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.

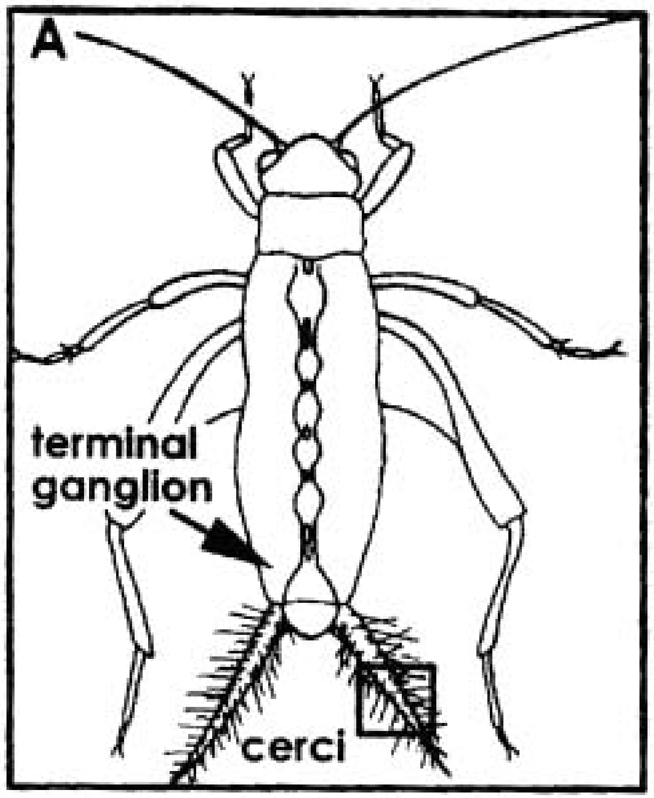
They test positive. What conclusion should we draw?

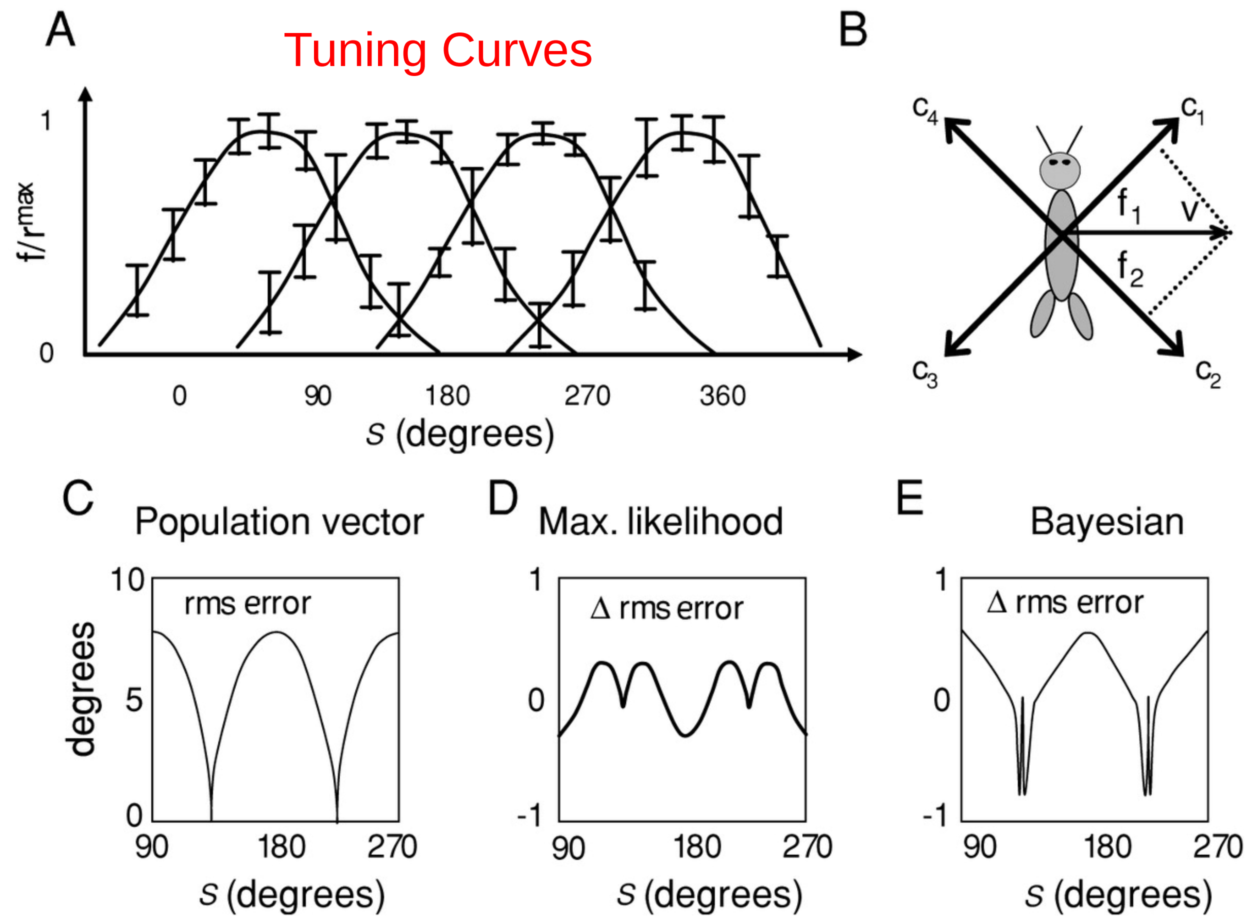
- P(d) *prior* has the disease
- P(t&d) *joint* tests positive *and* has the disease
- P(t|d) *likelihood* tests positive *given* has the disease
- P(d|t) *posterior* has disease *given* test is positive
- P(t) *evidence* test is positive (aka “marginal likelihood”)

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





Error relative to population vector.

