Motivating and validating Bayesian and neural circuit models of decisions

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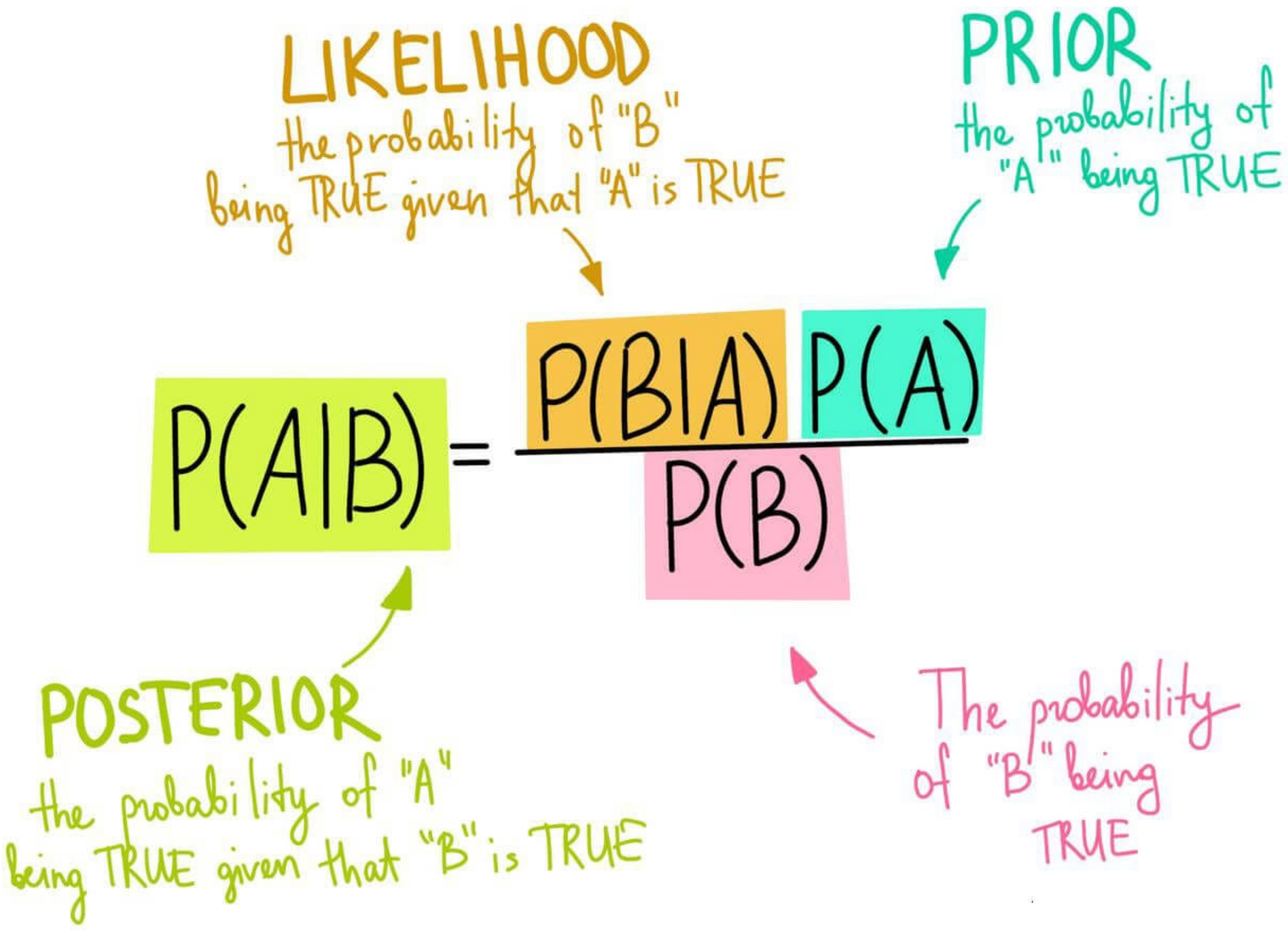

