Probabilistic Population Codes in Cortex

Computational Models of Neural Systems

Lecture 7.2

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Probability: Bayes' Rule

We want to know if a patient has disease d. Test them.

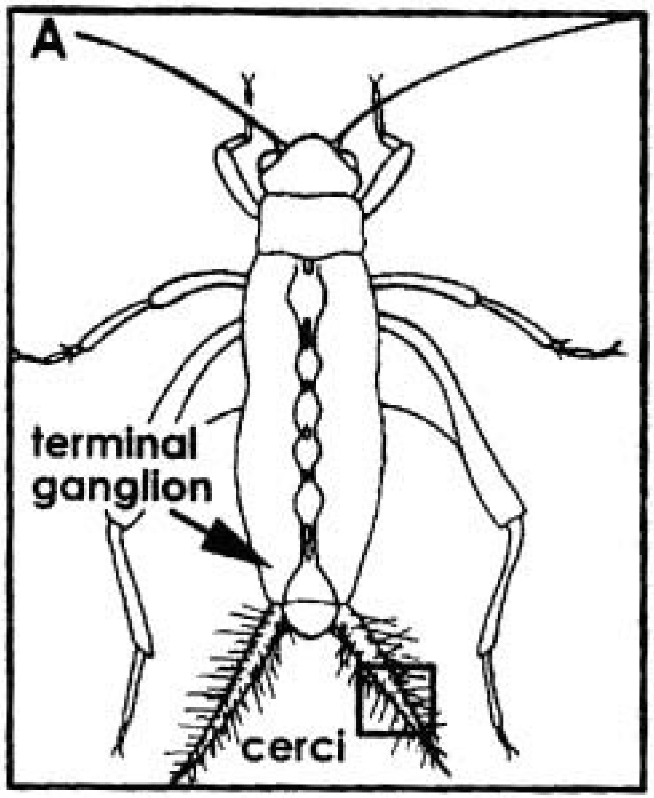
They test positive. What conclusion should we draw?

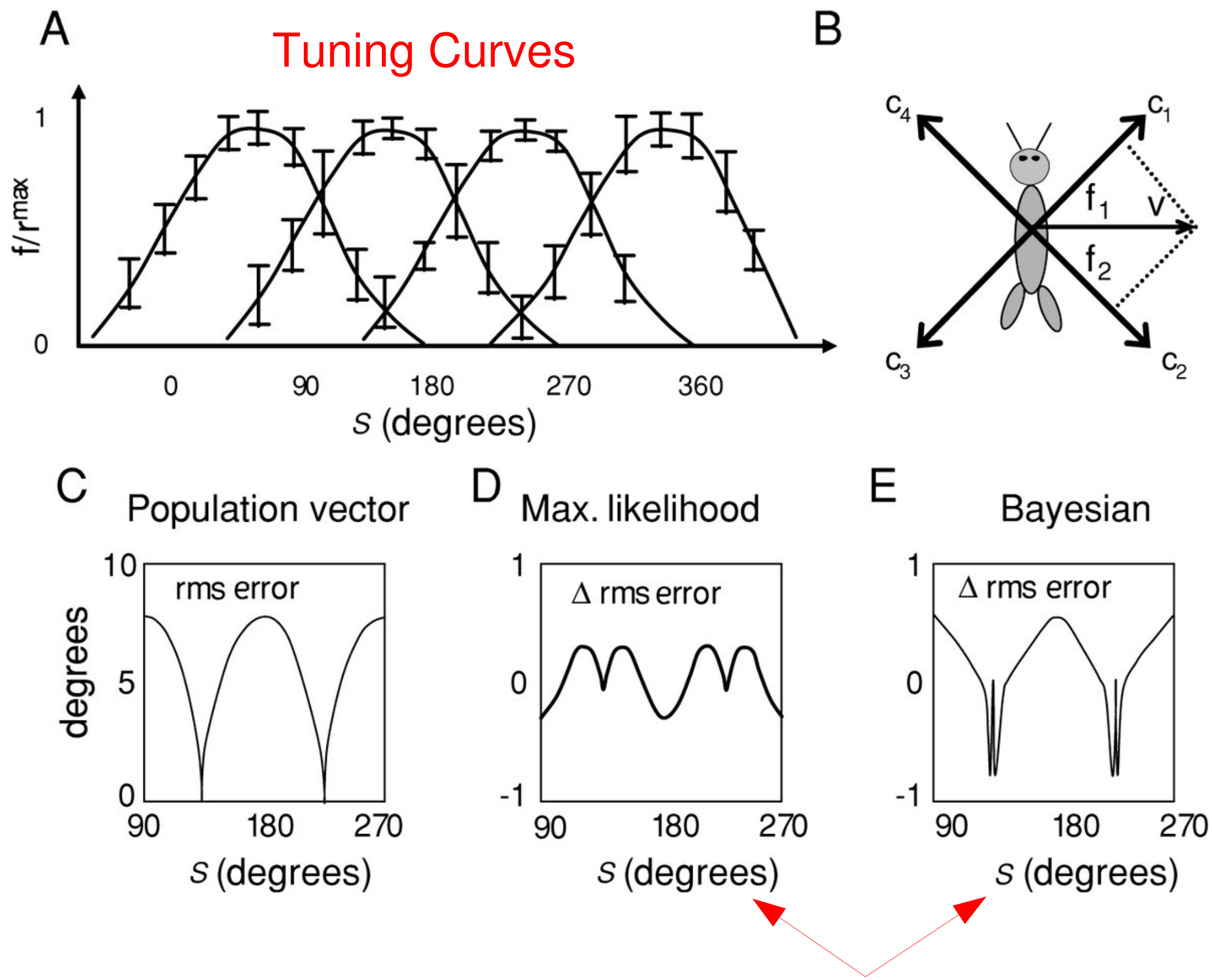
- P(d) *prior* has the disease
- P(t&d) *joint* tests positive *and* has the disease
- P(t|d) *likelihood* tests positive *given* has the disease
- P(d|t) *posterior* has disease *given* test is positive
- P(t) *evidence* test is positive (aka “marginal likelihood”)

Bayes' Rule:

$$P(d|t) = \frac{P(d \,\&\, t)}{P(t)} = \frac{P(t|d) \cdot P(d)}{P(t)}$$

Cricket Cercal System Encodes Wind Direction Using Four Sensory Neurons





Max firing rate ~ 40 Hz; baseline 5 Hz. Assume a Poisson spike rate distribution. Bayesian method gives lowest total decoding error.

Population Vector

- Term introduced by Georgopoulos to describe a method of decoding reaching direction in motor cortex.
- Given a set of neurons with preferred direction unit vectors v_i and firing rates r_i, compute the direction V encoded by the population as a whole.
- Solution: weight each preferred direction vector by its normalized firing rate r_i/r_{max}.

$$\vec{V} = \frac{1}{N}\sum_{i=1}^{N} \frac{r_i}{r_{max}} \cdot \vec{v}_i$$

- This is a simple decoding method, but not optimal when neurons are noisy.