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

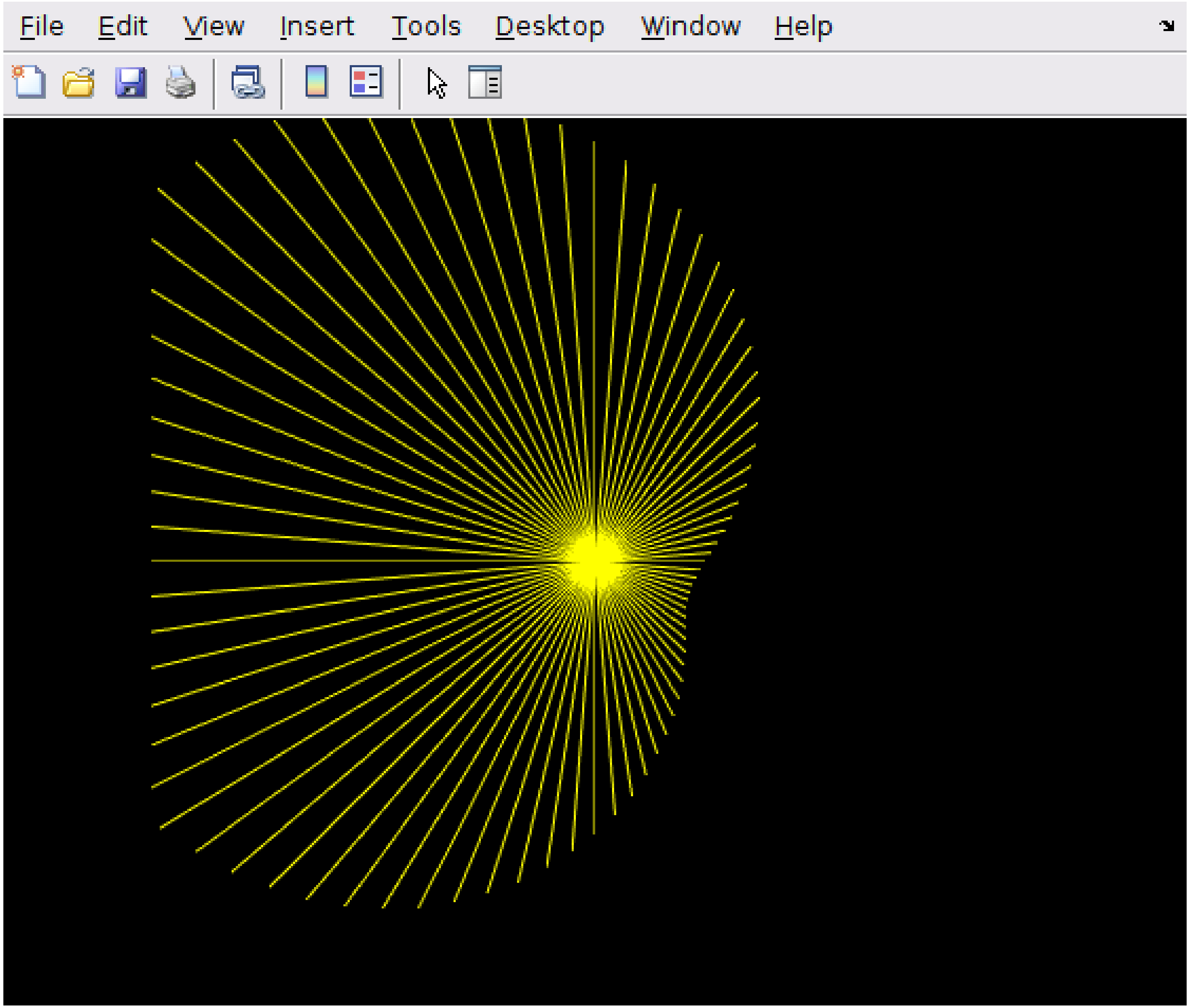
Population Vector

- 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.

popvec demo



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:

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

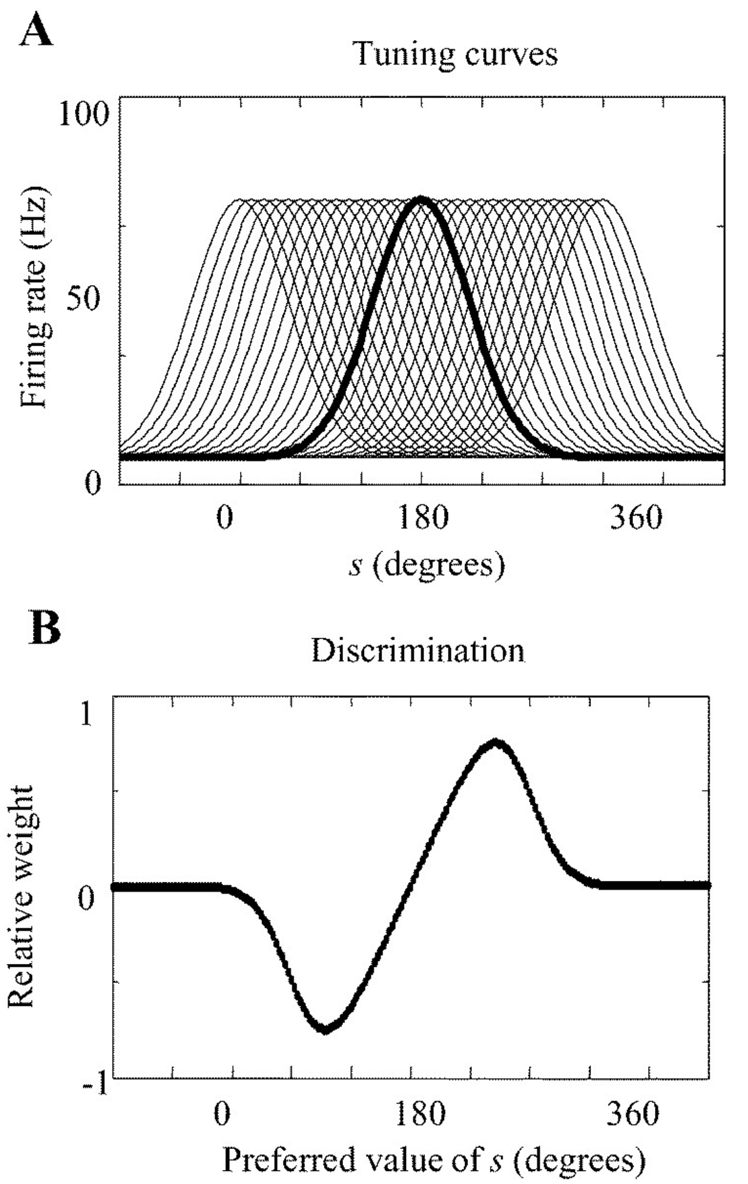
Homogeneous Population Code for Orientation in V1

- Gaussian tuning curves with $\sigma = 15^o$. Baseline firing rate = 5 Hz.

- Optimal linear decoder weights to discriminate a stimulus $s^* - \delta s$ from a stimulus $s^* + \delta s$, where $s^* = 180^o$. Note that the weight on the unit coding for 180^o is zero.