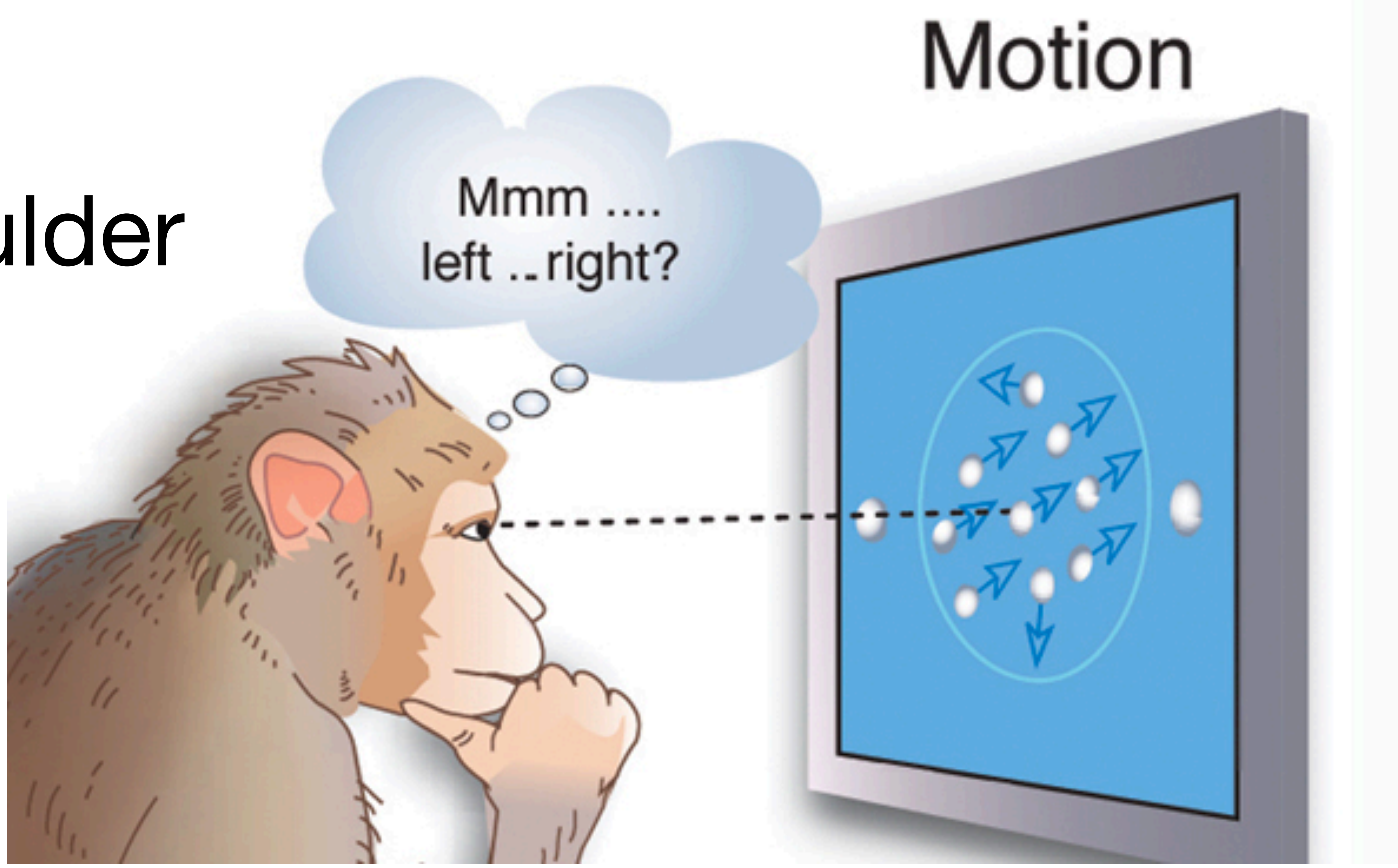

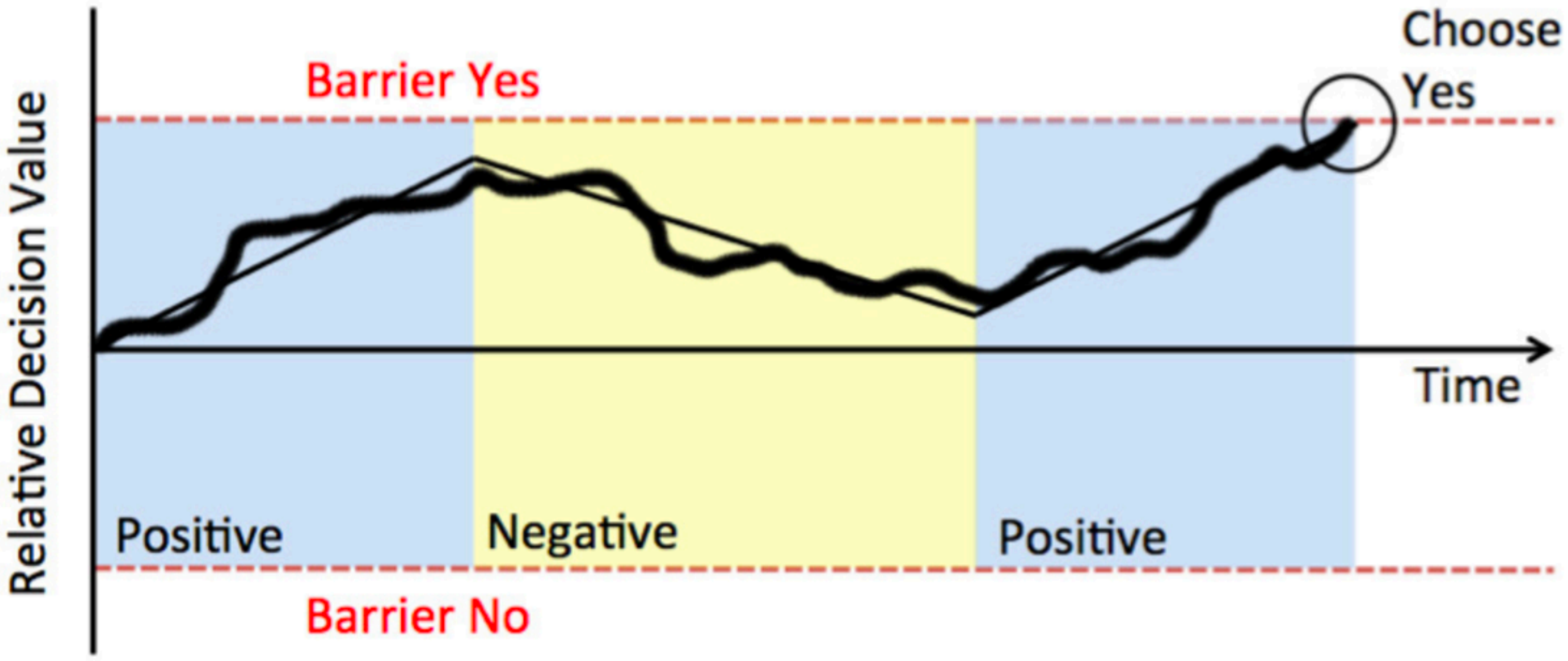

Outline

1. Bayes Rule and Bayesian inference
    1.1. Combining priors and observations
    1.2. Combing multiple observations within/across modalities
2. Two choice tasks
    2.1. Log likelihood ratio update and evidence accumulation
    2.2. Drift-diffusion model and decision statistics
3. Fitting models to data
    3.1. Maximum likelihood estimation
    3.2. Bayes factors for model identification
4. Competitive neural circuit models
    4.1. Mutual inhibition and winner take all networks
    4.2. Dependence of attractor structure on inputs


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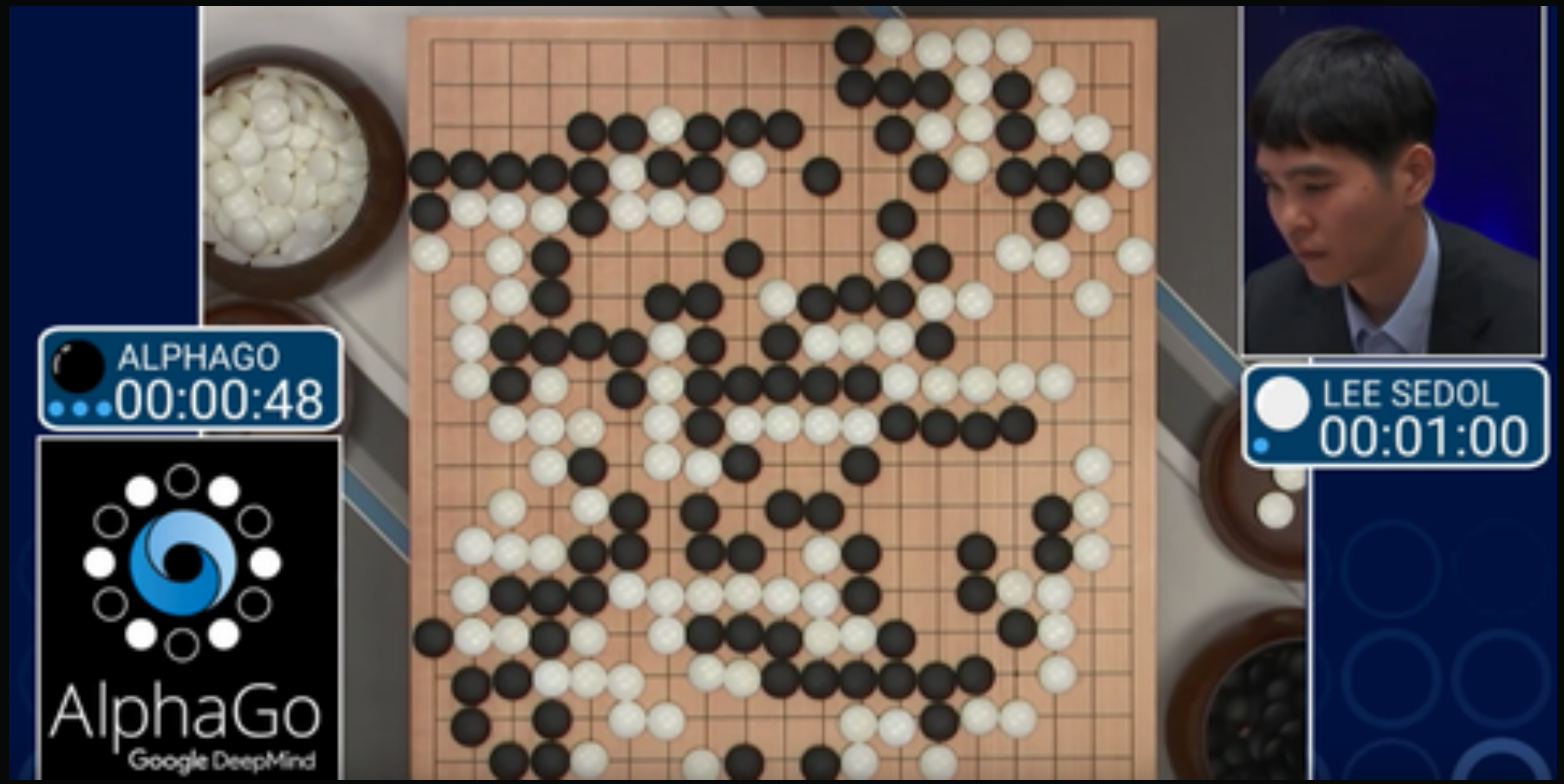
ALPHAGO
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AlphaGo
Google DeepMind
LEE SEDOL
00:01:00


Certificate of Marriage
STATE OF WASHINGTON
is to certify, that the undersigned, a
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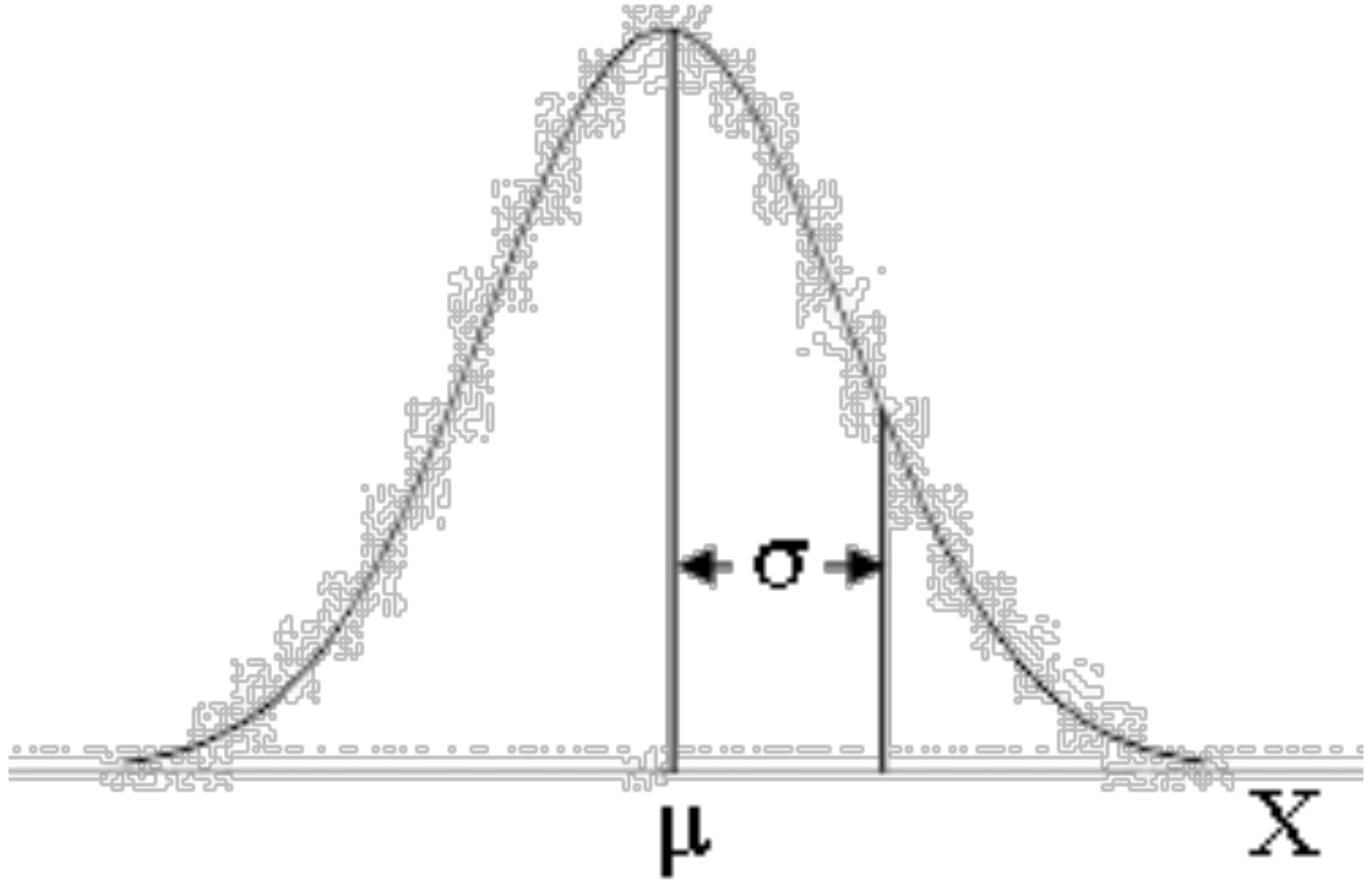
Probability primer (notation, etc)

