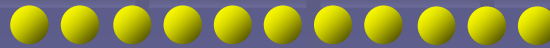
Maximum performance for an unbiased estimator

Fisher information

Maximum likelihood

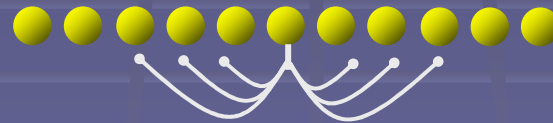
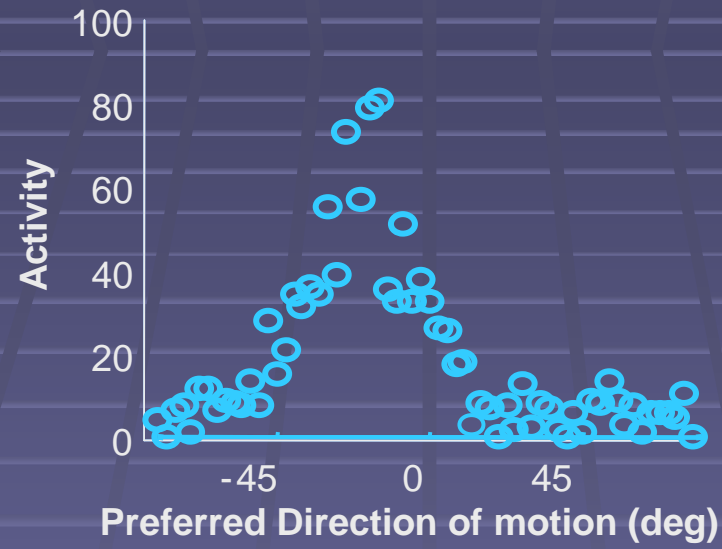


$$\hat{x}_{ML} = \arg \max_x (p(\mathbf{r} | x))$$

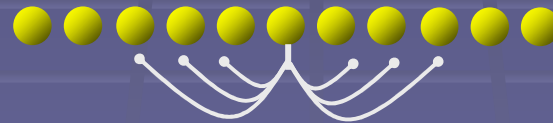
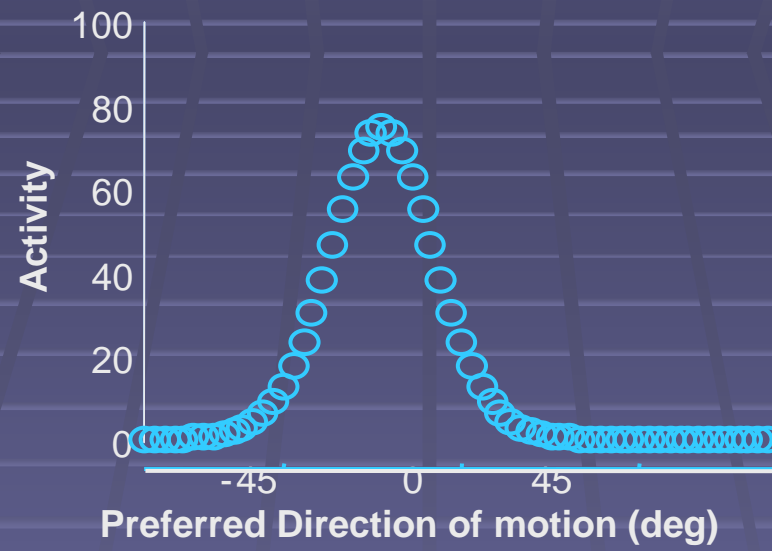


$$\sigma_{ML}^2 = \frac{1}{I(x)}$$

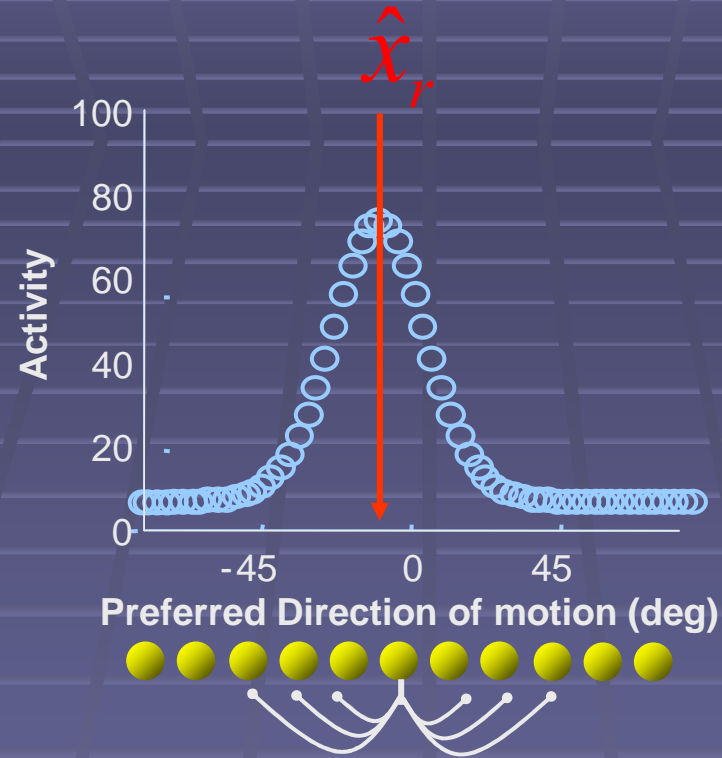
How to decode?