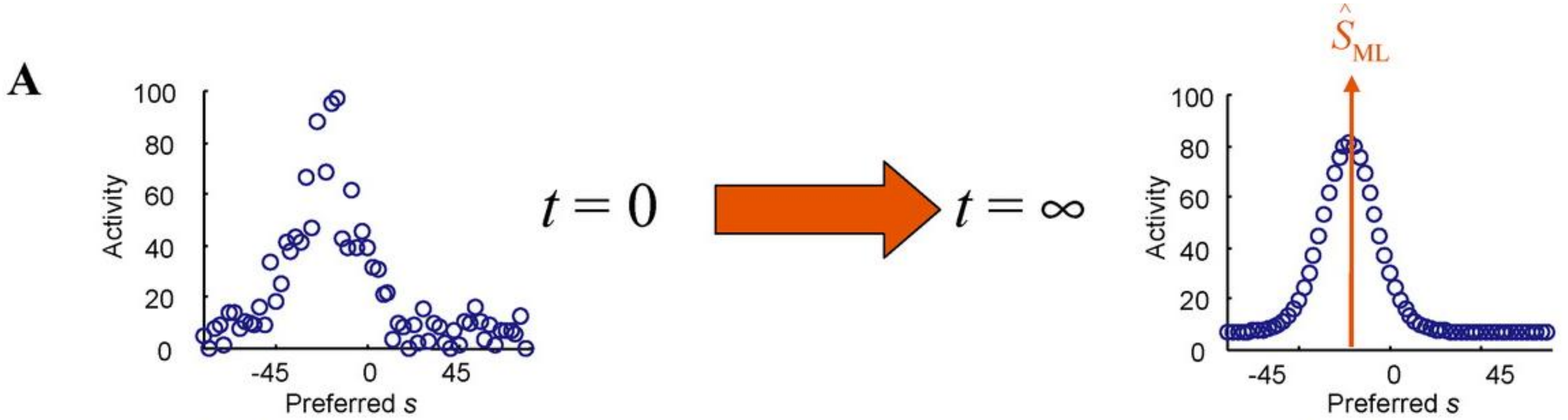
$$t(\boldsymbol{r}) = \sum_i r_i w_i$$

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



Cleaning Up Noise With Recurrent Connections

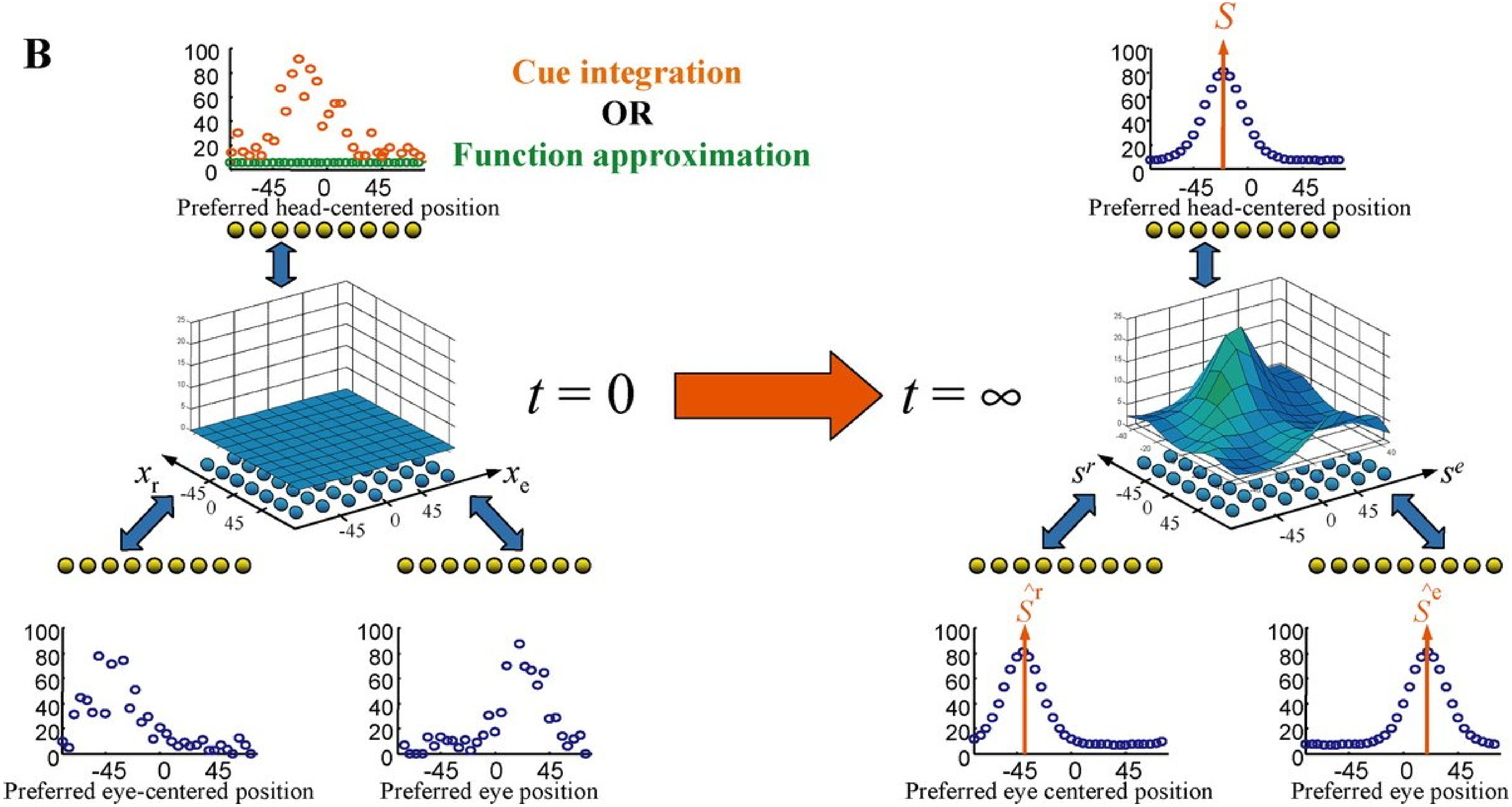
- Construct an <u>attractor</u> network whose attractor states correspond to perfect (noise-free) representations of stimulus values.
  - For a 1D linear variable, this would be a line attractor.
  - For a direction variable like head direction, use a ring attractor.
- The attractor network will map 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

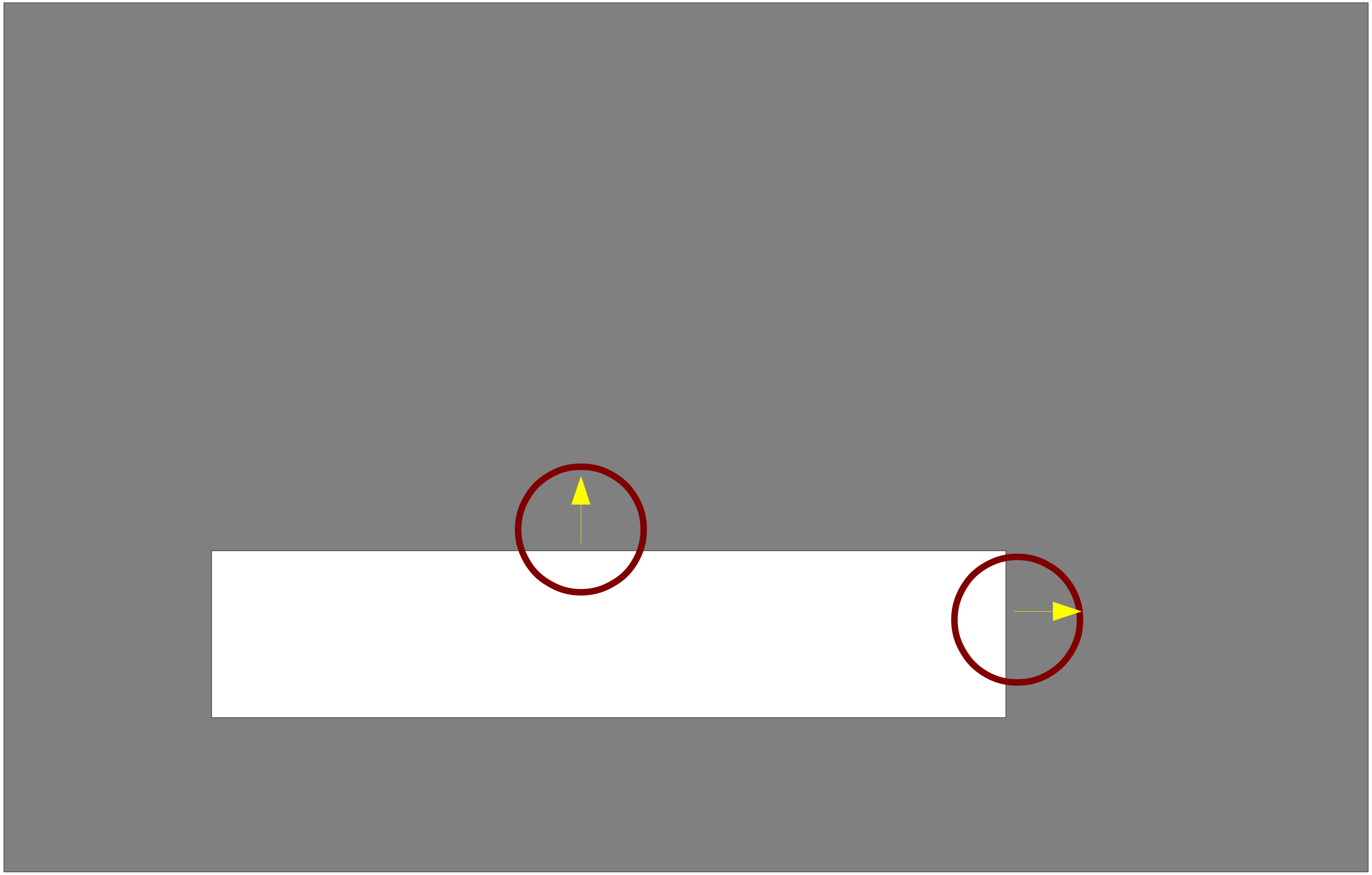
- The previous decoding exercise assumed that the activity vector was a noisy encoding of a single value.