probability density function $p(x)$

probability a *random variable* X has a value between x and $x + \Delta$ is about $\Delta \cdot p(x)$



example: normal

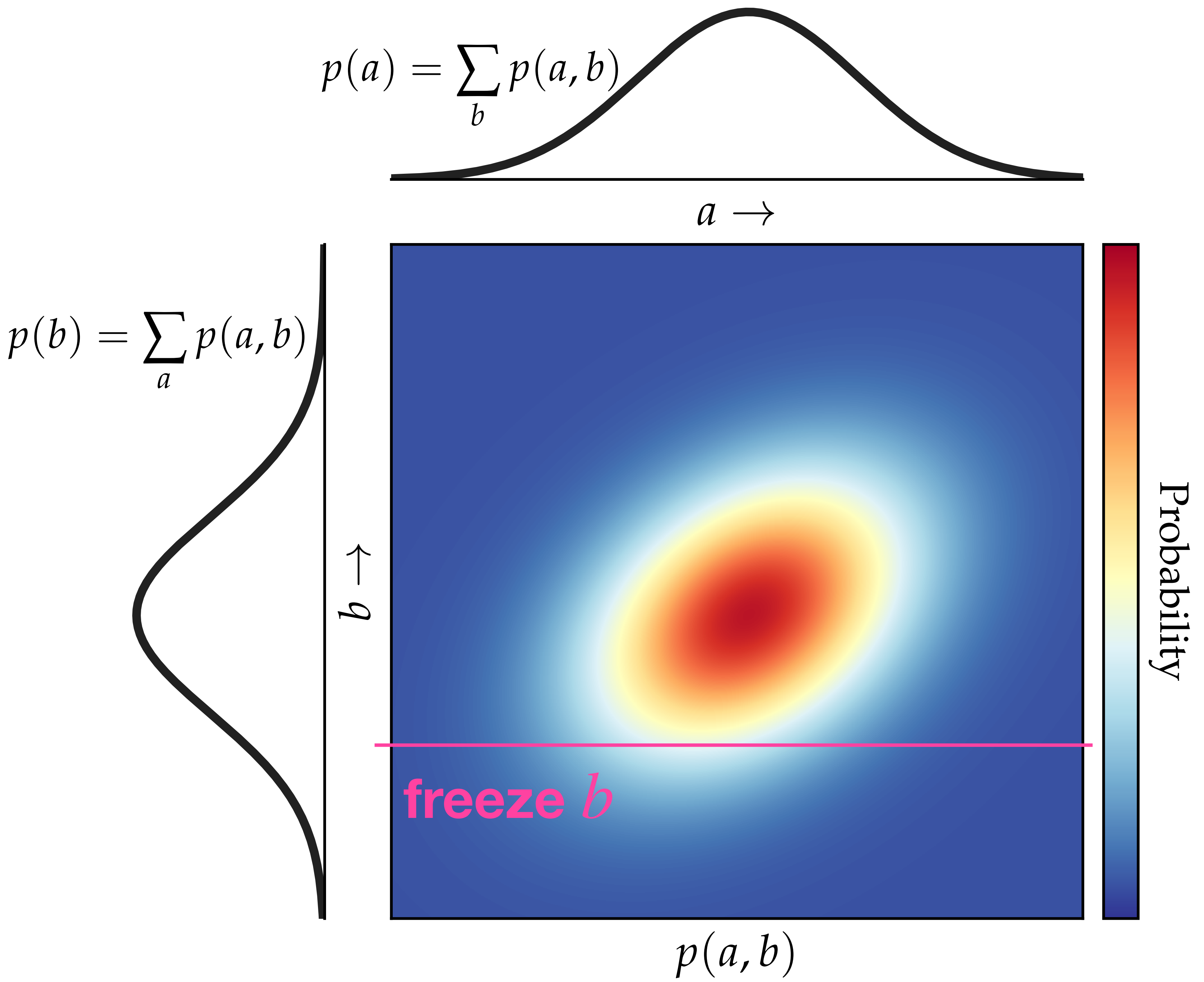
$$p(x) = \frac{1}{\sqrt{2\pi\sigma}} e^{-(x-\mu)^2/2\sigma^2}$$

"drawing" a random variable from a normal distribution

also written $\mathcal{N}(+\mu, \sigma^2)$ $\quad X \sim \mathcal{N}(+\mu, \sigma^2)$

conditional probability $p(x \,|\, y)$

probability density of X given the value y of another "event"



event could be: a completely different but correlated random variable, a condition on the random variable X

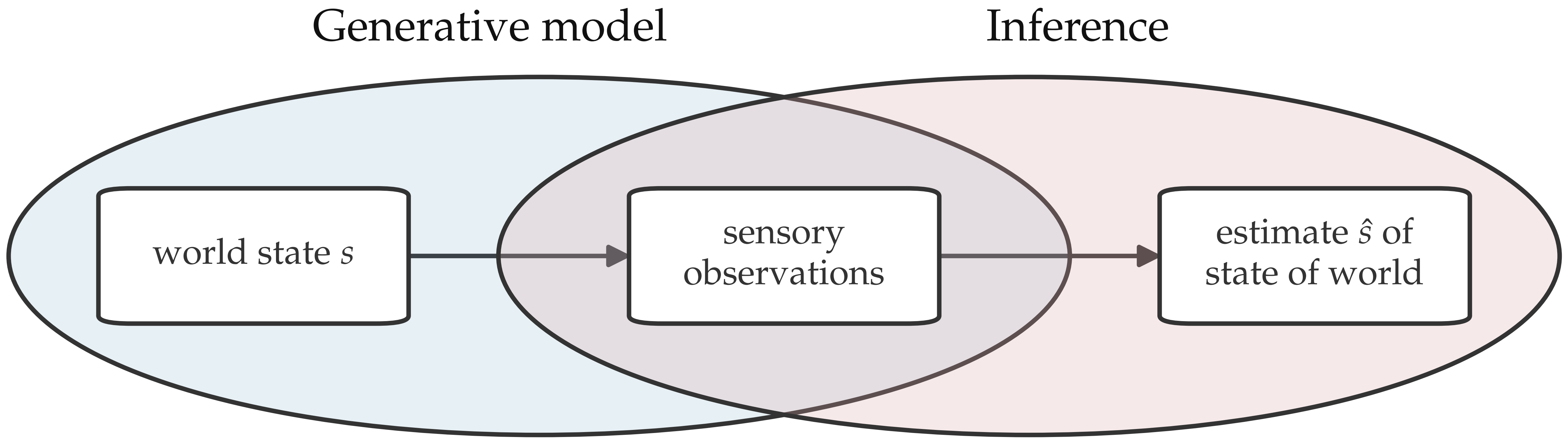
example: correlated normal random variables

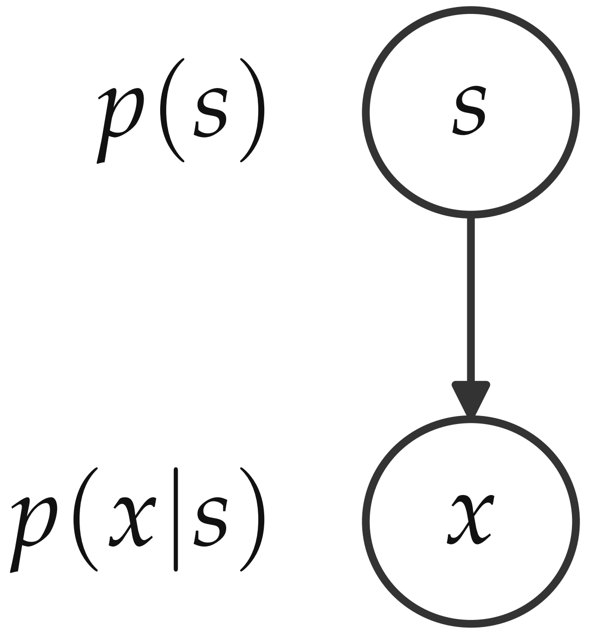
$$p(a \,|\, b) = \frac{p(a,b)}{p(b)}$$

could be:

- height & weight of an animal
- latitude & mean temp of city
- observed visual & auditory stimuli from common source