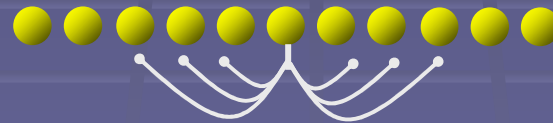
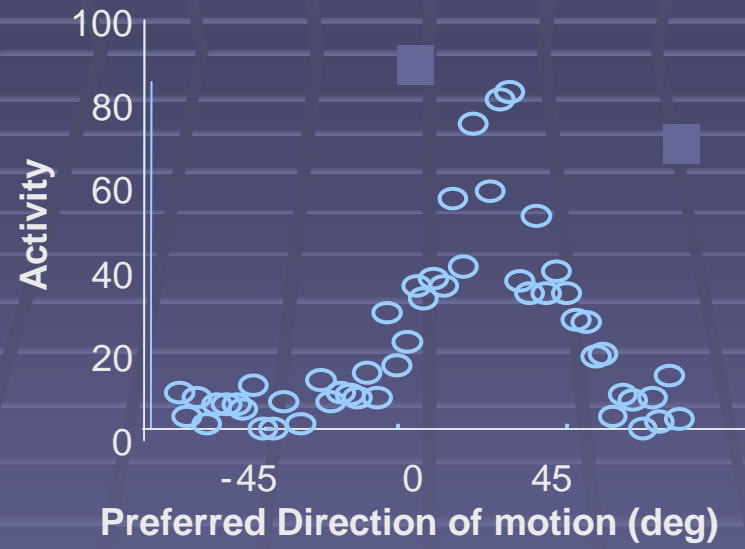
How to decode?



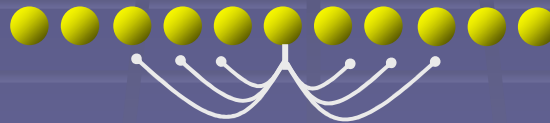
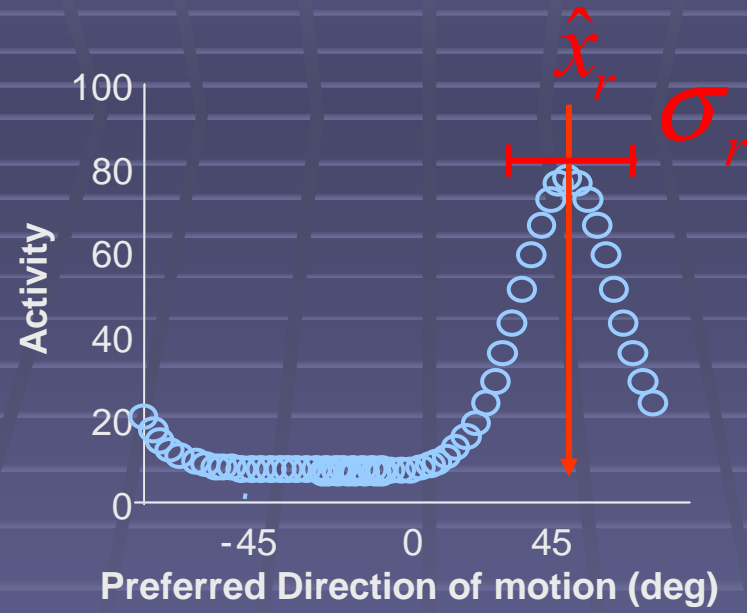
Recurrent network



How to decode?

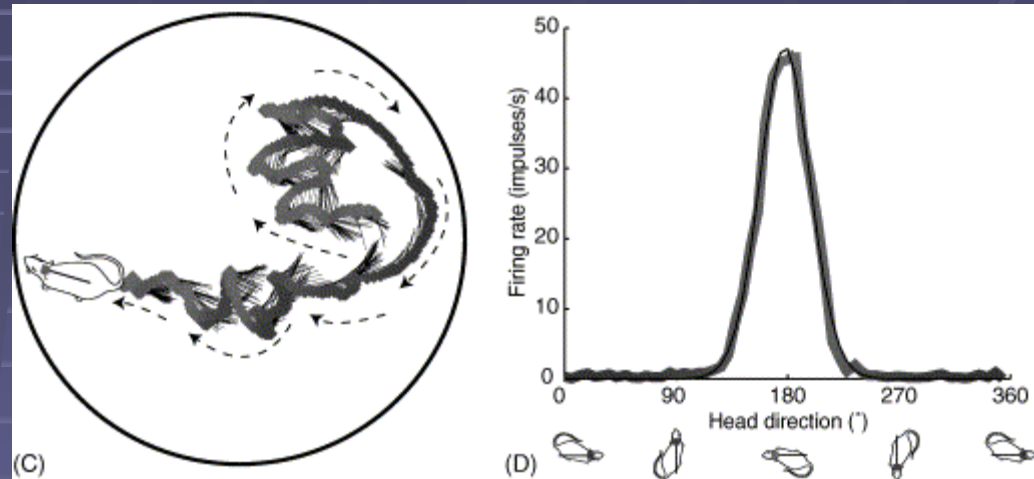


How to decode?