- 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?



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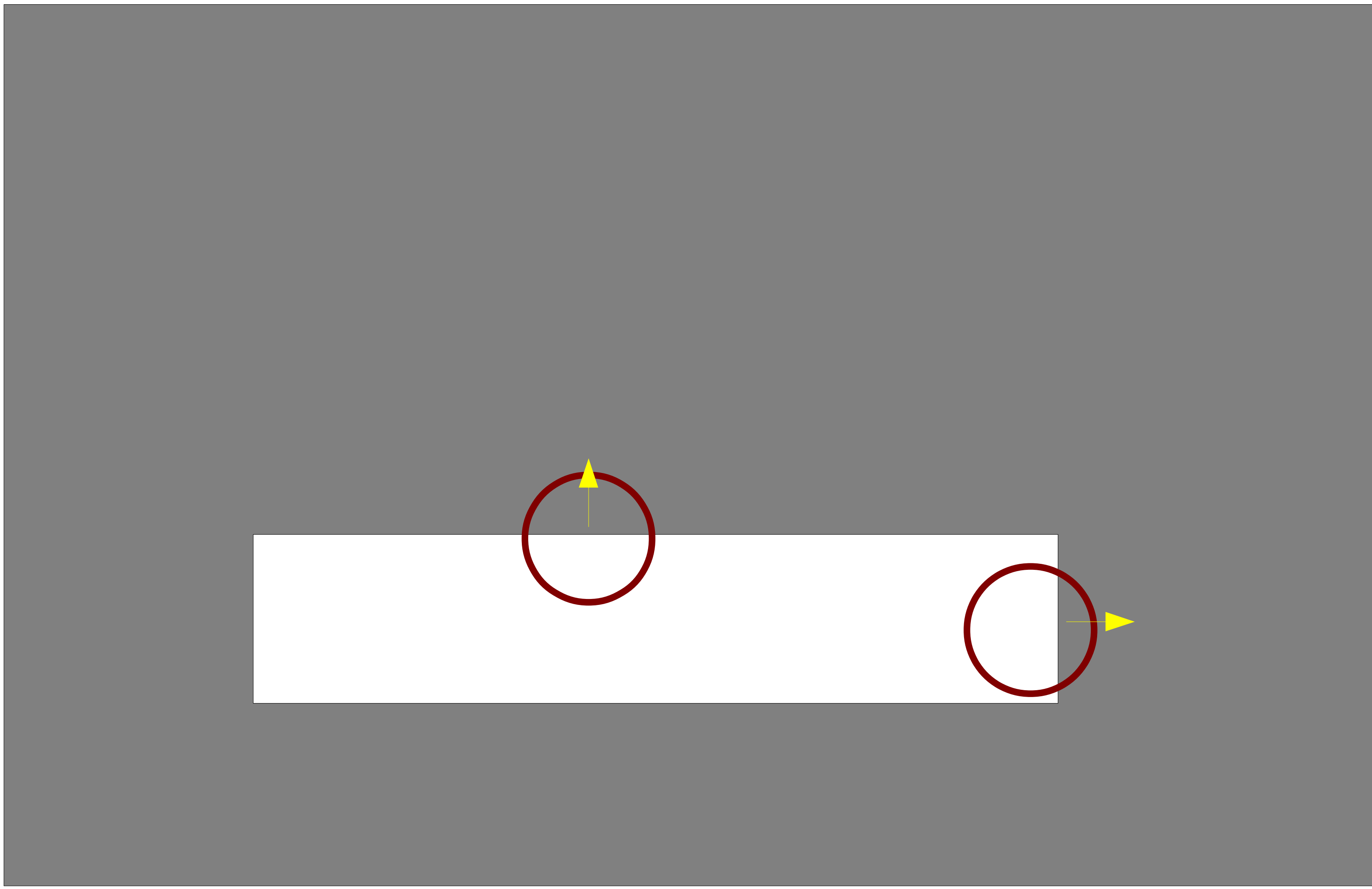
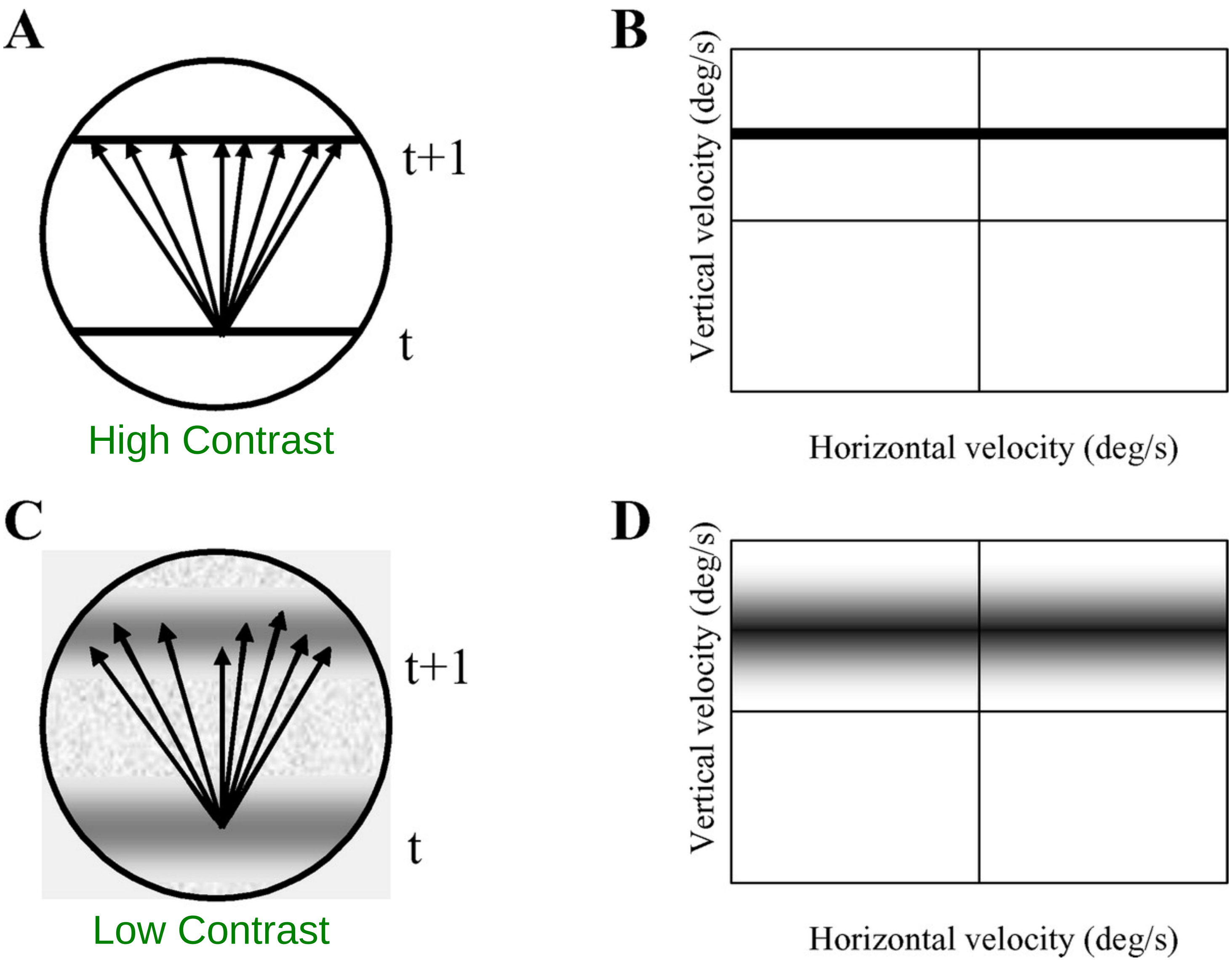
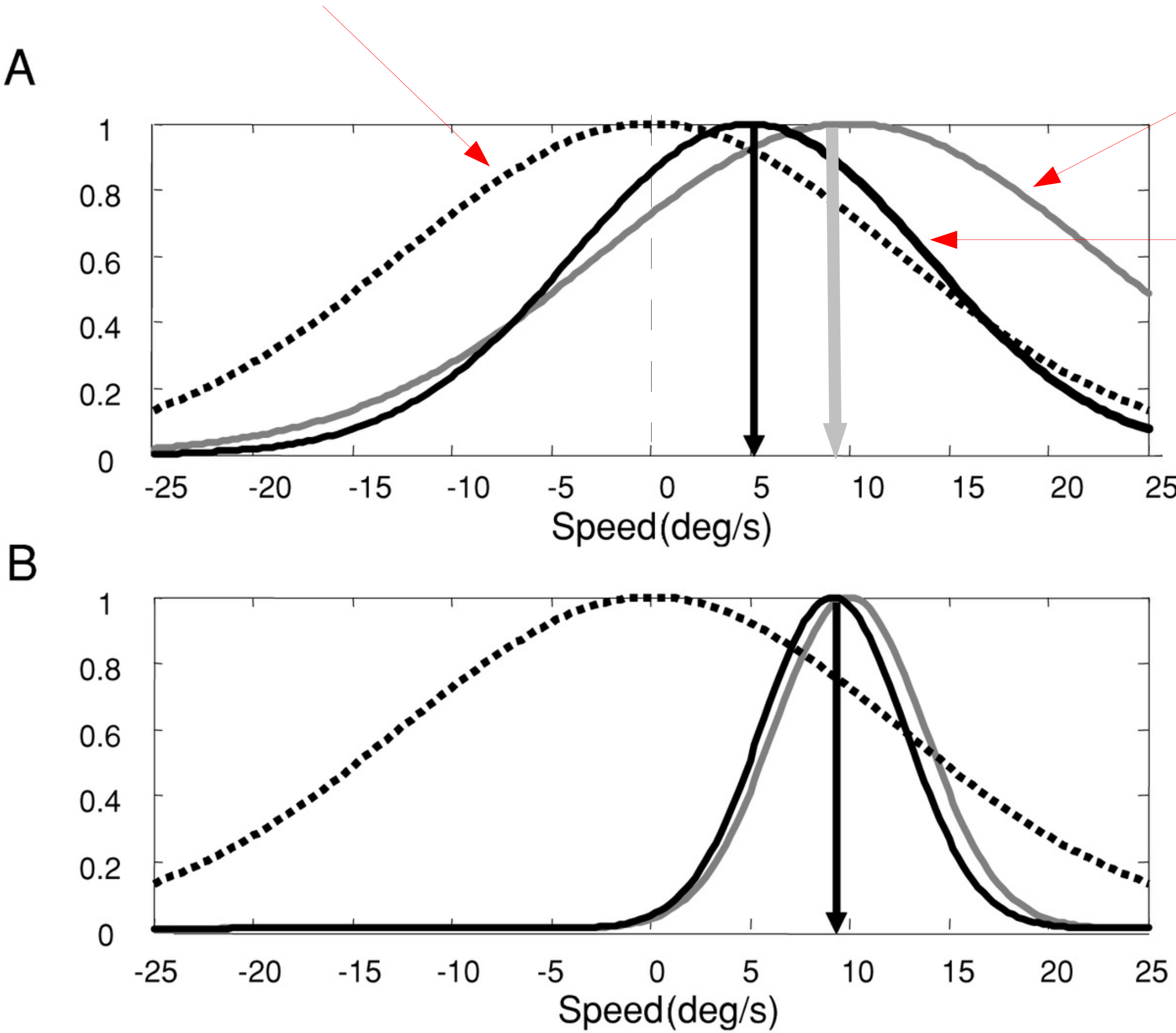