Bayesian model of the world & Bayes rule





stimulus

object feature

auditory source

observation

perceived feature value

perceived sound position

Bayes Rule

$$p(s\,|\,x) = \frac{p(x\,|\,s)p(s)}{p(x)}$$

$p(s\,|\,x)$ **posterior**

$p(x\,|\,s)$ **likelihood function**

$p(s)$ **source prior**

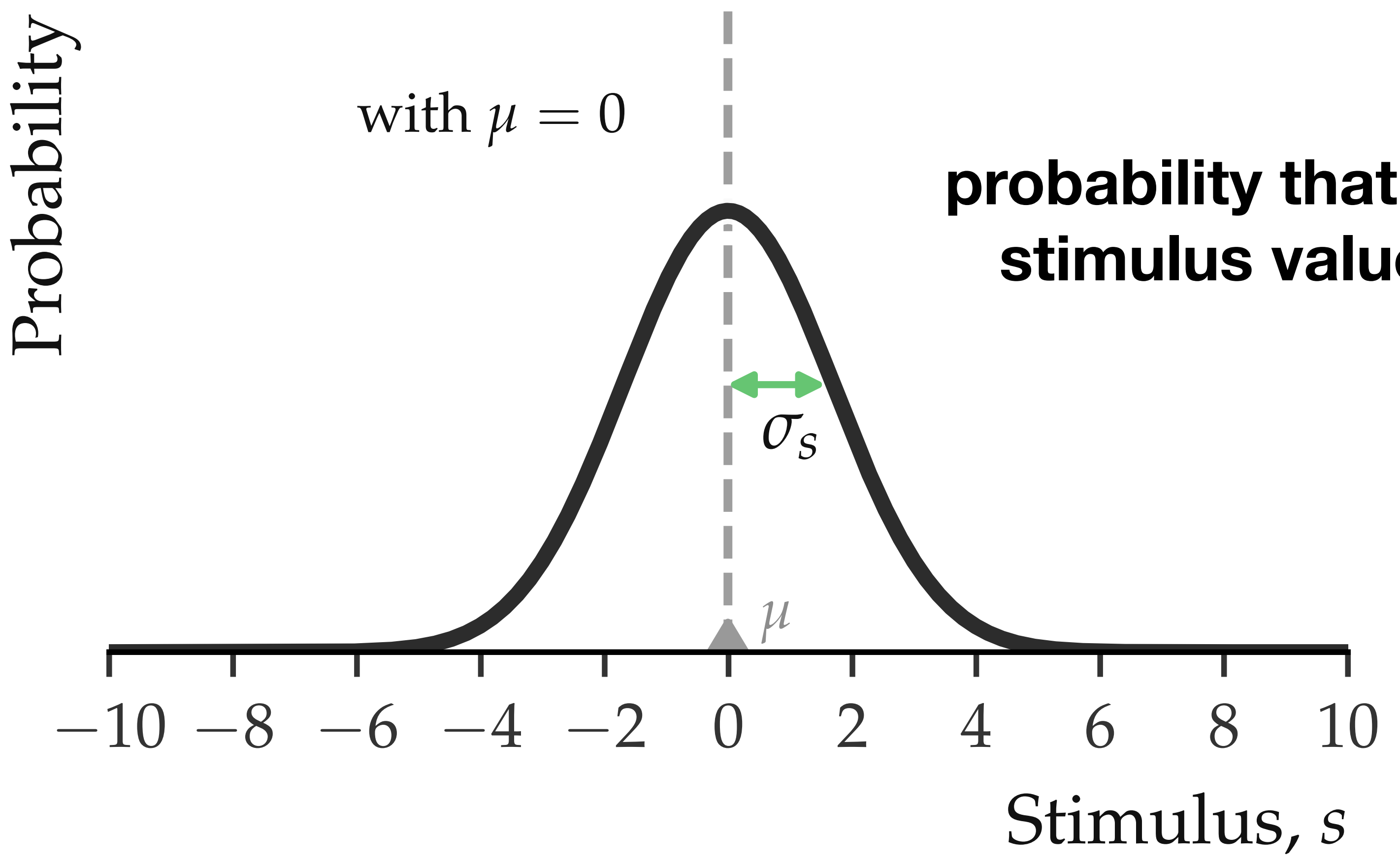
$p(x)$ **observation prior**

Example

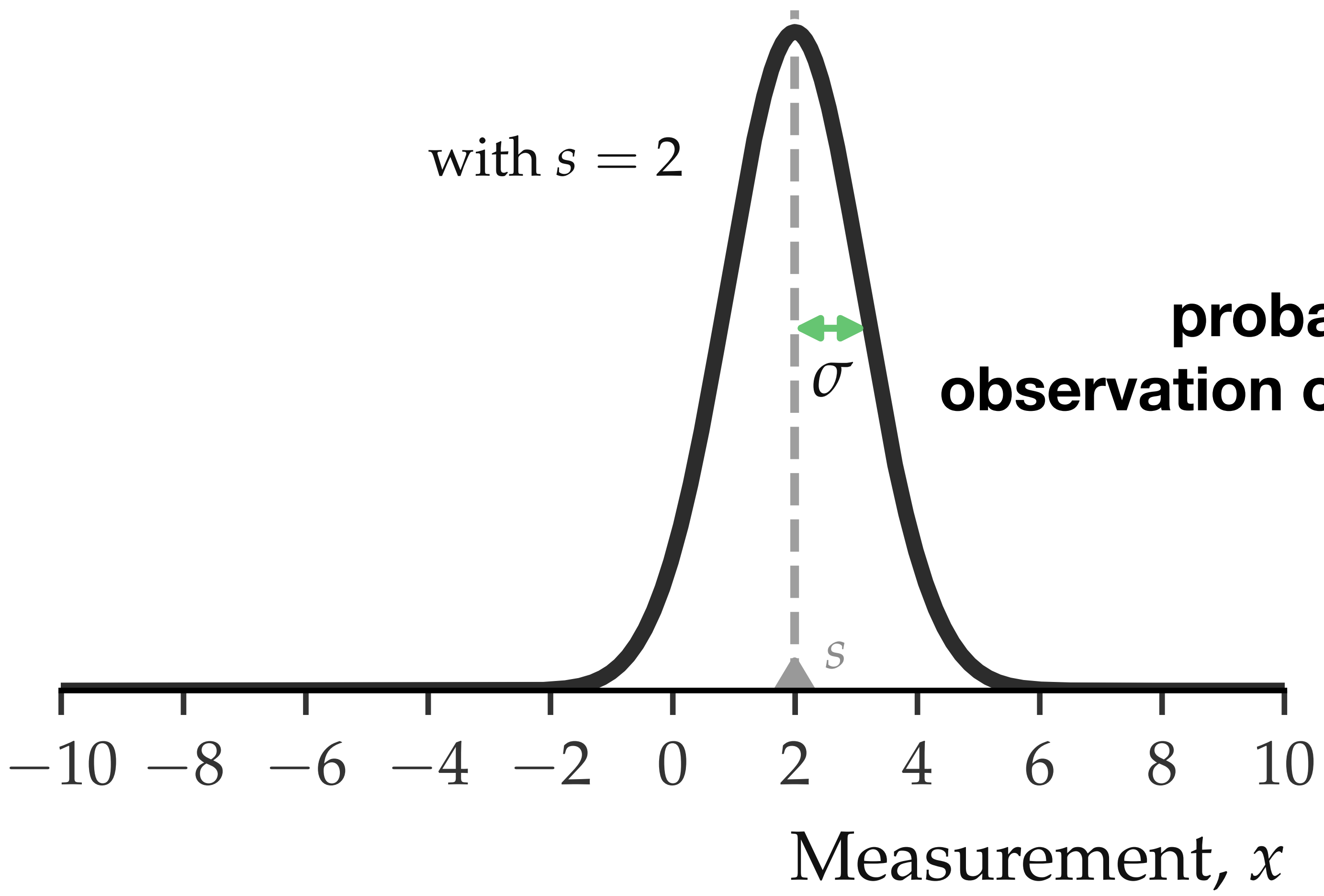
normal distribution

$$p_s(s) = \frac{1}{\sqrt{2\pi\sigma_s^2}}\, e^{-\frac{(x-\mu)^2}{2\sigma_s^2}}$$

$$p_{x|s}(x|s) = \frac{1}{\sqrt{2\pi\sigma^2}}\, e^{-\frac{(x-s)^2}{2\sigma^2}}$$