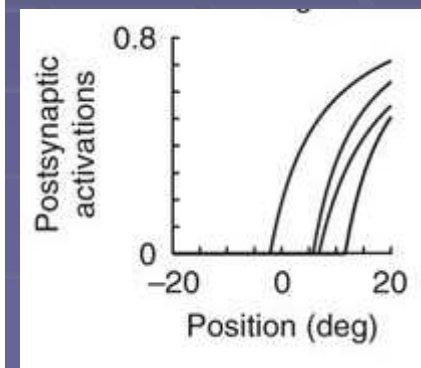
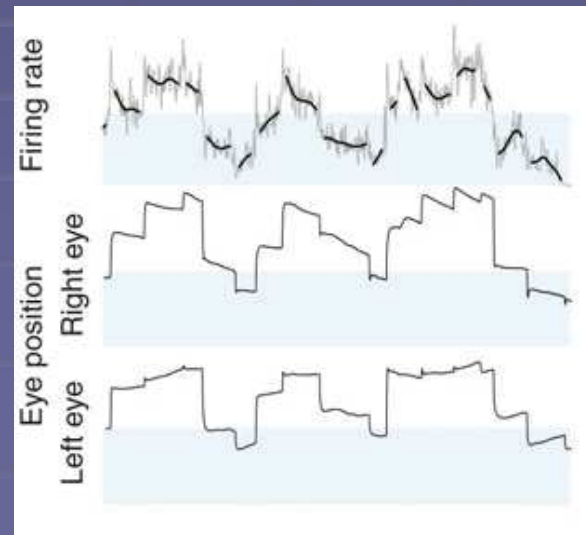