Maximum Likelihood Estimator

- MLE uses information about the spike rate distribution to decide how likely is a population spike rate vector **r** given stimulus value *s*. For a Poisson spike rate distribution, where r_i is the spike count for true firing rate f_i:

$$P[\boldsymbol{r}|s] = \prod_{i=1}^{N} \exp[-f_i(s)\Delta t] \cdot (f_i(s)\Delta t)^{r_i \Delta t} \frac{1}{(r_i \Delta t)!}$$

- We can then use Bayes' rule to assign a probability to each possible stimulus value. Assume that all stimulus values are equally likely. Then:

$$P[s|\boldsymbol{r}] \approx \frac{P[\boldsymbol{r}|s]}{P[\boldsymbol{r}]}$$

Bayesian Estimator

- If we know something about the distribution of stimulus values P[s], we can use this information to derive an even better estimate of the stimulus value.
- For example: the cricket may know that not all wind direction values are equally likely, given the behavior of its predators.
- From Bayes' rule:

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

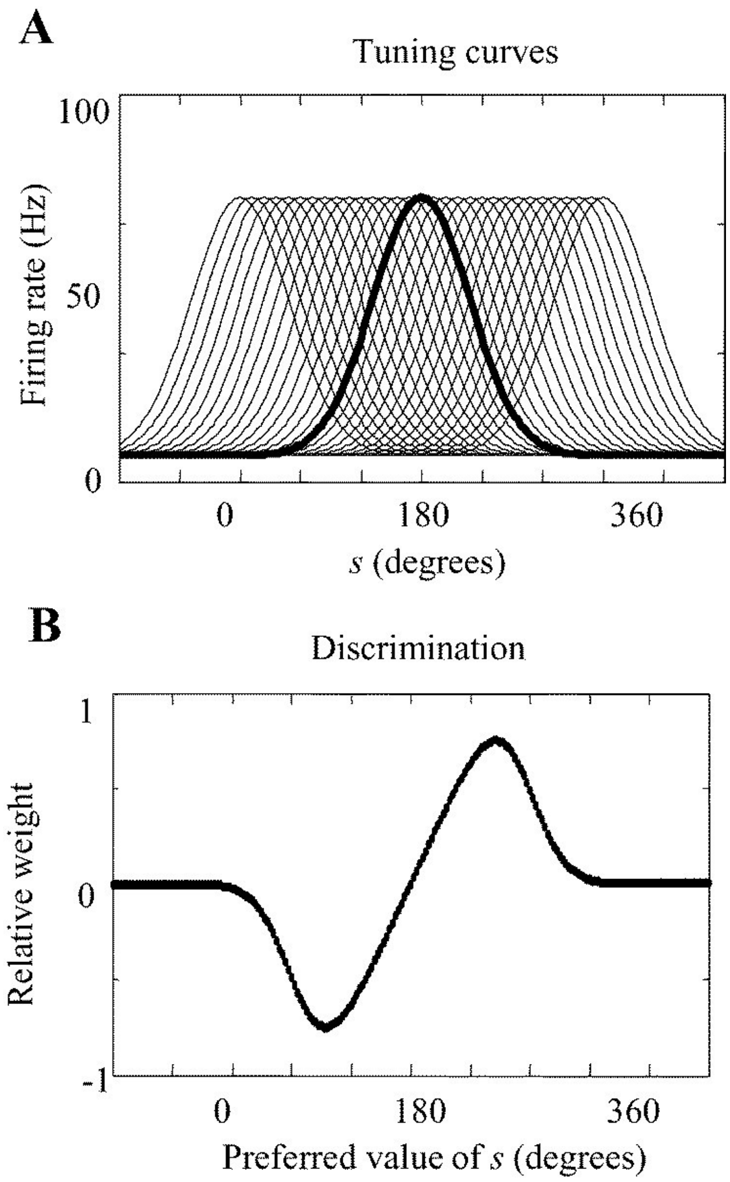
Homogeneous Population Code for Orientation in V1

- Gaussian tuning curves with σ = 15°. Baseline firing rate = 5 Hz.

- Optimal linear decoder weights to discriminate a stimulus s* – δs from a stimulus s* + δs, where s* = 180°. Note that the weight on the unit coding for 180° is zero.

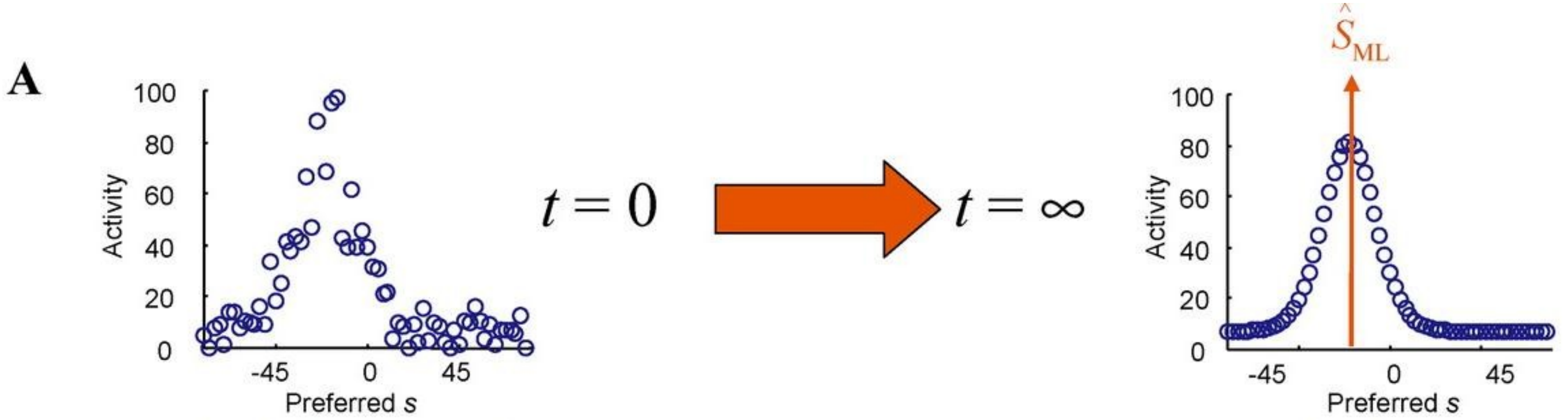
$$t(\boldsymbol{r}) = \sum_i r_i w_i$$

If t(**r**) > 0 conclude that stimulus > s.