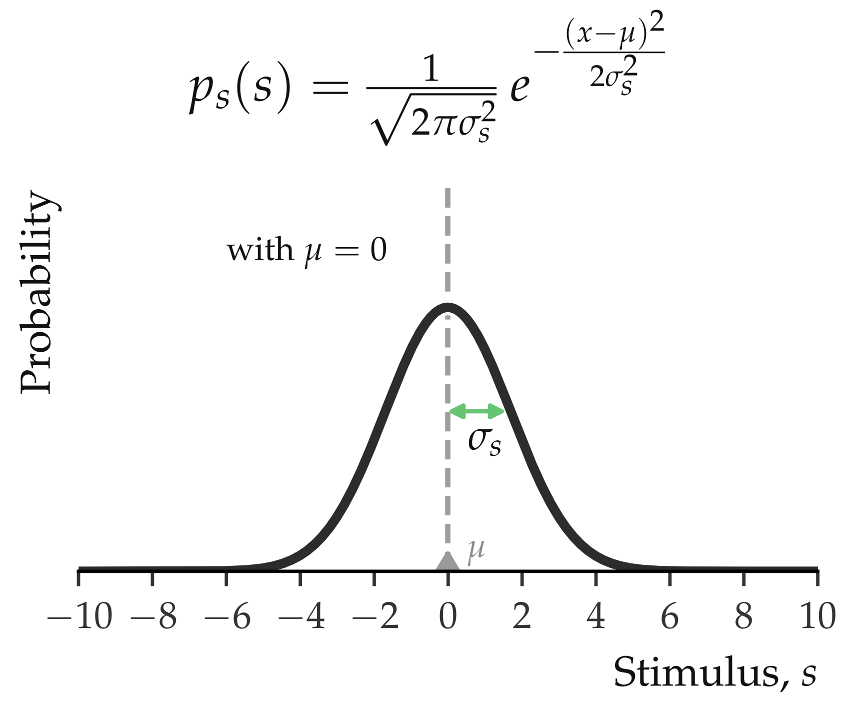


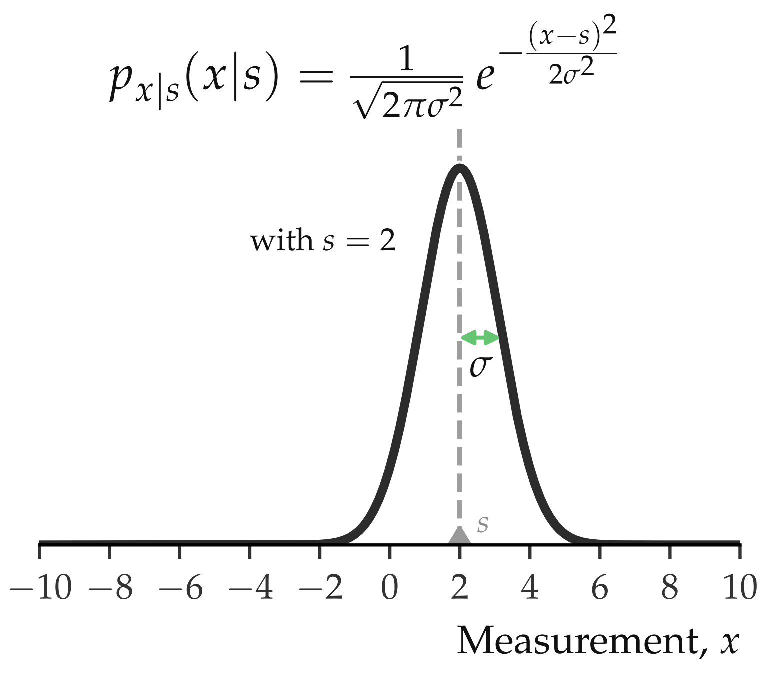
probability that a particular stimulus value is drawn



probability that a particular observation of that stimulus value is drawn

Combining evidence with priors





$$p(s\,|\,x_1) = \frac{p(x_1\,|\,s)p(s)}{p(x_1)} \propto p(x_1\,|\,s)p(s)$$

scaling factor doesn't matter, just the shape!

long calculation

e.g., normal distributions

$$p(s\,|\,x_1) \propto \exp\left[-\frac{(x_1 - s)^2}{2\sigma^2}\right] \cdot \exp\left[-\frac{(s-\mu)^2}{2\sigma_s^2}\right] \propto C \cdot \exp\left[-\frac{(s - \mu_{\text{post}})^2)}{2\sigma_{\text{post}}^2}\right]$$

where

$$\mu_{\text{post}} = \frac{J_1 x_1 + J_s\mu}{J_1 + J_s} \quad \textbf{and} \quad \sigma_{\text{post}}^2 = \frac{1}{J_1 + J_s} \quad \textbf{and} \quad J_1 = \frac{1}{\sigma^2} \quad \textbf{and} \quad J_s = \frac{1}{\sigma_s^2}$$

stimulus estimate | **uncertainty on estimate** | **"precisions"**

precisions differentially weight prior and observation

$$w_1 = \frac{J_1}{J_1 + J_s} \longrightarrow \mu_{\text{post}} = w_1 x_1 + (1 - w_1)\mu$$

bias due to prior

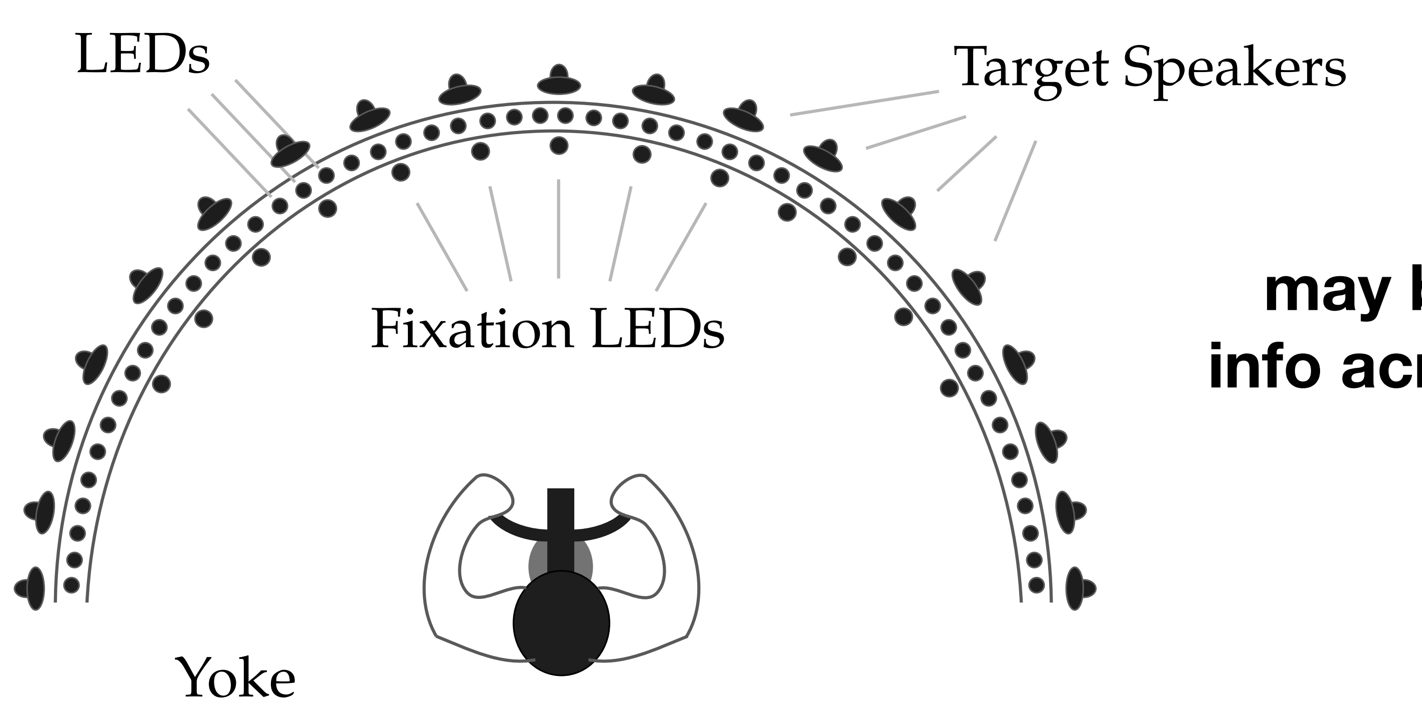
$$\text{Bias}\left[\mu_{\text{post}}\,|\,s\right] = E\left[\mu_{\text{post}}\,|\,s\right] - s = w_1\langle x_1\rangle + (1-w_1)\mu - s = w_1 s - s + (1-w_1)\mu = (1-w_1)(\mu - s)$$

variance reduced by prior

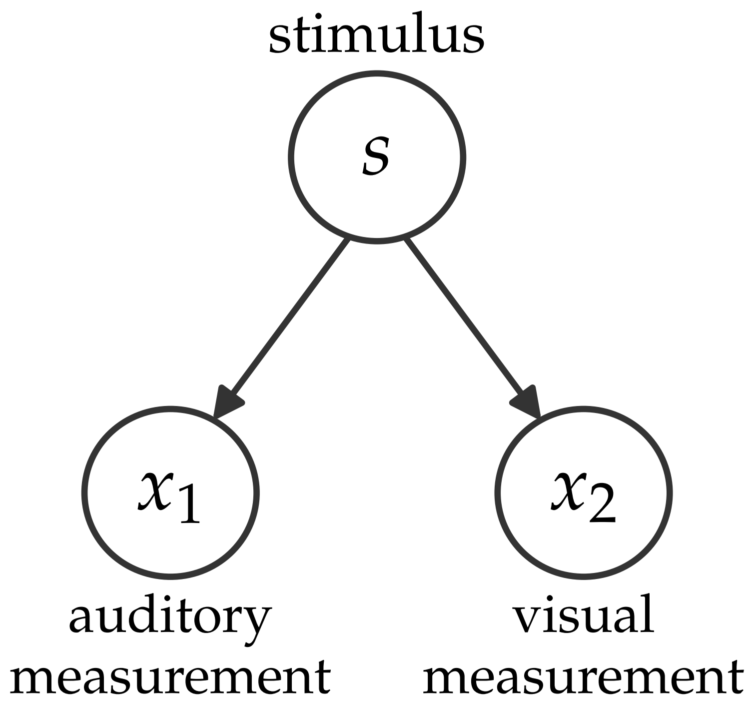
$$\text{Var}\left[\mu_{\text{post}}\,|\,s\right] = w_1^2\text{Var}\left[x_1\,|\,s\right] = w_1^2 \cdot \sigma^2 < \sigma^2$$