Exemple of line attractors

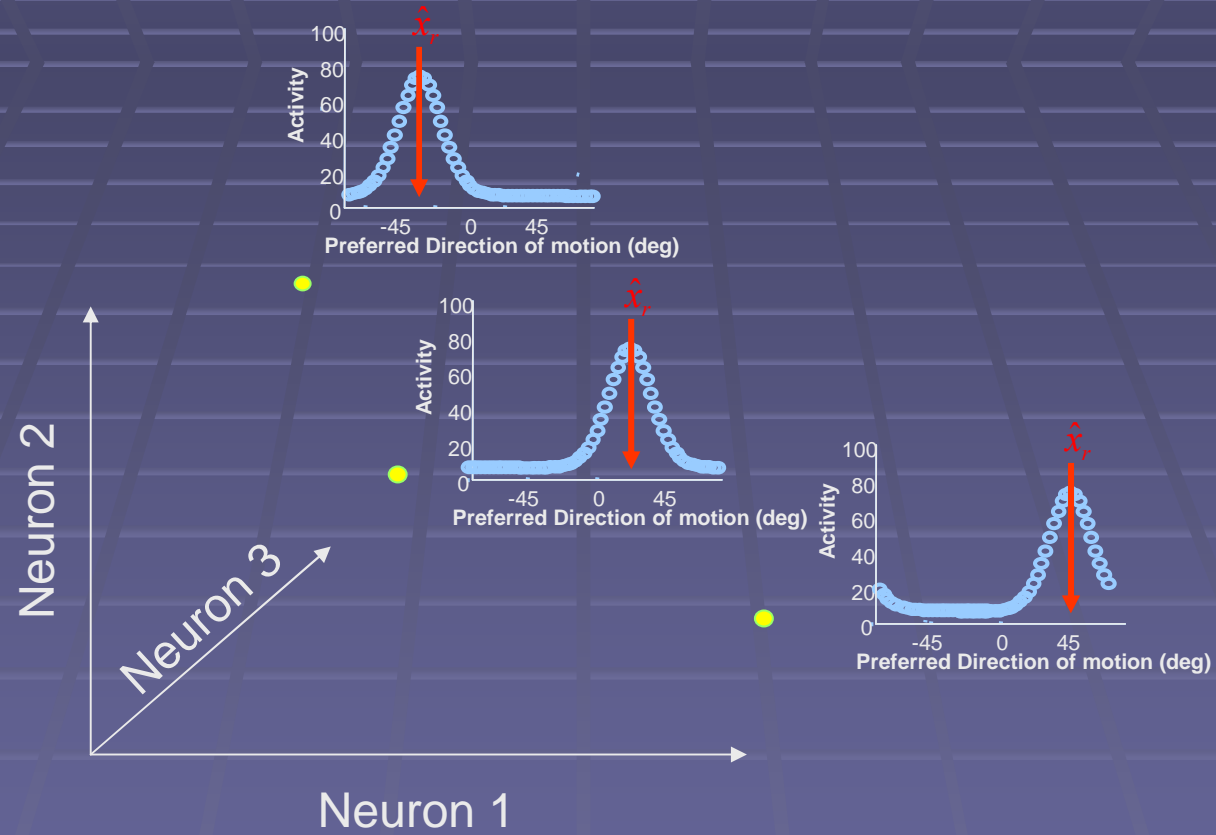
Head direction cells in the hippocampus



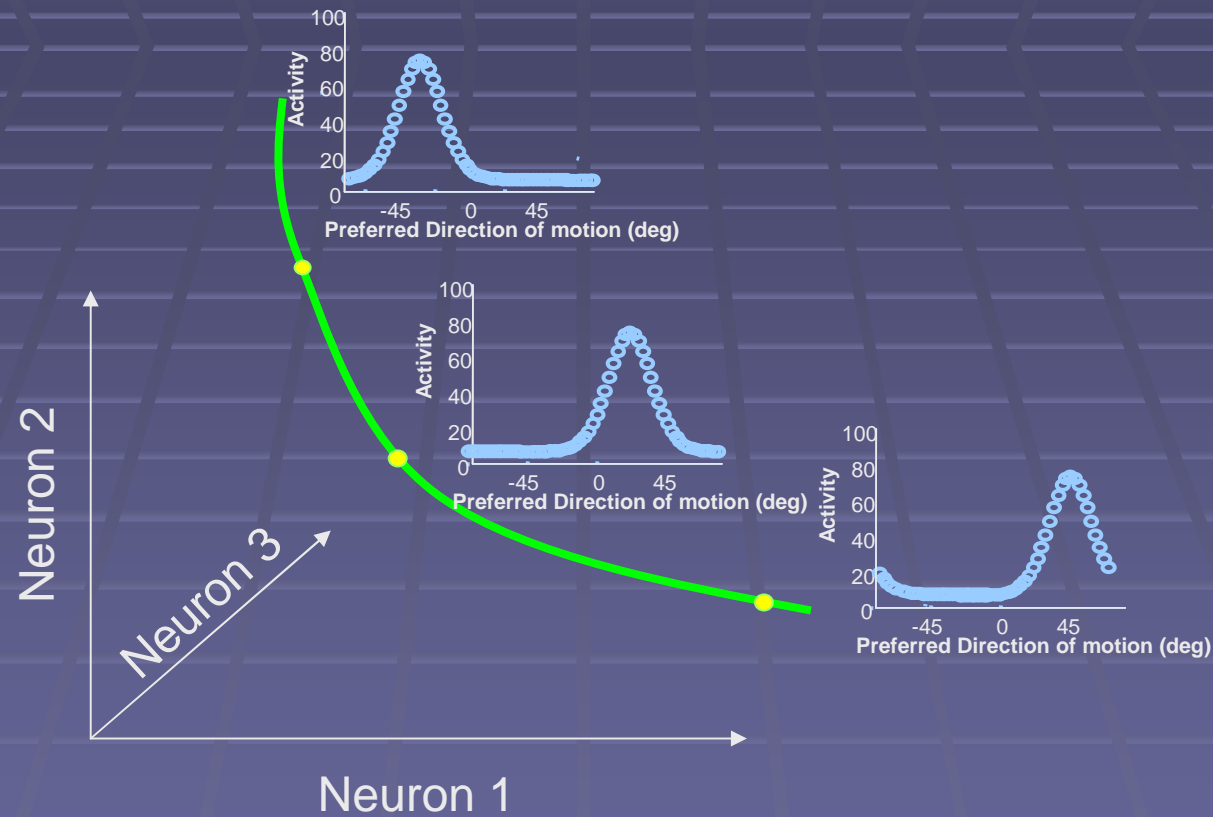
Oculomotor integrator:
Graded firing rate as a function of gaze angle