Cleaning Up Noise With Recurrent Connections

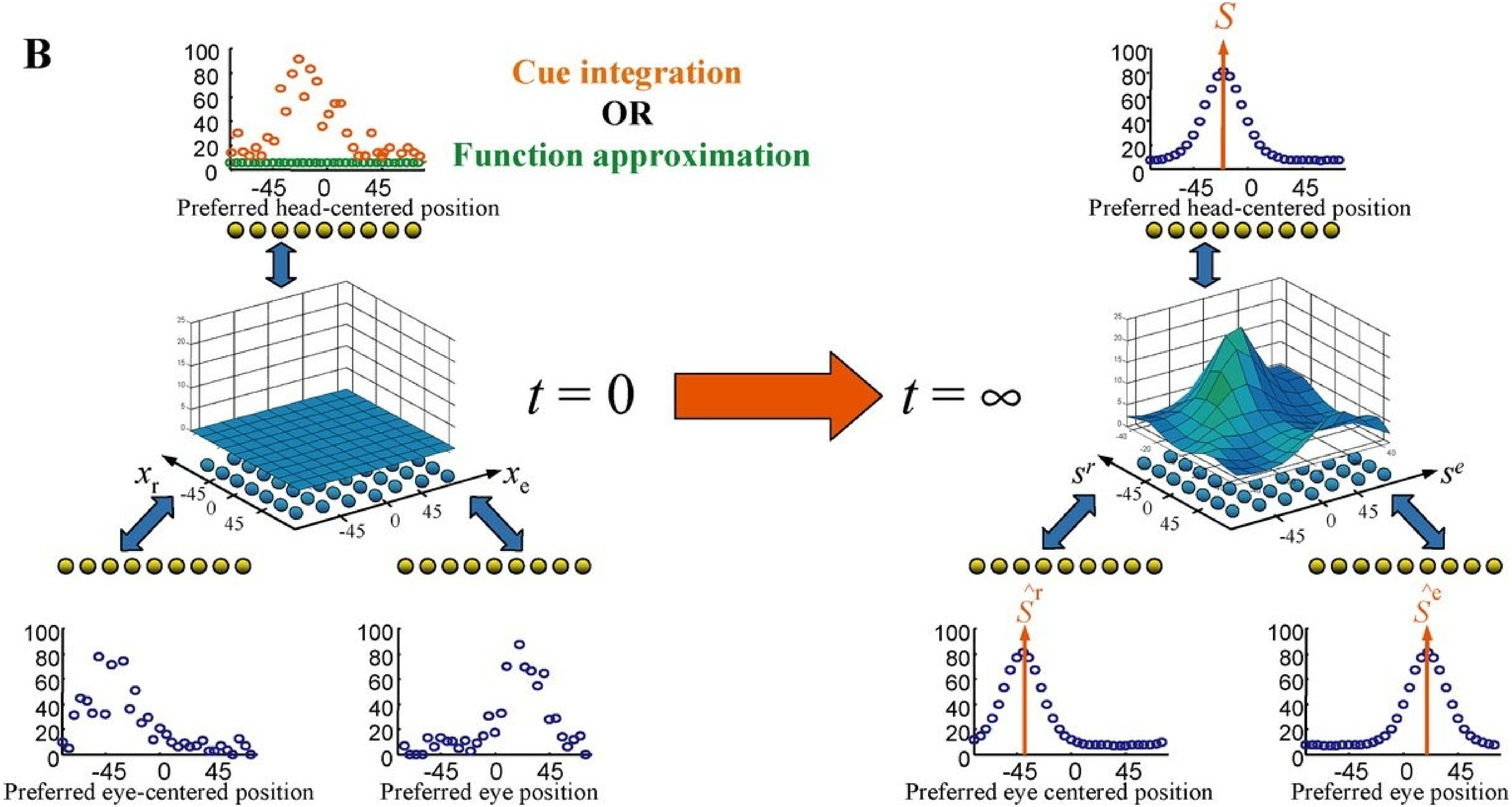
- Construct an <u>attractor</u> network whose attractor states correspond to perfect (noise-free) representations of stimulus values.
  - For a 1D linear variable, this would be a line attractor.
  - For a direction variable like head direction, use a ring attractor.
- The attractor network will map a noisy activity vector **r** into a cleaner vector **r*** encoding the stimulus value that is most likely being encoded by **r**.



Basis Functions

- You can think of the neurons' tuning curves as a set of basis functions from which to construct a linear decoding function.
- But instead of decoding, we can also use these basis functions to transform one representation into another.
- Or use them to do arithmetic.
- Example: calculating head-centered coordinates from retinal position plus eye position.

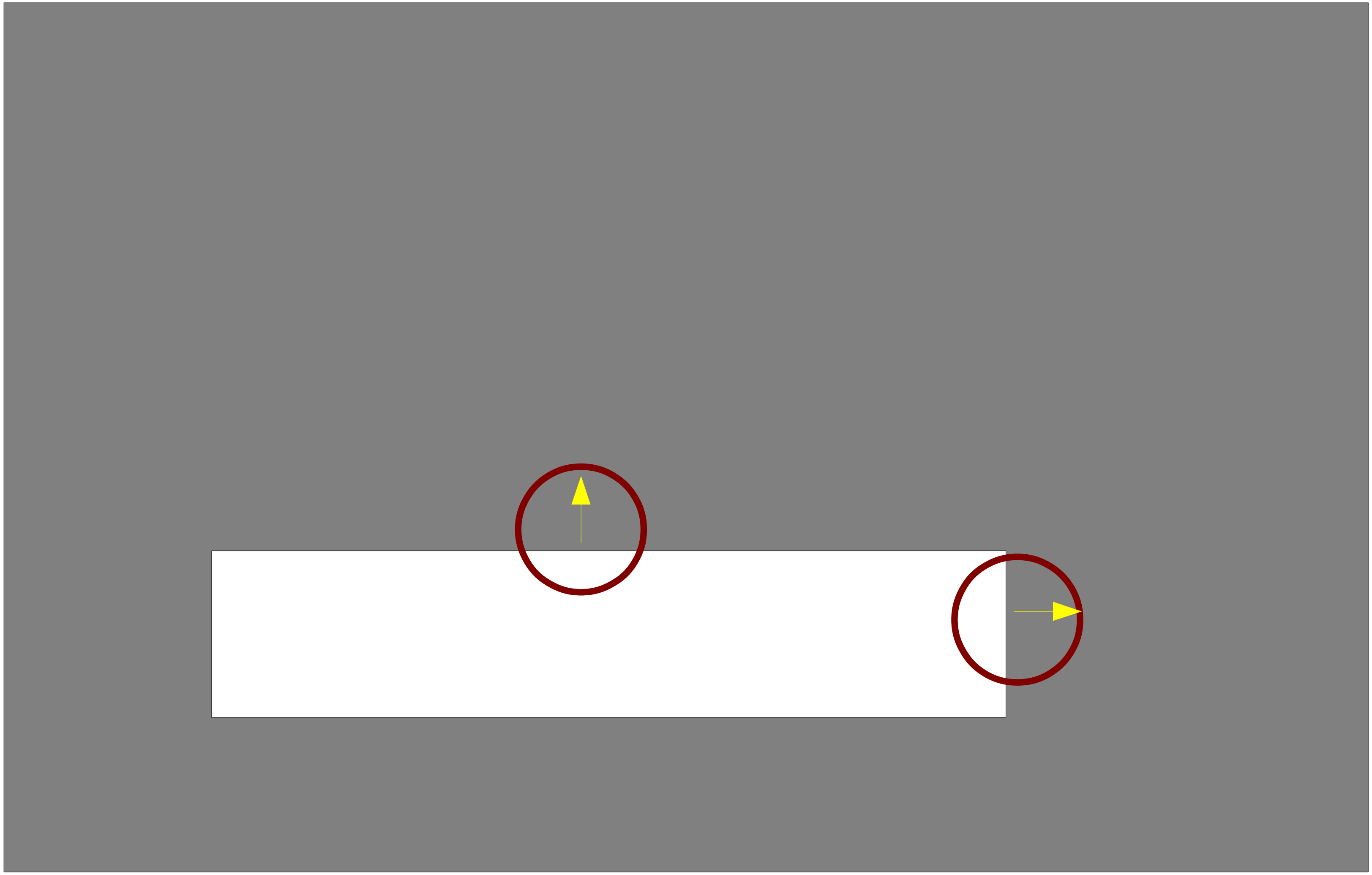
Recurrent Network Maintains Proper Relationships Between Retinal, Eye, and Head Coordinates