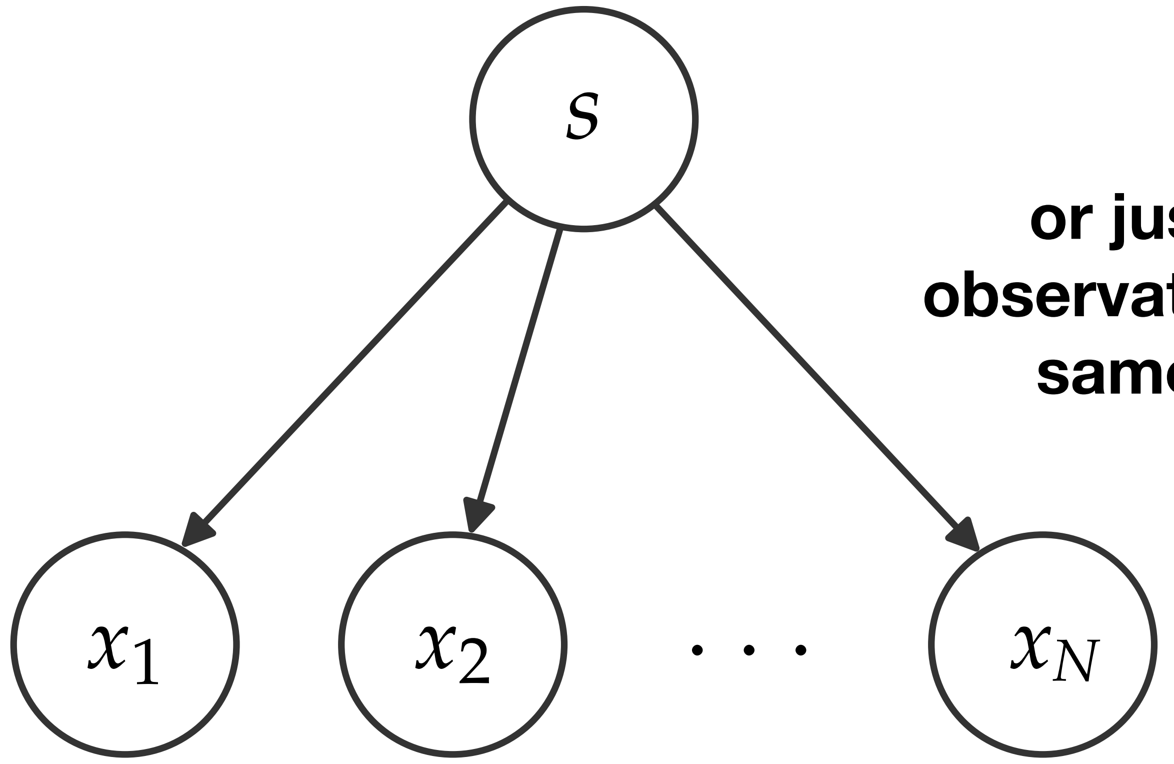
these two quantities "tradeoff" as prior is adjusted

Combining multiple pieces of evidence



may be combining info across modalities





or just multiple observations from the same stimulus

two observation case

$$p(x_1, x_2 \mid s) = p(x_1 \mid s)p(x_2 \mid s)$$

if observations are <u>conditionally independent</u>

assume normally distributed observations & prior

$$p(x_j \mid s) = \frac{1}{\sqrt{2\pi}\sigma_j} \exp\left[-\frac{(x_j - s)^2)}{2\sigma_j^2}\right]$$

$$p(s \mid x_{1:2}) \propto p(x_1 \mid s)p(x_2 \mid s)p(s) \longrightarrow p(s \mid x_{1:2}) = C \exp\left[-\frac{(s - \mu_{\text{post}})^2}{2\sigma_{\text{post}}^2}\right]$$

$$\mu_{\text{post}} = w_1 x_1 + w_2 x_2 + (1 - w_1 - w_2)\mu \qquad \sigma_{\text{post}}^2 = \left[J_1 + J_2 + J_s\right]^{-1} = J_{\text{post}}^{-1} \qquad w_j = J_j / J_{\text{post}} \qquad J_j = \frac{1}{\sigma_j^2}$$

multiple observations

$$p(s \mid x_{1:N}) \propto p(x_1 \mid s)p(x_2 \mid s)\cdots p(x_N \mid s)p(s)$$

$$\mu_{\text{post}} = \sum_{n=1}^{N} w_n x_n + \left(1 - \sum_{n=1}^{N} w_n\right)\mu \qquad J_{\text{post}} = \sum_{n=1}^{N} J_j + J_s$$

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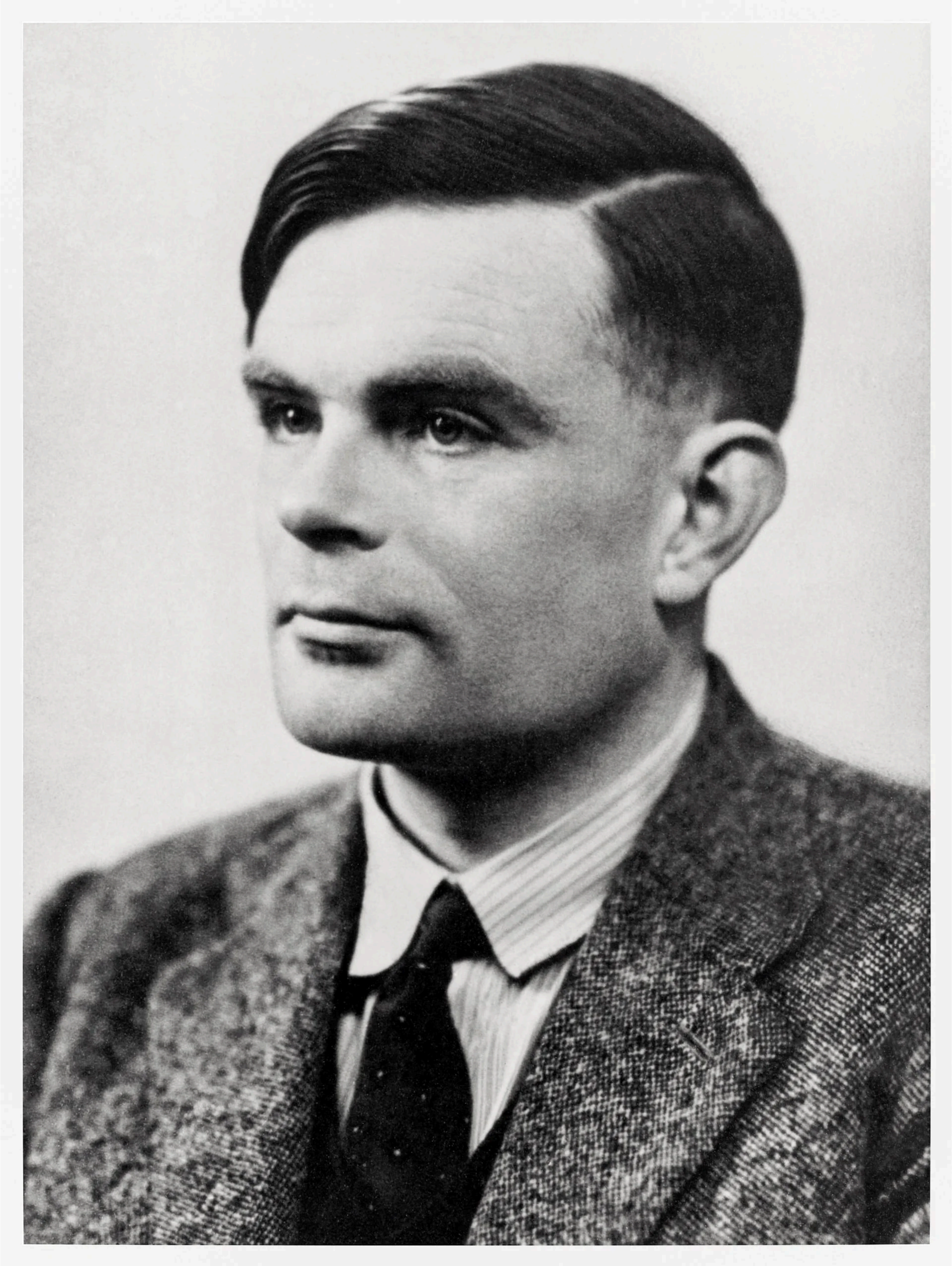
log likelihood ratio (LLR) update

$$\textbf{belief} = \log \frac{P(\textbf{choice A true} \mid \textbf{evidence})}{P(\textbf{choice B true} \mid \textbf{evidence})}$$