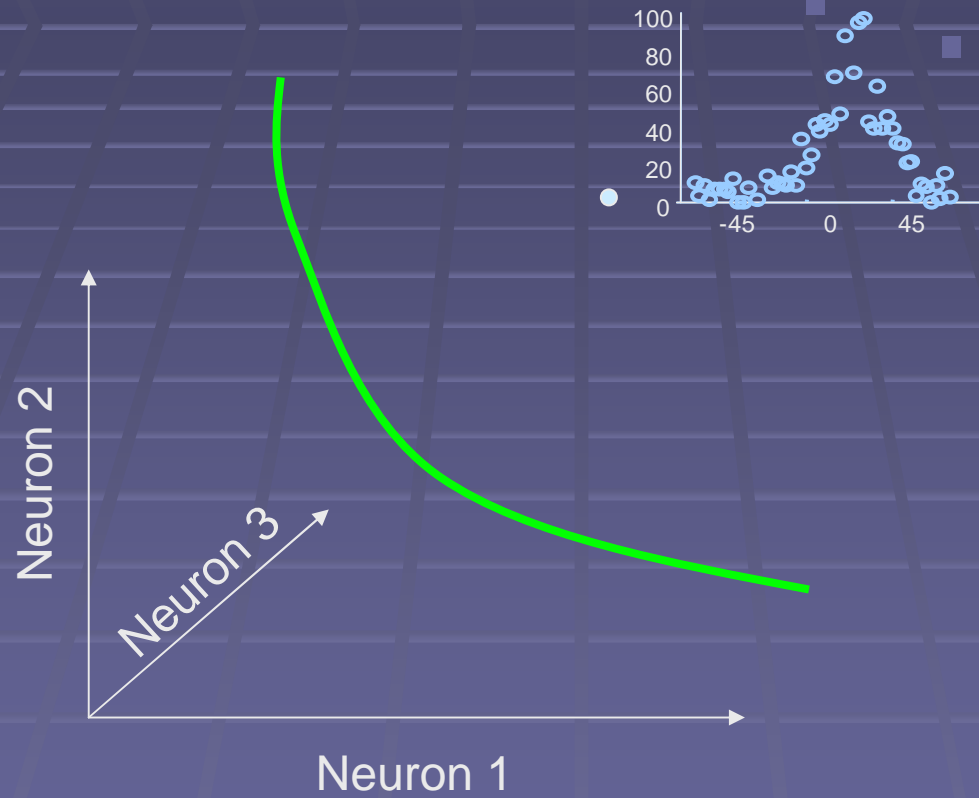
Line attractor networks



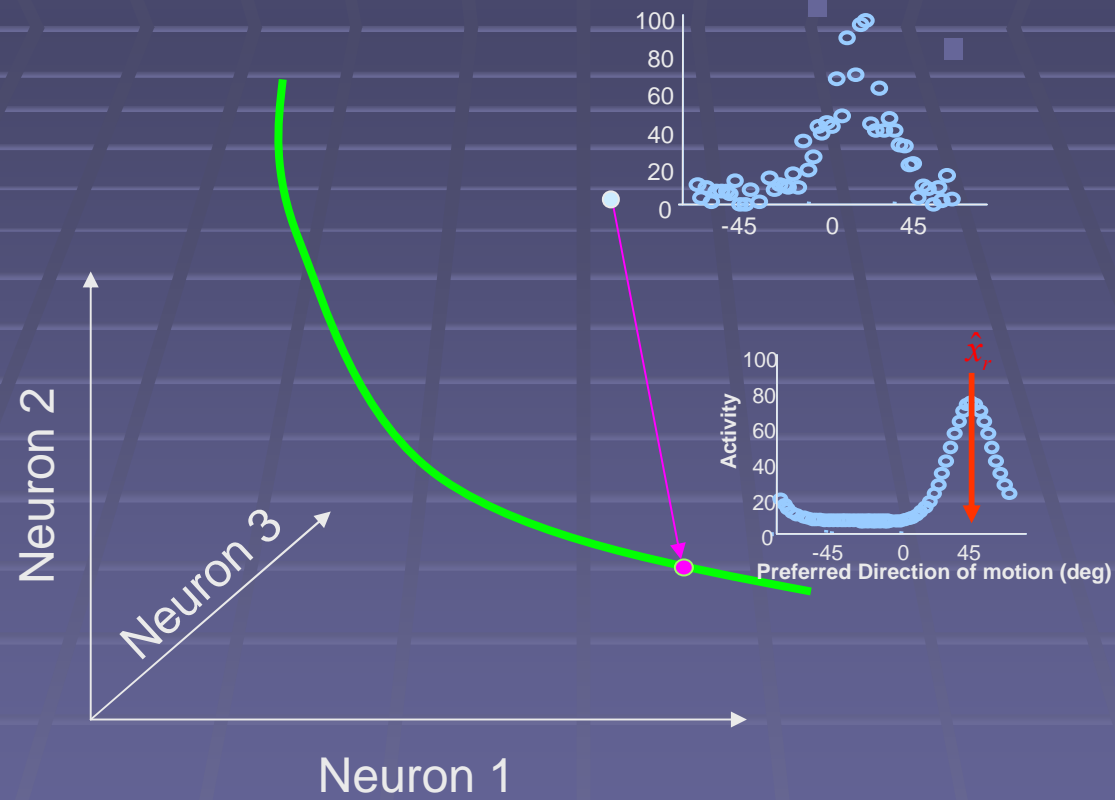
Line attractor networks



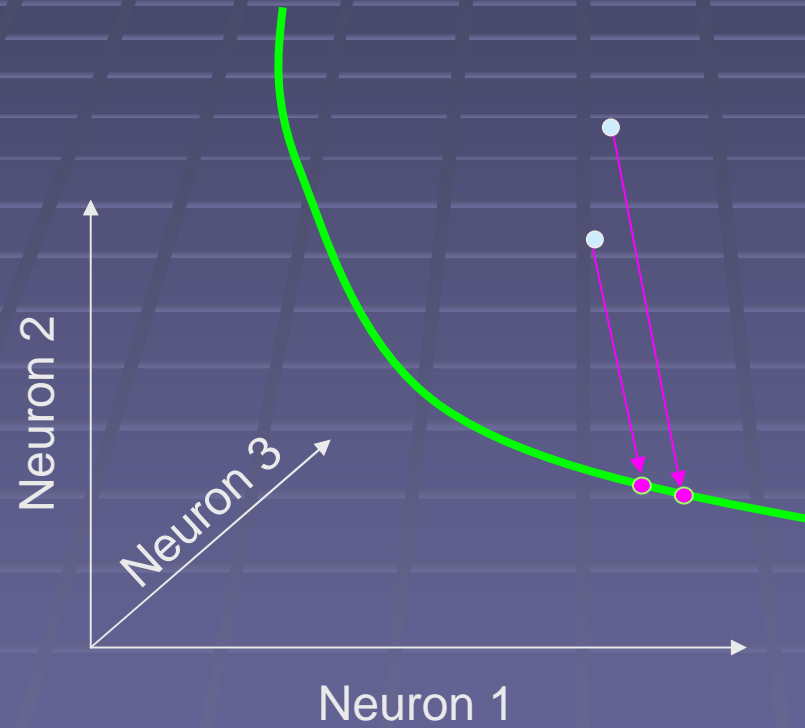
Line attractor networks



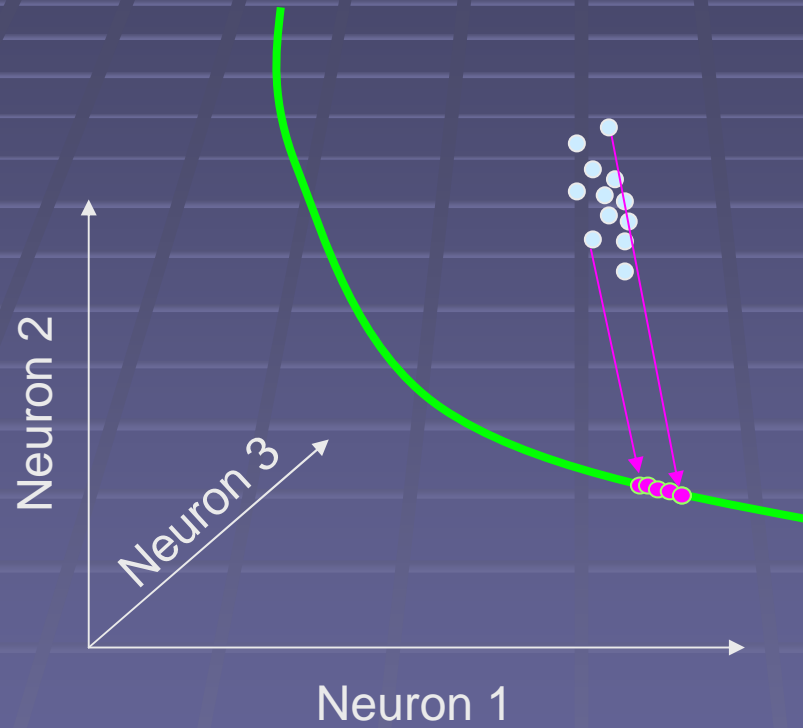
Line attractor networks



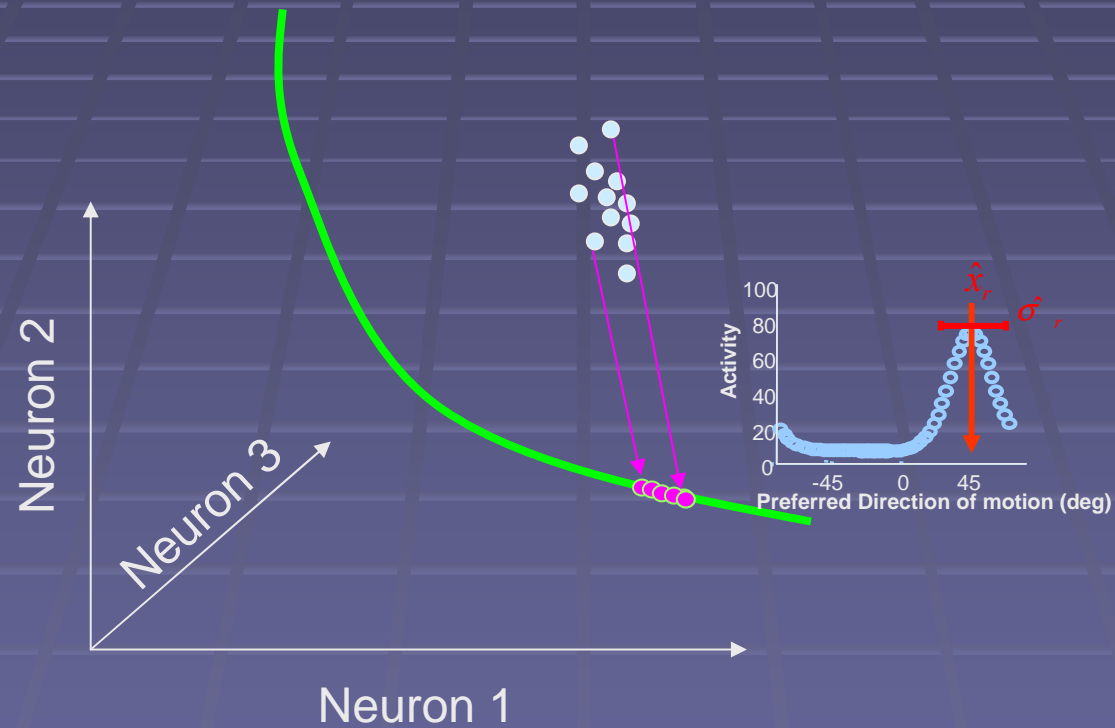
Line attractor networks



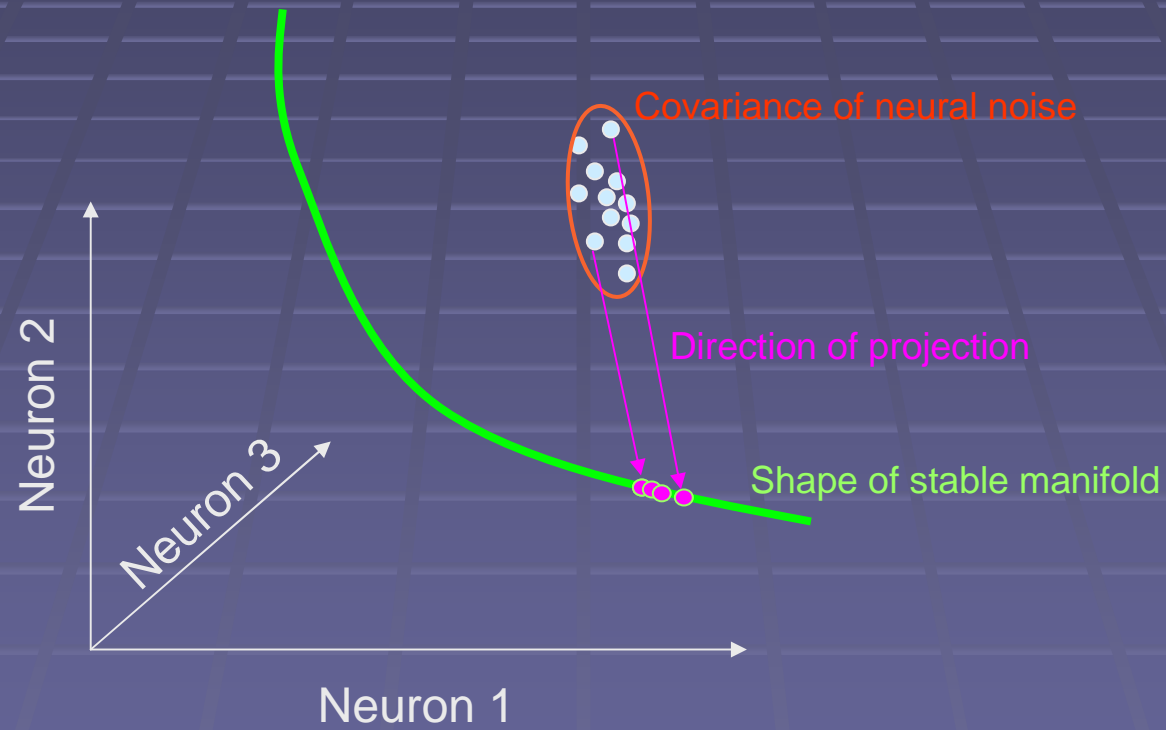
Line attractor networks