Horizontal Direction Uniformly Distributed Because No Information Available



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

Bayesian Estimation of Velocity: Prior P(s) is a Gaussian Centered on Zero



Likelihood P[**r**|s]

Posterior P[s|**r**]

Low Contrast Case

High Contrast Case

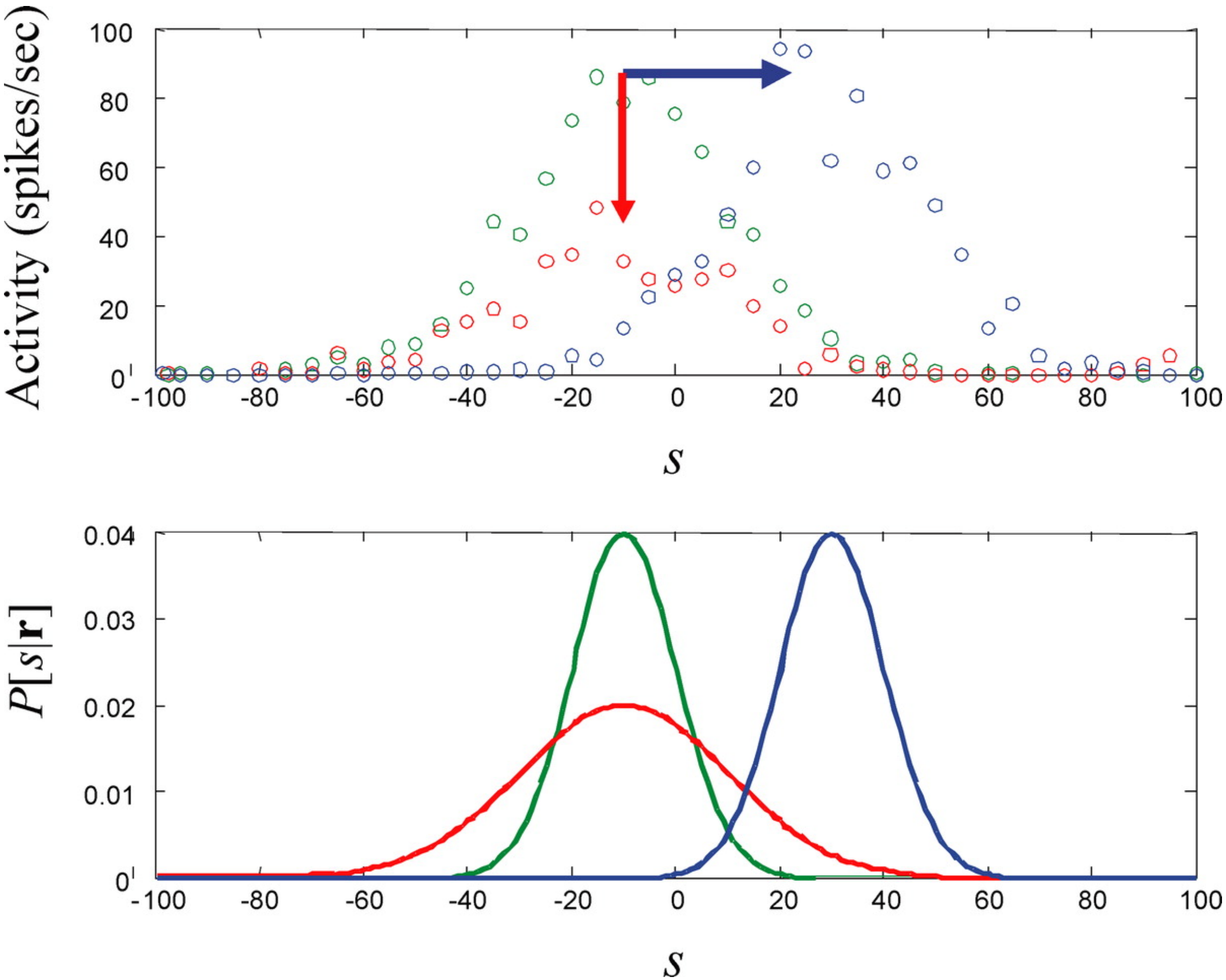
Likelihood peaked at same value but curve is narrower, so estimated velocity from posterior is higher.

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

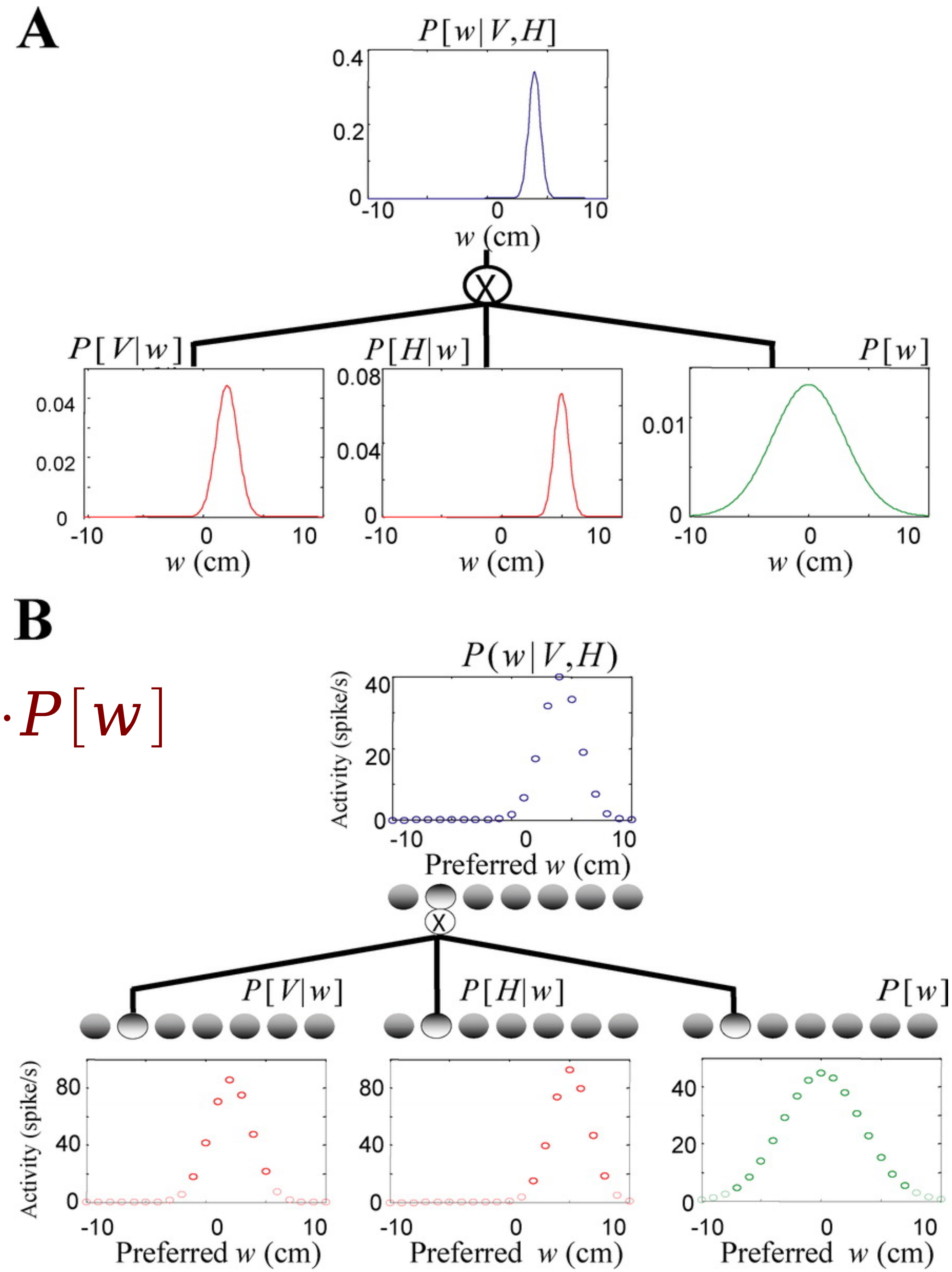
Estimating the width of a bar using both visual (V) and haptic (H) cues.

Population codes are computed by convolving with Gaussian kernels.