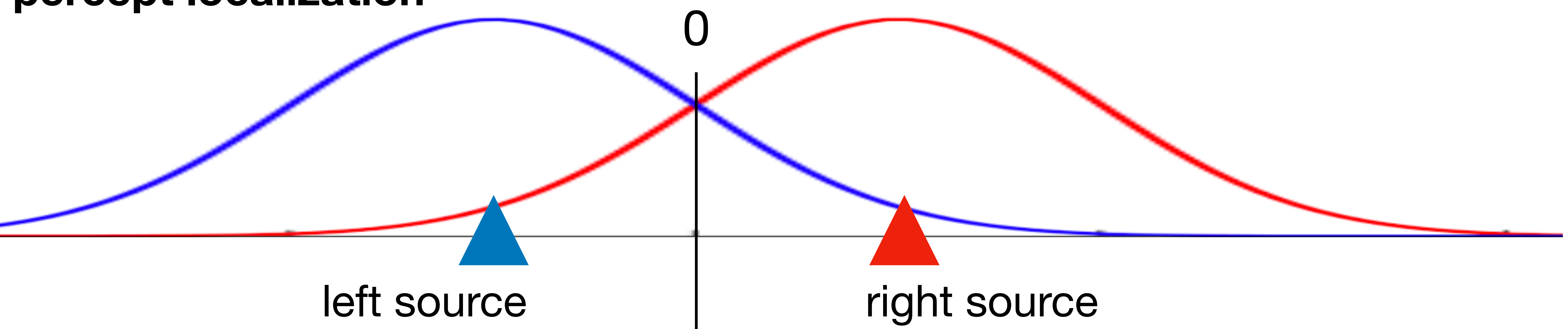
**(Neyman & Pearson 1933;
Turing 1942;
Wald & Wolfowitz 1948)**



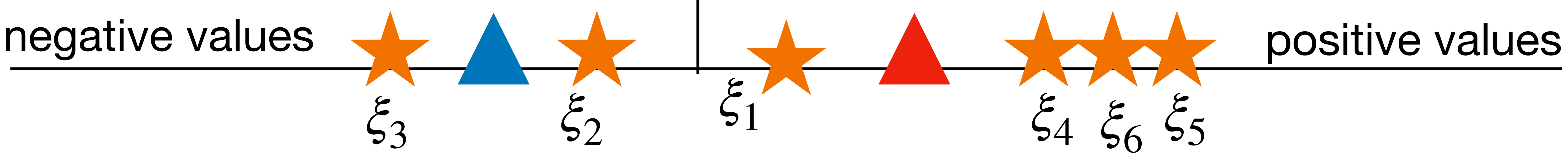
Log-likelihood ratio update

consider an observer who must determine the location of a stimulus (e.g., visual or auditory) source

percept localization



$$f_-(\xi) = \mathcal{N}(-\mu, \sigma^2) \qquad f_+(\xi) = \mathcal{N}(+\mu, \sigma^2)$$



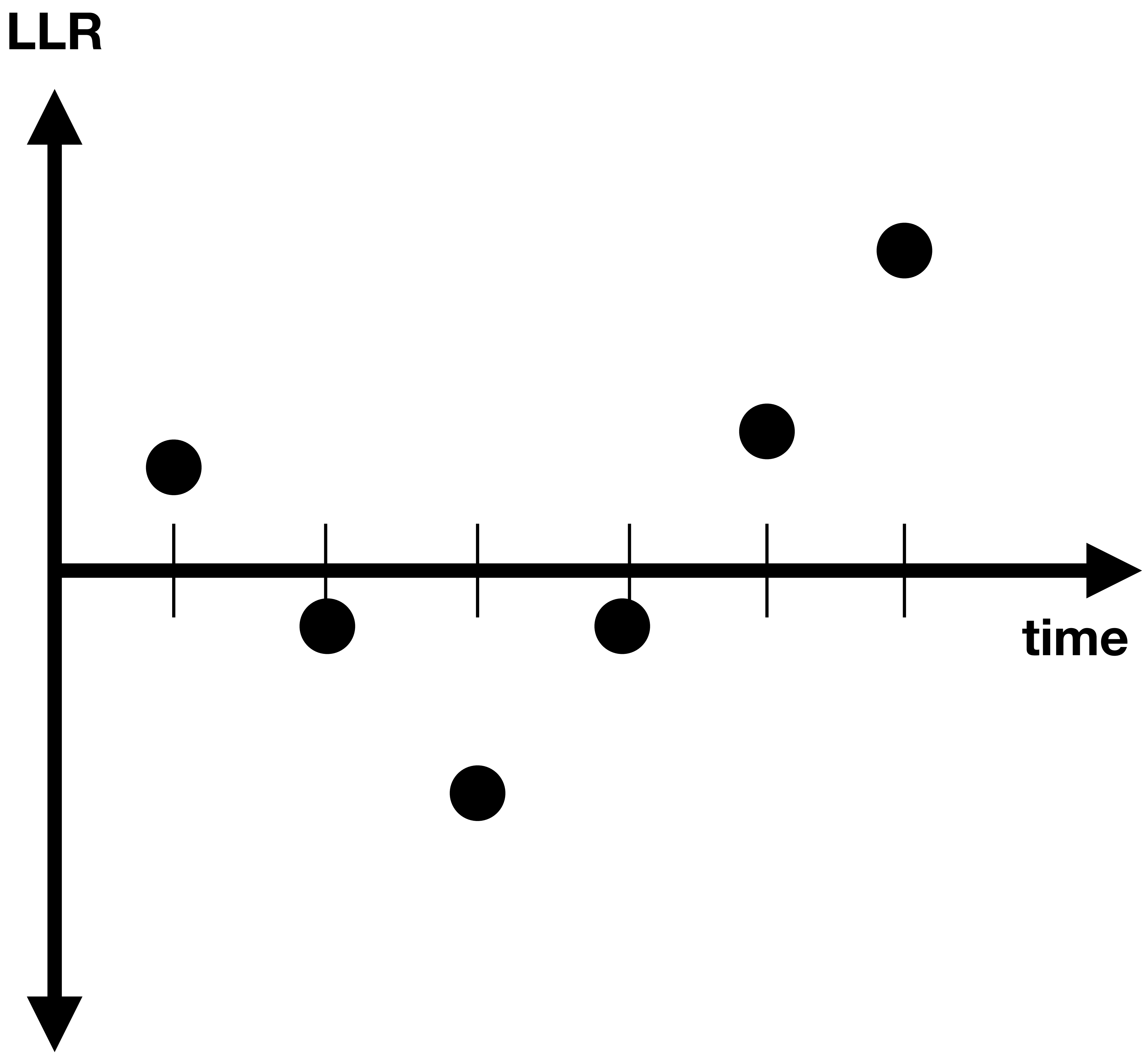
information from each observation: $\mathrm{LLR}(\xi) = \log \dfrac{f_+(\xi)}{f_-(\xi)} = \dfrac{2\mu}{\sigma^2}\xi$ if positive: *right more likely* if negative: *left more likely*

log likelihood ratio (LLR) update
(Wald 1947; Gold & Shadlen 2002; Bogacz et al 2006)

$$\mathrm{LLR}(\xi_{1:6}) = \frac{2\mu}{\sigma^2} \cdot \left[\xi_1 + \xi_2 + \xi_3 + \xi_4 + \xi_5 + \xi_6\right]$$