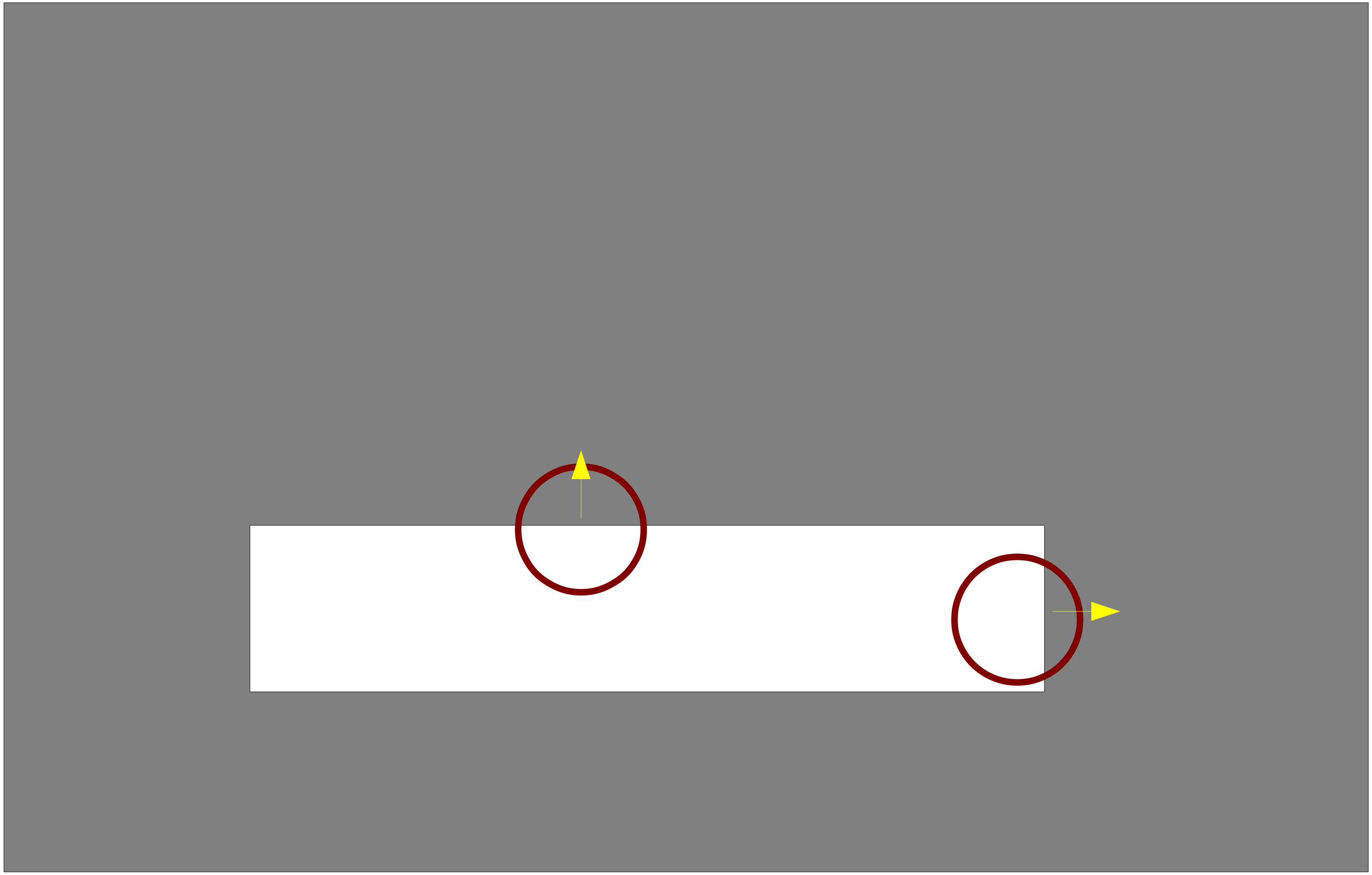
Encoding Probability Distributions

- The previous decoding exercise assumed that the activity vector was a noisy encoding of a single value.
- What if there were inherent uncertainty as to the value of a variable?
- The brain might want to encode its beliefs about the *distribution* of possible values.
- Hence, population codes might represent probability distributions.

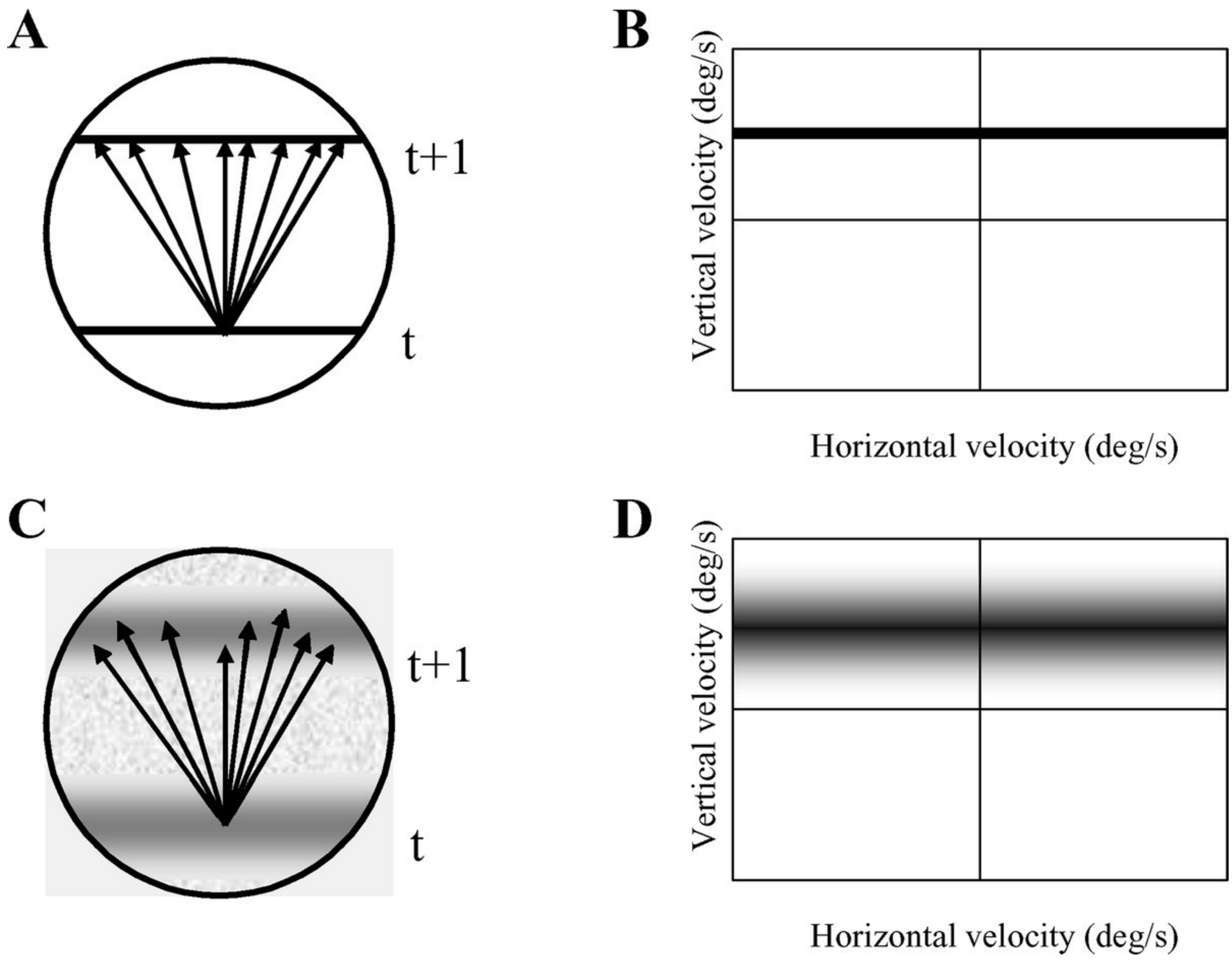
Aperture Problem: In What Direction Is the Bar Moving?



Aperture Problem: In What Direction Is the Bar Moving?