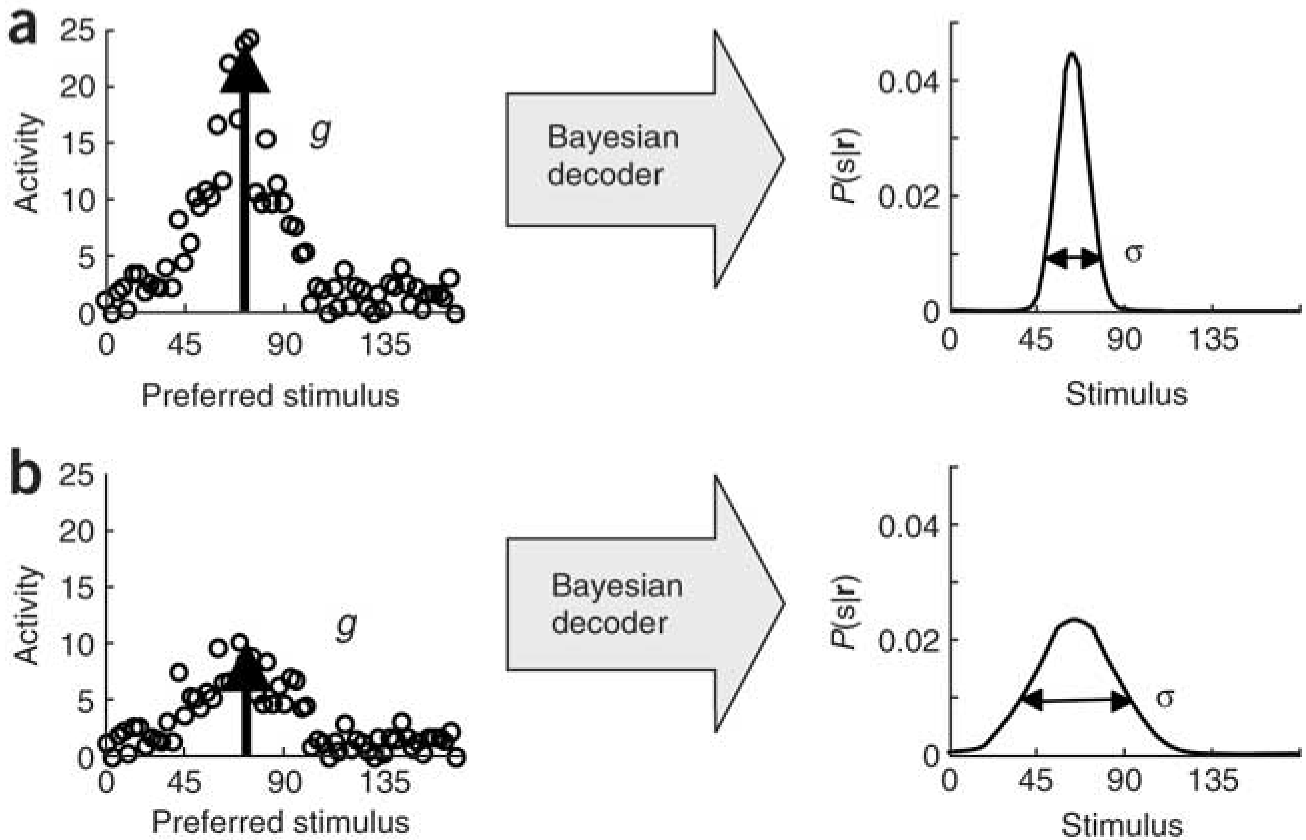
$$P[w|V,H] \propto P[V|w]\cdot P[H|w]\cdot P[w]$$

“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

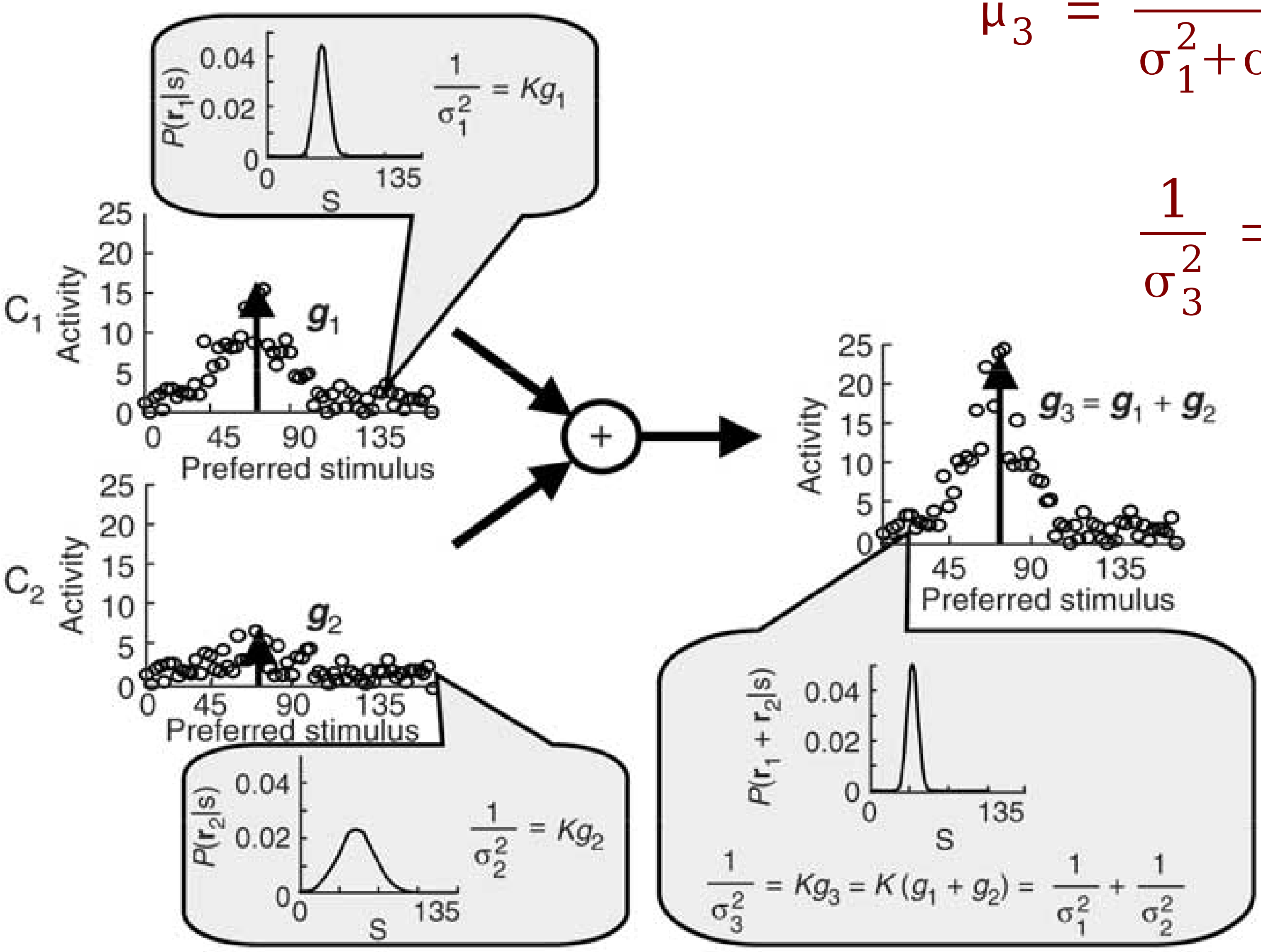


Lower amplitude means broader variance.

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.