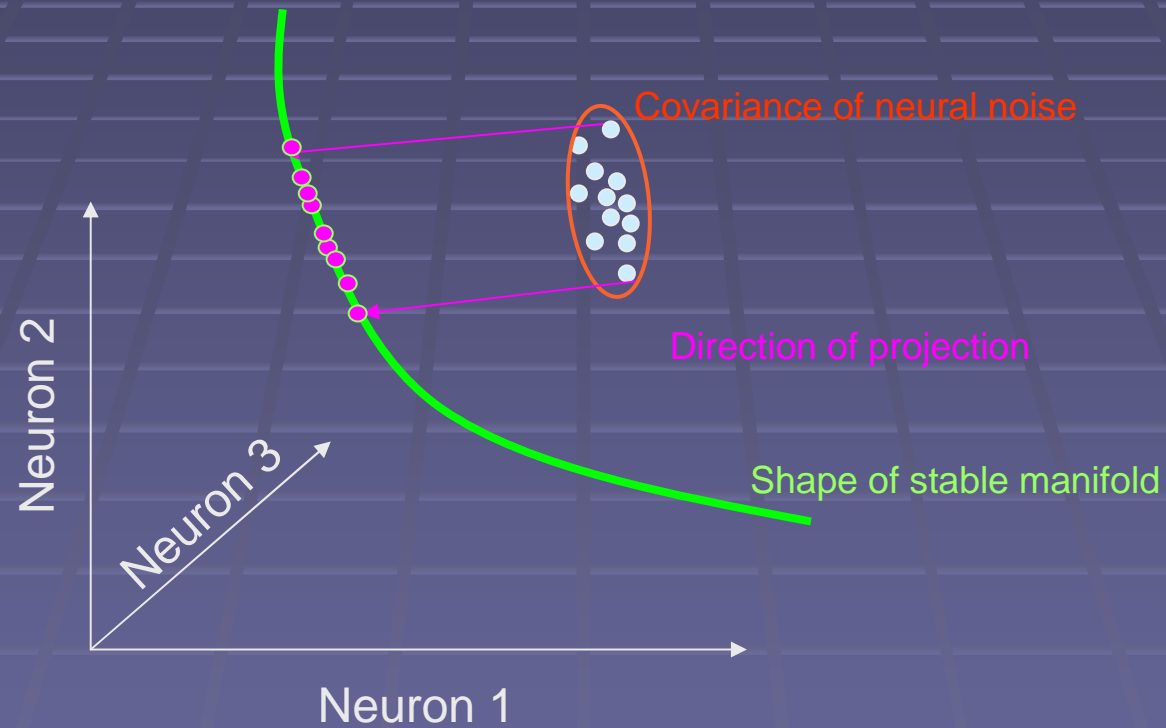
Line attractor networks



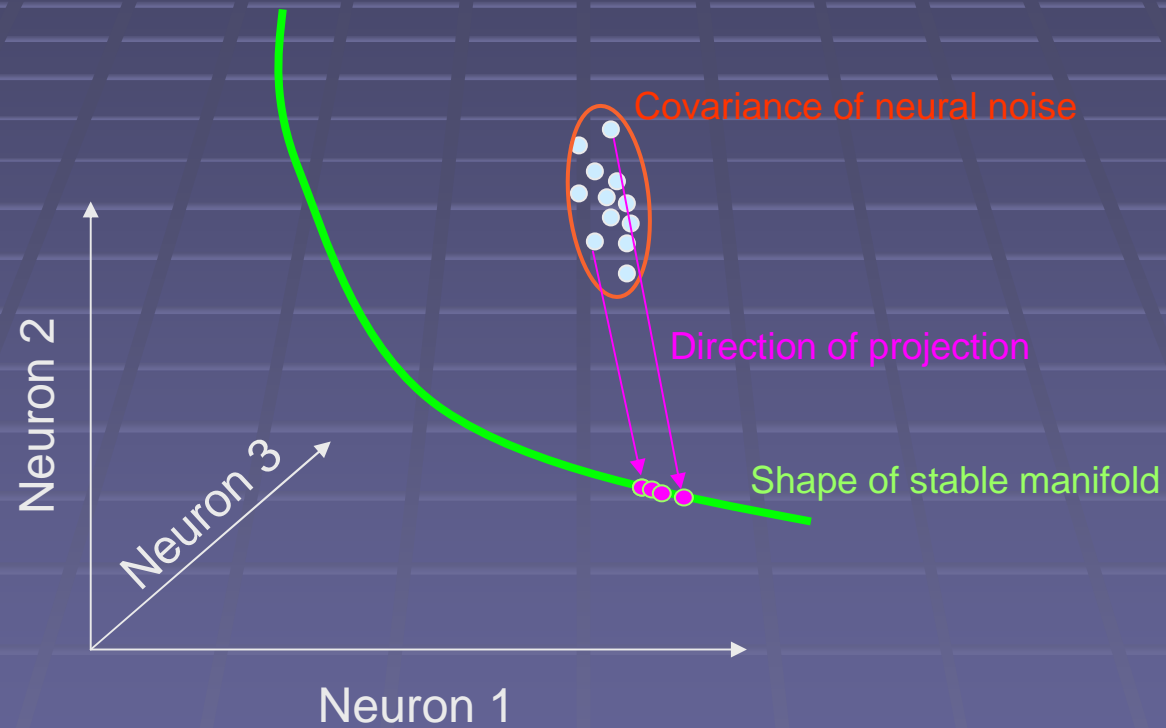
Line attractor networks



Line attractor networks



Line attractor networks



$$\Sigma^{-1} \frac{\partial \mathbf{r}^T}{\partial t} = \nu(W)$$

Conclusion

- Sensory and motor variables are represented with noisy population codes.
- It is possible to compute the precision of these codes. It is the inverse of the Fisher information, a function the slope of the tuning curve, the neural noise, and the number of neurons.
- But this information is difficult to get. The most often used methods (linear estimator, population vectors) are not optimal. They are not ideal observers.
- The best one can do is find the variable that maximize the probability of the neural response, the maximum likelihood estimator.
- The maximum likelihood estimate can be recovered by a line attractor network.

Problems...

- Persistent Line attractors are rare. There is no trace of them in purely sensory areas.
- Neurons are never noiseless. The smooth stable state does not exist.
- There is no time to converge in the real world.
- How is the attractor reset or updated by new inputs?