Horizontal Direction Uniformly Distributed Because No Information Available

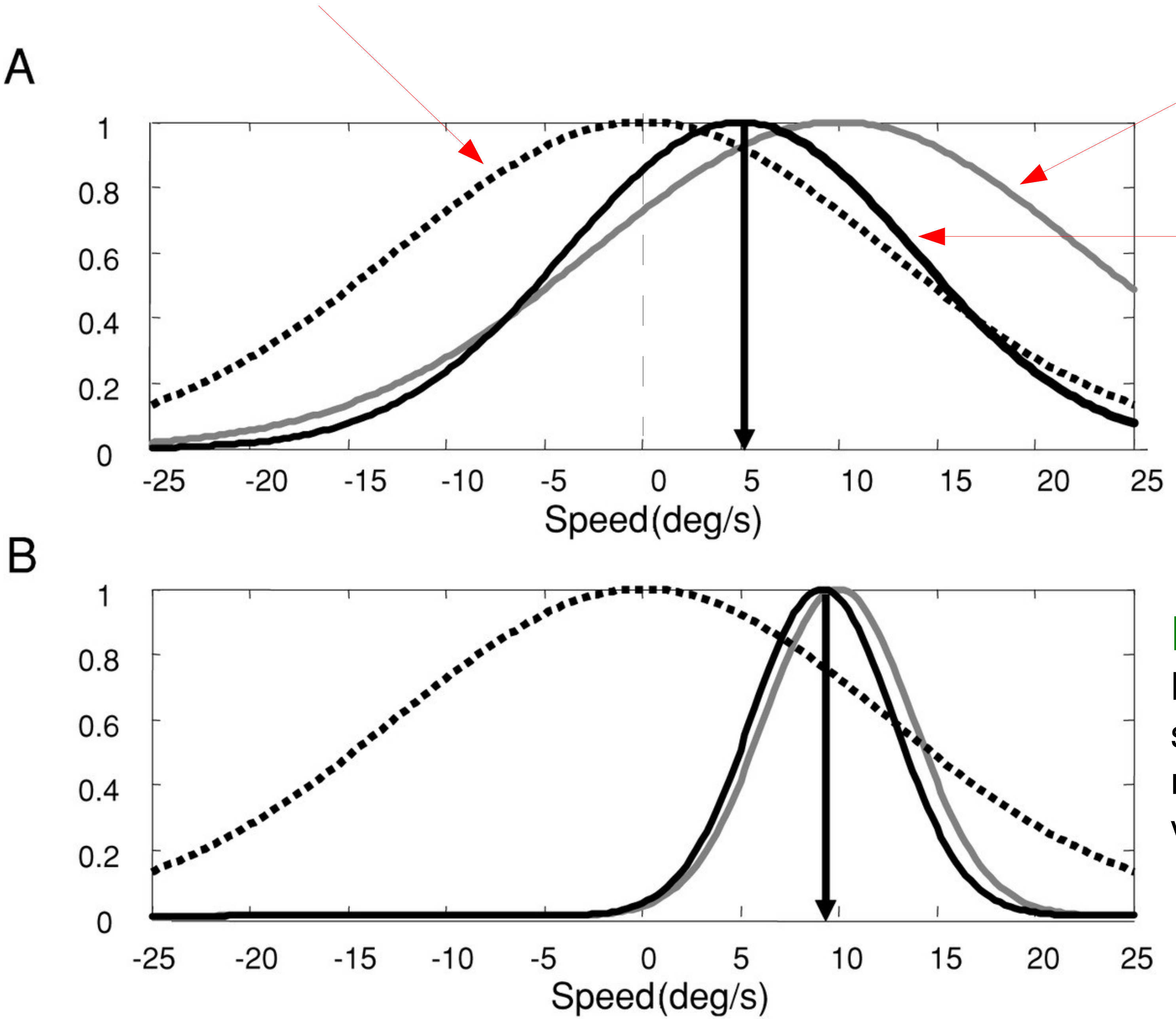


Some uncertainty about vertical velocity yields a distribution of possible values.

Bayesian Estimation of Velocity: Prior is a Gaussian Centered on Zero

Likelihood P[**r**|s]

Posterior P[s|**r**]



Low Contrast Case

High Contrast Case

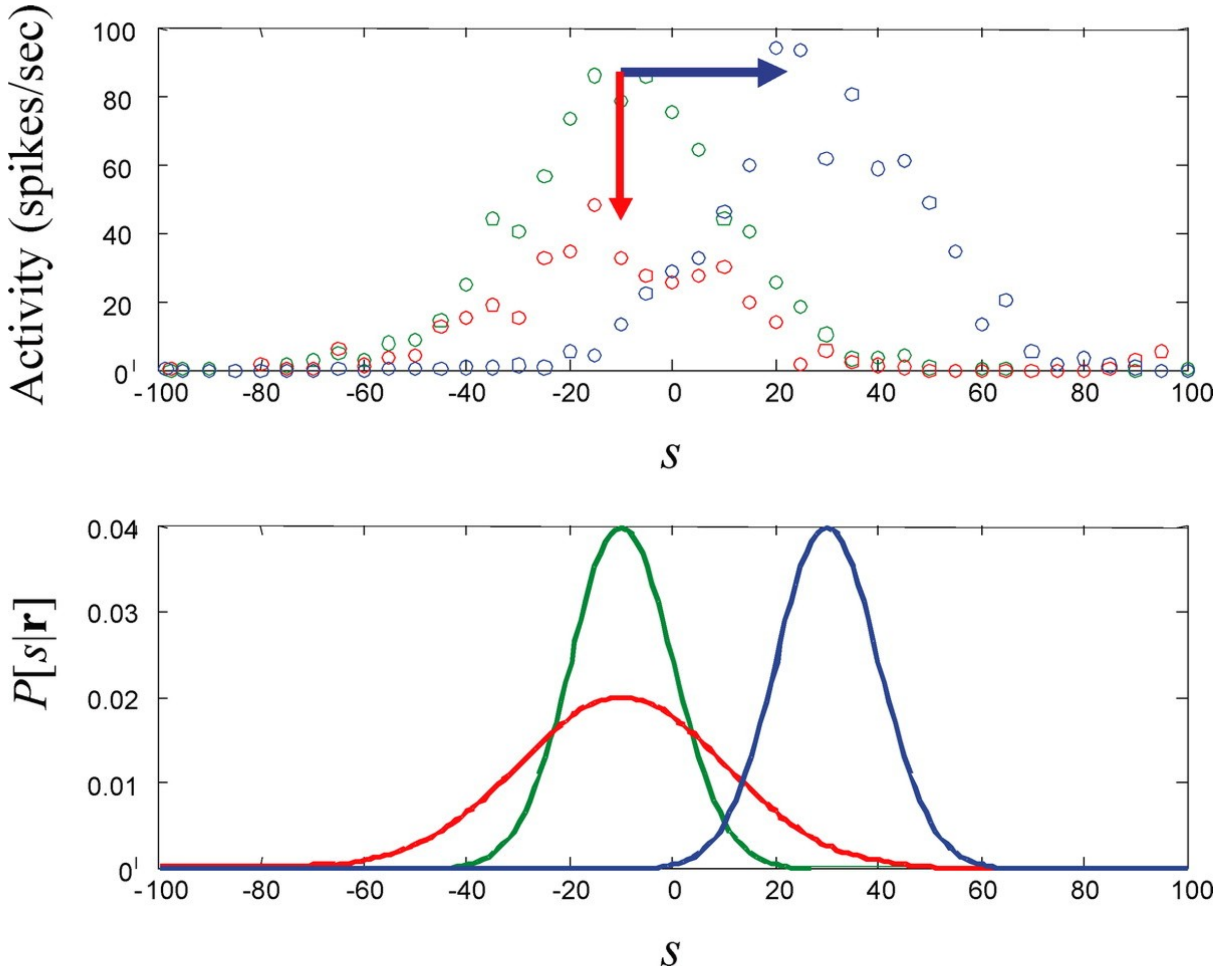
Likelihood peaked at same value but curve is narrower, so estimated velocity is higher.

Psychophysical Argument for Representing Distributions Instead of Expected Values

- People estimate velocities as higher when the contrast is greater. How to account for this?
- The Bayesian estimator produces this effect. Humans behave as predicted by Bayes' law.
- Why does this model work? Because:
  - The width of the likelihood distribution is explicitly represented
- Other psychophysical experiments confirm the view of humans as Bayesian estimators.
- This suggests that the nervous system utilizes probability distribution information, not just expected values.

Decoding Gaussian Signals with Poisson Noise

- Translation (blue) shifts the probability distribution but does not change the shape from the original (green).
- Scaling down (red) broadens the variance.