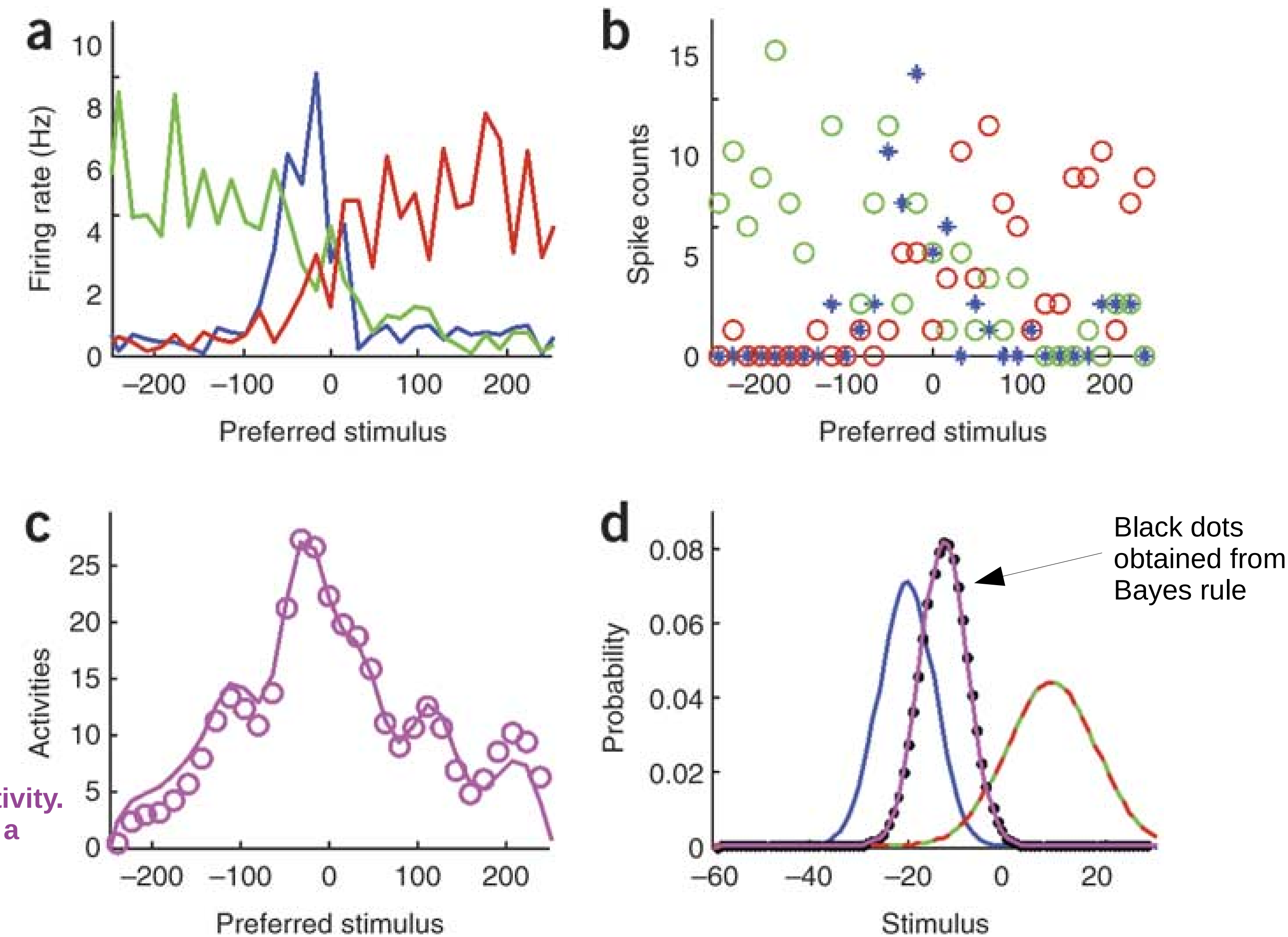
- But we can still combine tuning curves using linear coefficients A_k, provided the $\mathbf{h}_k$(s) functions are drawn from a common basis set.

$$\boldsymbol{r}_3 = A_1^T \boldsymbol{r}_1 + A_2^T \boldsymbol{r}_{\mathbf{2}}$$

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

Inputs:

Outputs:



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

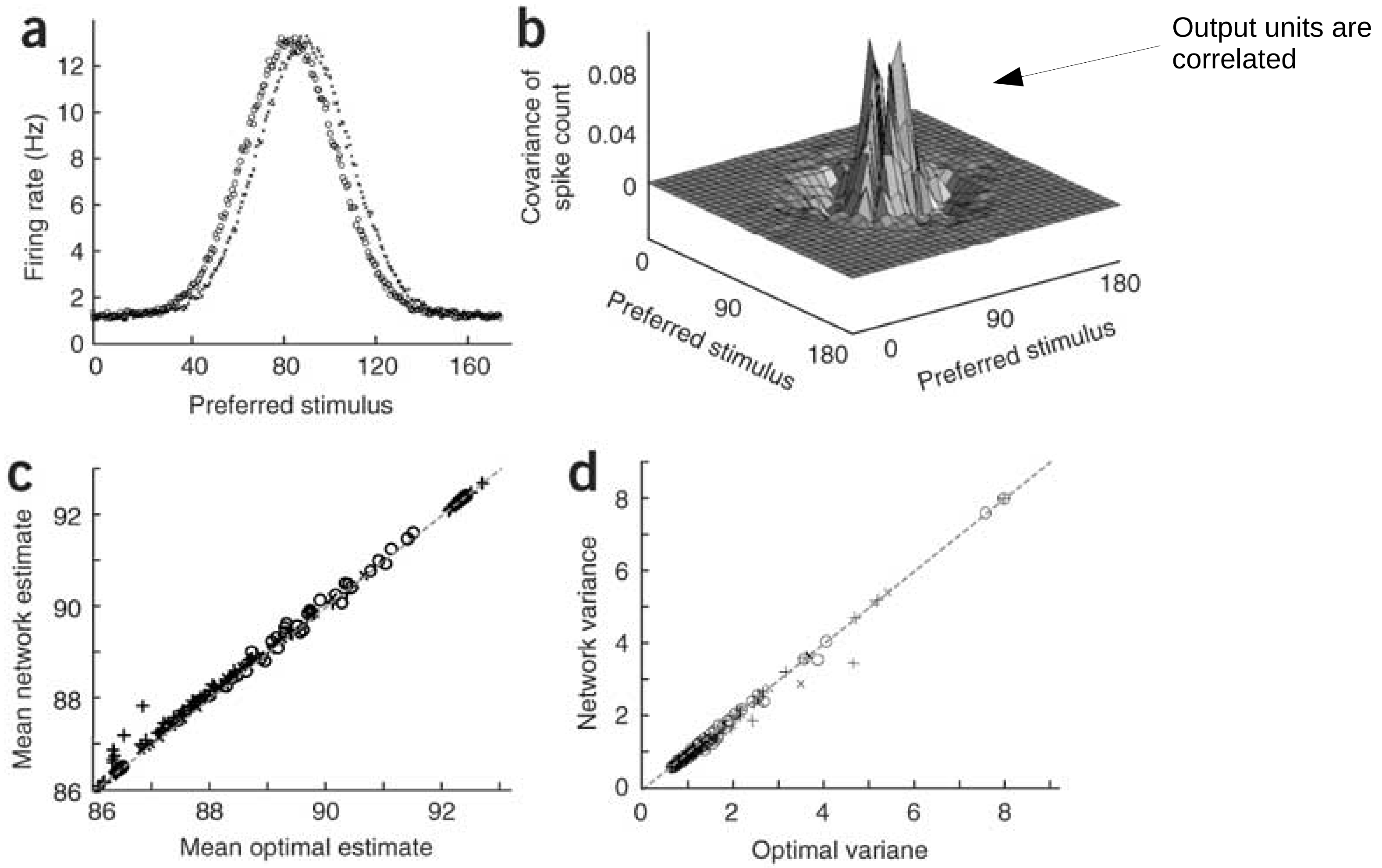
Simulation with Integrate-and-Fire Neurons

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.