Convolutional Encodings

- For other types of probability distributions we don't want to use uniform Gaussian tuning curves. Instead, convolve the probability distribution with a set of basis functions.
- Fourier encoding (sine wave basis functions):

$$f_i(P[s|\boldsymbol{r}]) = \int ds \cdot \sin(w_i s + \phi_i) \cdot P[s|\boldsymbol{r}]$$

- Gaussian kernels:

$$f_i(P[s|\boldsymbol{r}]) = \int ds \cdot \exp\left(-\frac{(s - s_i)^2}{2\sigma_i^2}\right) \cdot P[s|\boldsymbol{r}]$$

- Decoding of these representations is tricky.

Ernst & Banks Experiment

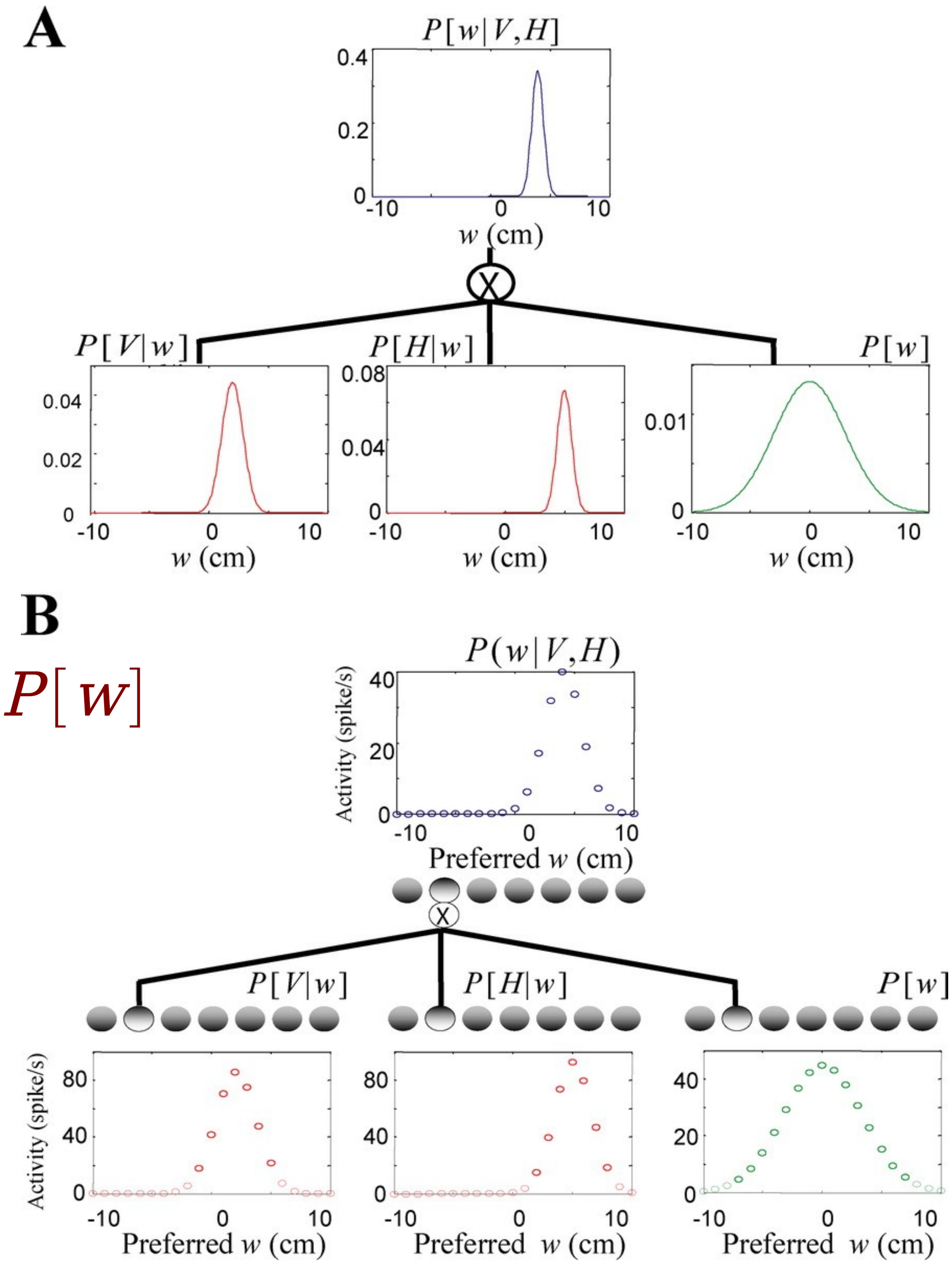
Estimating the width of a bar using both visual (V) and haptic (H) cues.

Population codes are computed by convolving with Gaussian kernels.

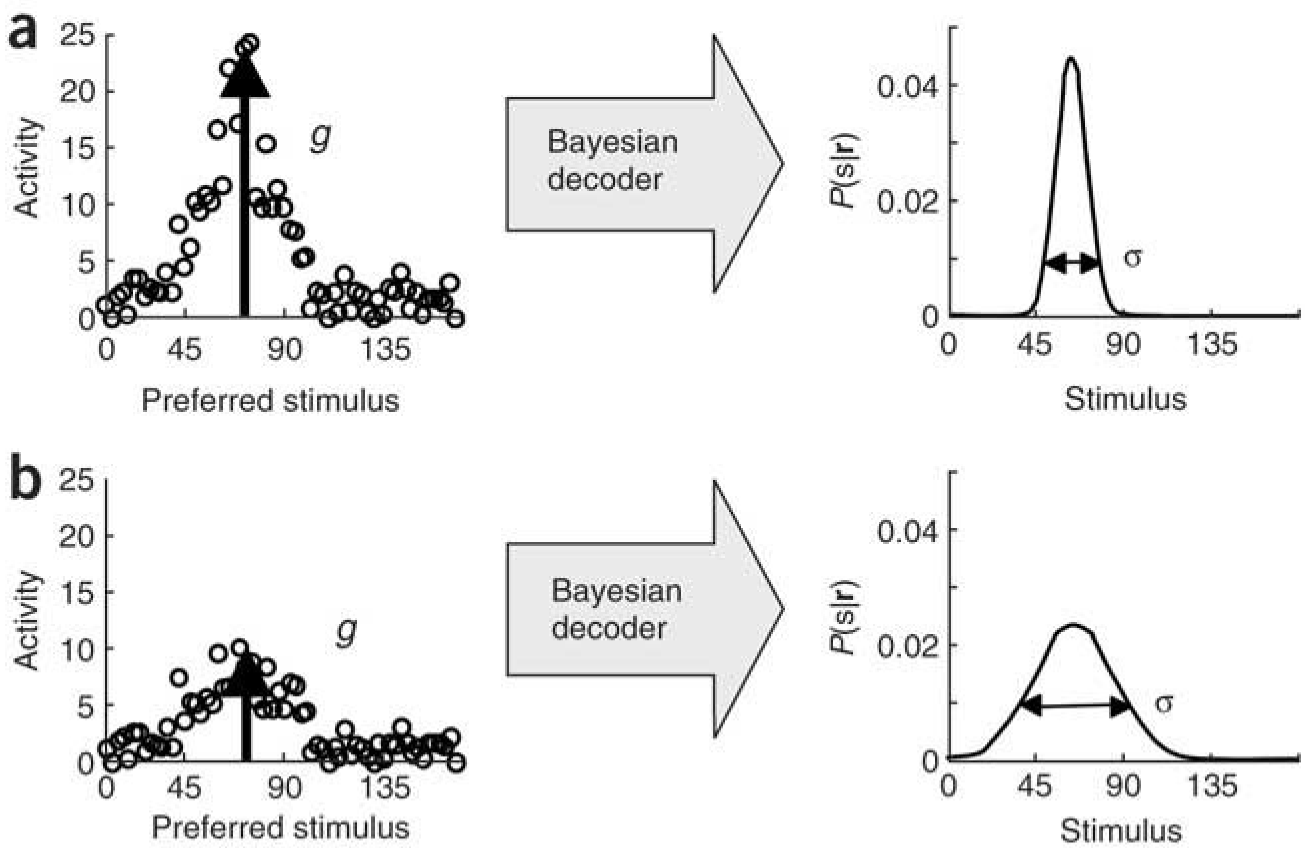
$$P[w|V,H] \propto P[V|w]\,P[H|w]\,P[w]$$

“Neural” model does three-way element-wise multiplication.

In this way, we can do inference using noisy population codes.



Ma et al. (2006): Bayesian Inference with Population Codes

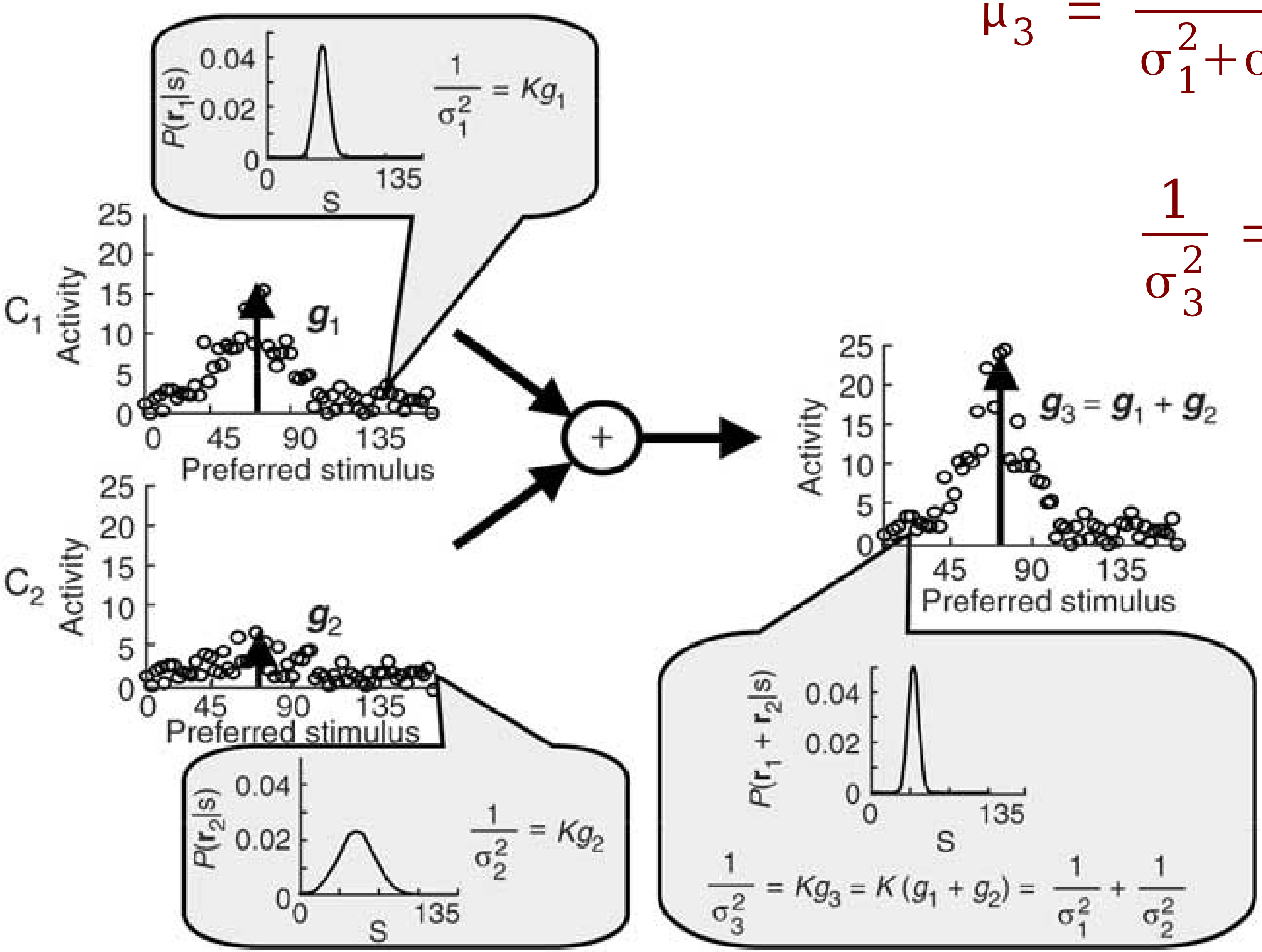


Lower amplitude means broader variance.

Sensory Integration of Gaussians w/Poisson Noise

$$\mu_3 = \frac{\sigma_2^2}{\sigma_1^2+\sigma_2^2}\mu_1 + \frac{\sigma_1^2}{\sigma_1^2+\sigma_2^2}\mu_2$$

$$\frac{1}{\sigma_3^2} = \frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2}$$



Generalizing the Approach

- Gaussians with Poisson noise are easy to combine: we can do element-wise addition of firing rates, and the resulting representation is Bayes-optimal.
- Can we generalize to non-Gaussian functions and other types of noise, and retain Bayes-optimality?
- $\mathbf{r}_3 = \mathbf{r}_1 + \mathbf{r}_2$ is Bayes-optimal if $p(s|\mathbf{r}_3) = p(s|\mathbf{r}_1)\, p(s|\mathbf{r}_2)$.
- This doesn't hold for most distributions but it does for some that are “Poisson-like”.

Poisson-Like Distributions

$$P(\boldsymbol{r}_k | s, g) = \phi(\boldsymbol{r}_k, g_k) \cdot \exp(\boldsymbol{h}^T(s)\boldsymbol{r}_k)$$

$$\boldsymbol{h}'(s) = \Sigma_k^{-1}(s, g_k)\,\boldsymbol{f}'(s, g_k)$$

Σ_k is the covariance matrix of $\boldsymbol{r}_k$

gain $g_k = K/\sigma_k^2$

$\boldsymbol{f}_k(s)$ is the tuning curve function

For identical tuning curves and Poisson noise:

$$\boldsymbol{h}(s) = \log \boldsymbol{f}(s)$$

$$\phi_k(\boldsymbol{r}_k, g_k) = \exp(-c\,g_k) \prod_i \exp(r_{ki} \log g_k) / r_{ki}!$$

Non-Identical Tuning Curves

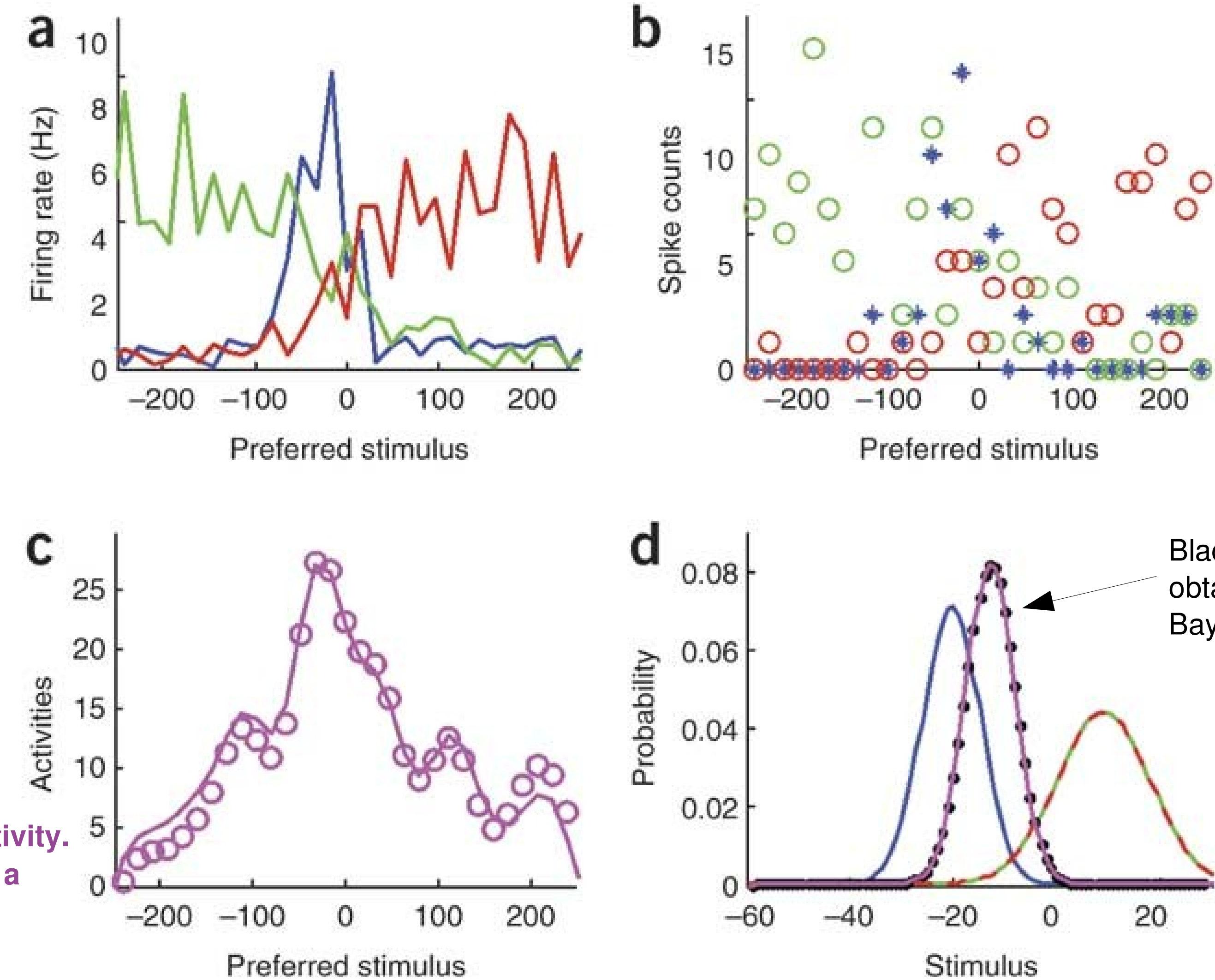
- When tuning curve functions $\mathbf{f}_k$ are not the same, $\mathbf{h}(s)$ is not the same for all tuning curves. Simple addition doesn't work.
- But we can still combine tuning curves using linear coefficients A_k, provided the $\mathbf{h}_k(s)$ functions are drawn from a common basis set.

$$\boldsymbol{r}_3 = A_1^T \boldsymbol{r}_1 + A_2^T \boldsymbol{r}_2$$

Combining Three Poisson-Like Populations Using Different Types of Tuning Curves

Inputs:

Outputs:



Solid line: mean activity.
Circles: activity on a single trial.

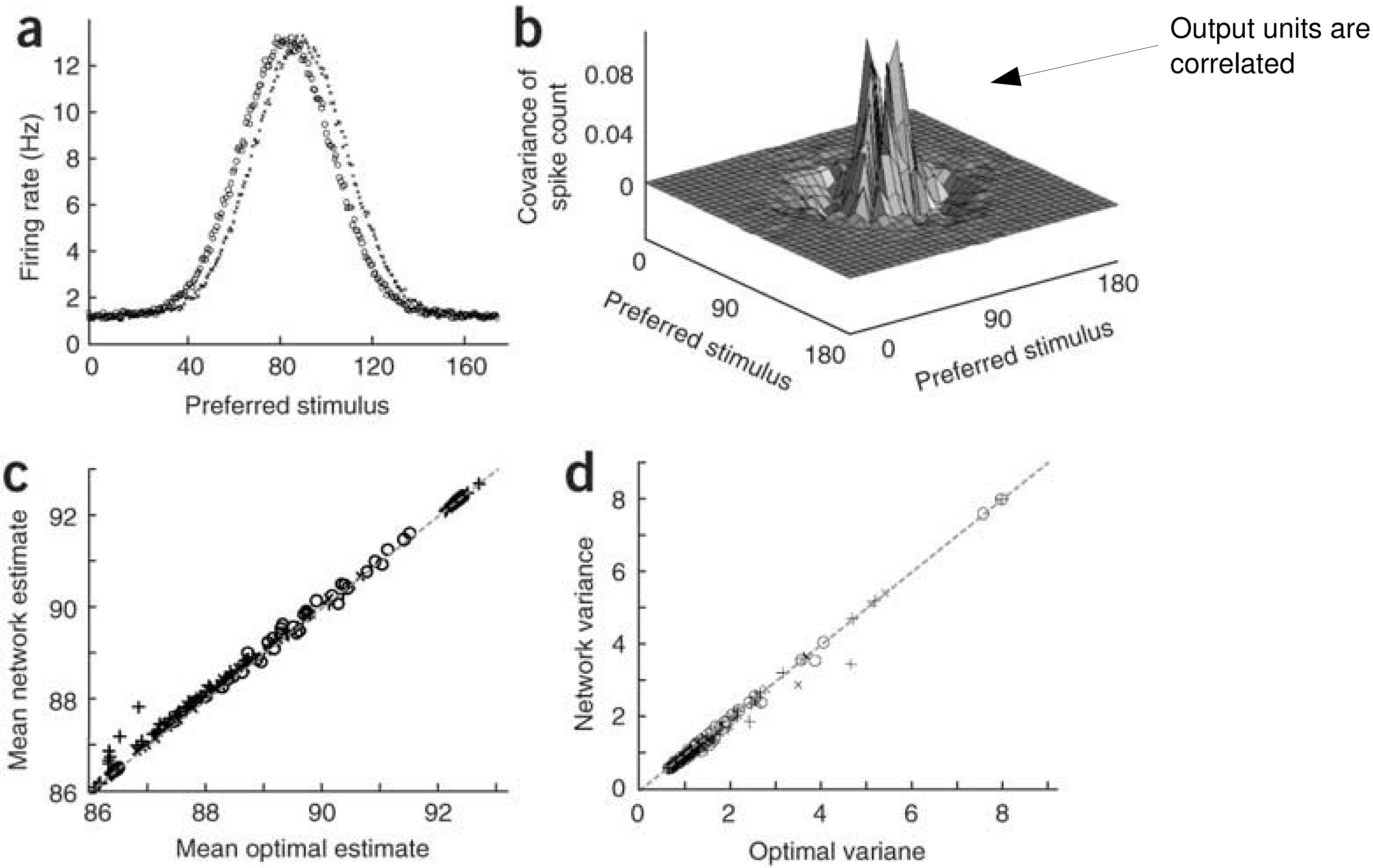
Simulation with Integrate-and-Fire Neurons

Inputs:

$\mu_1 = 86.5$

$\mu_2 = 92.5$

Simulates cue conflict.



Combined estimate is Bayes-optimal!

Summary

- Population codes are widely used in the brain (visual cortex, auditory cortex, motor cortex, head direction system, place codes, grid cells, etc.)
- The brain uses these codes to represent more than just a scalar value. They can encode <u>probability distributions</u>.
- We can do arithmetic on probability distributions if the population code satisfies certain constraints.
  - Codes that are Poisson-like are amenable to this.
- The population code serves as a basis set.
  - Populations can be combined via linear operations, and in the simplest case, element-wise addition.