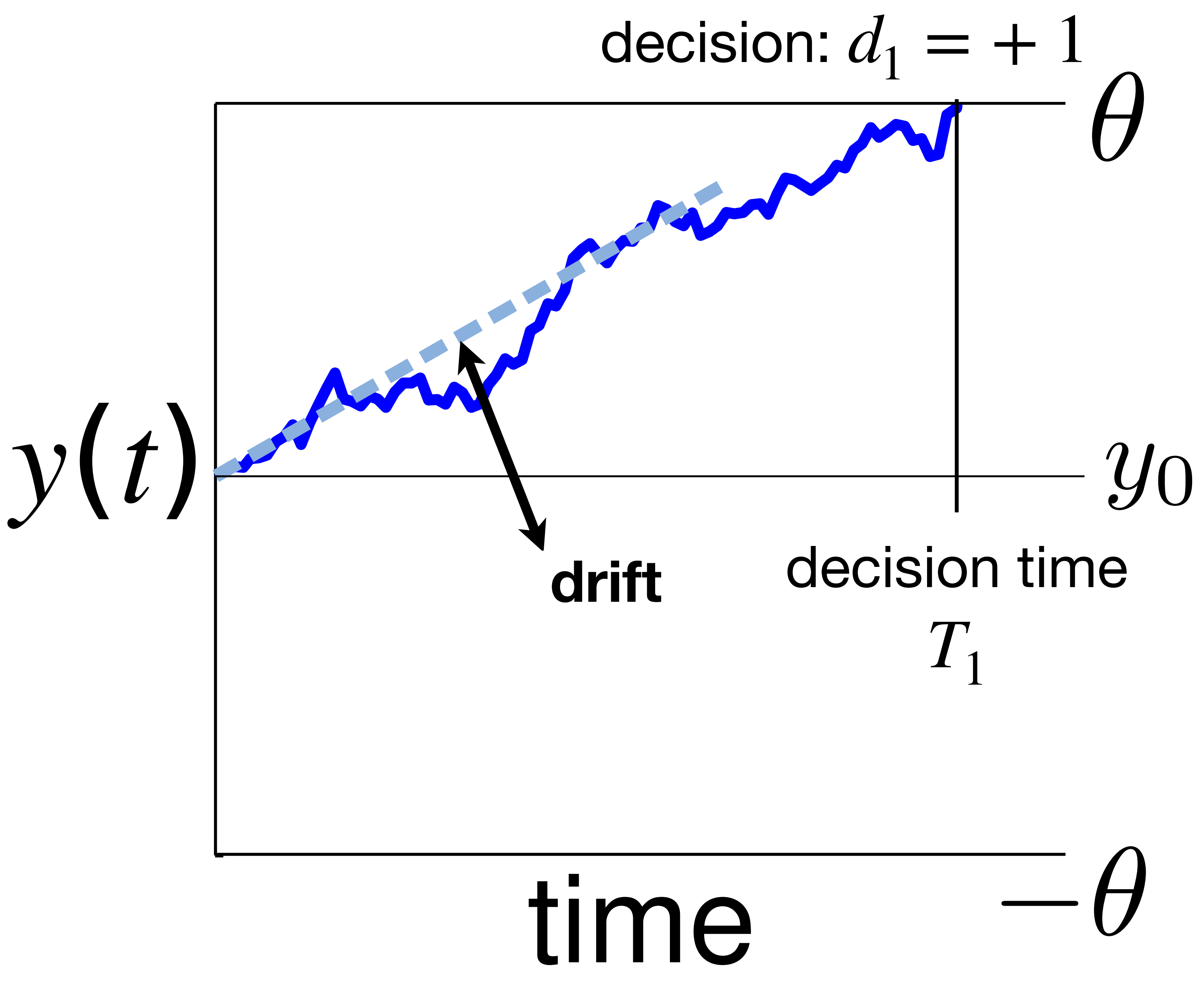
define $y_t = \mathrm{LLR}(\xi_{1:t})$:

$$\boxed{y_t \equiv y_{t-1} + \mathrm{LLR}(\xi_t)}$$



Drift diffusion model and decision statistics

$$y_n - y_{n-1} = \mathrm{LLR}(\xi_n) \quad \mapsto \quad \frac{dy}{dt} = \pm 1 + \sqrt{2} \cdot \xi(t)$$



decrease speed/
increase accuracy

increase speed/
decrease accuracy

trial-wise data

(d_1, T_1)	(d_2, T_2)	(d_3, T_3)	(d_4, T_4)	$\cdots$
trial 1	**trial 2**	**trial 3**	**trial 4**	

accuracy $$\mathrm{Acc} = \frac{1}{N_{\mathrm{trials}}} \sum_{n=1}^{N_{\mathrm{trials}}} \delta_{d_n,+1}$$

$$\log \frac{P(H^+ \mid \xi_{1:t})}{1 - P(H^+ \mid \xi_{1:t})} = \theta \quad \rightarrow \quad P(H^+ \mid \xi_{1:t}) = \frac{1}{1 + e^{-\theta}}$$

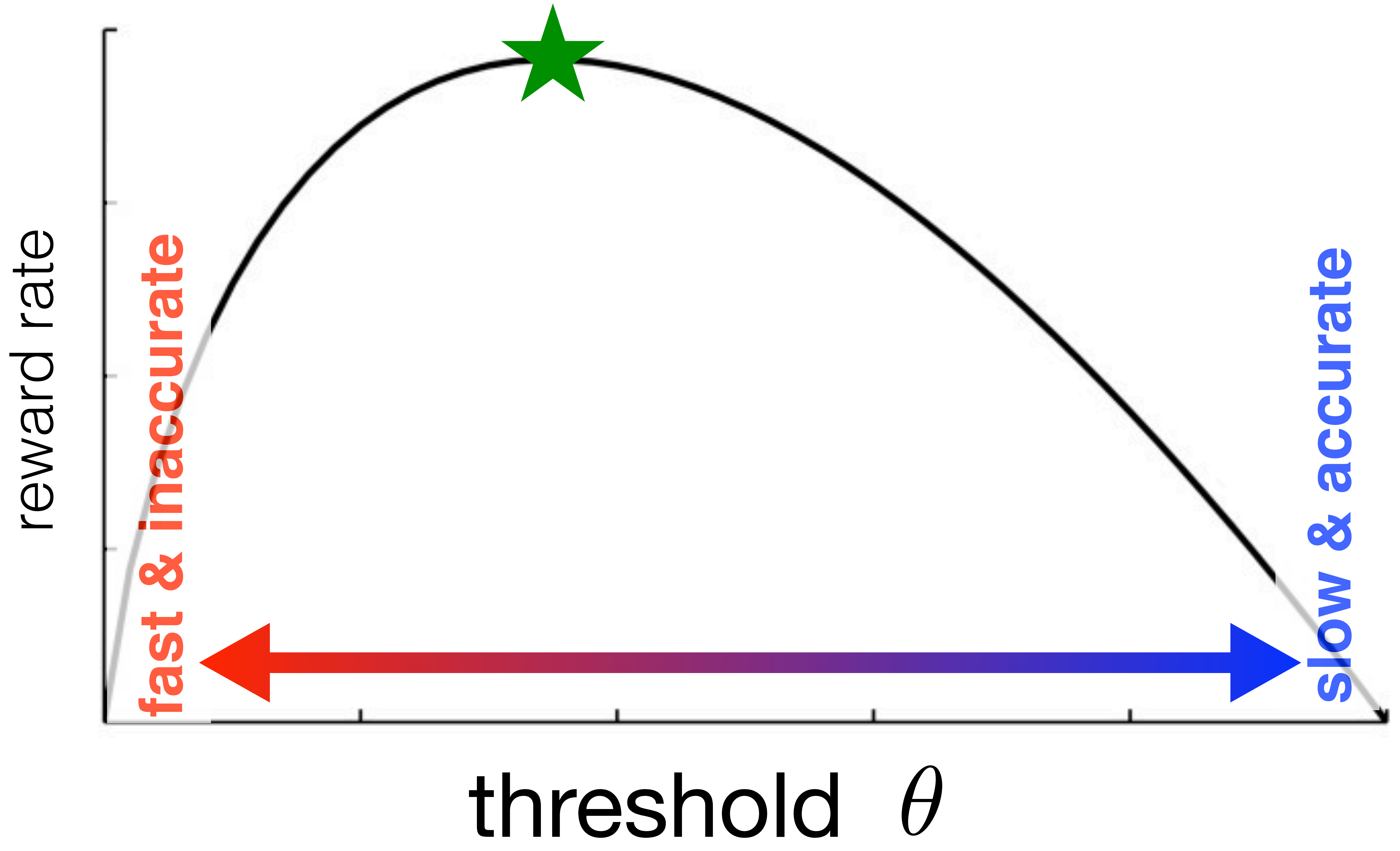
decision time distribution: bin T_n into histograms

mean decision time: $$\bar{T} = \frac{1}{N_{\mathrm{trials}}} \sum_{n=1}^{N_{\mathrm{trials}}} T_n$$

Reward rate

$$RR = \frac{\text{percent correct}}{(\text{decision time}) + (\text{penalty time})}$$

(Wald & Wolfowitz 1948;
Gold & Shadlen 2002)



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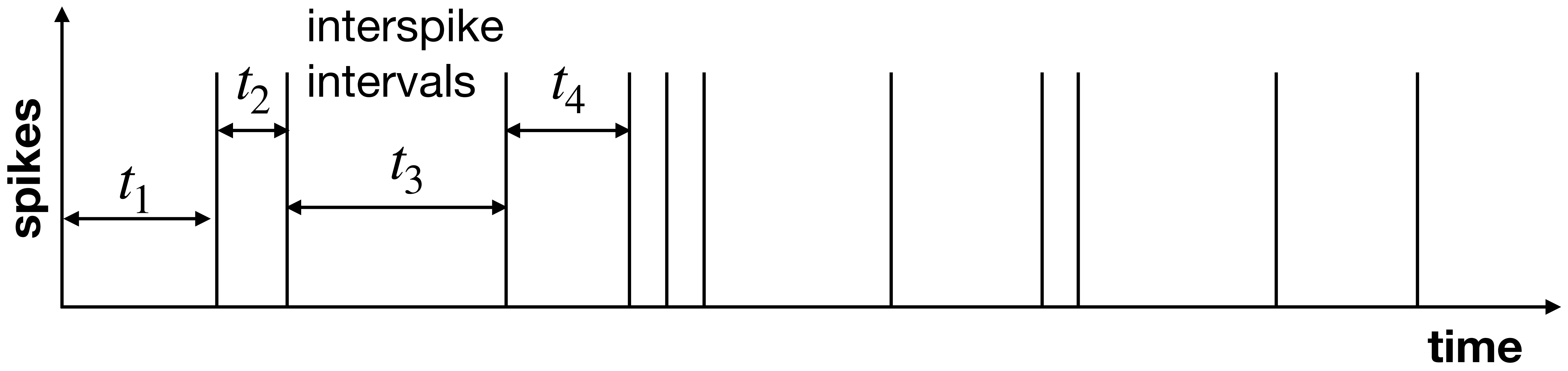
Bayesian parameter fitting

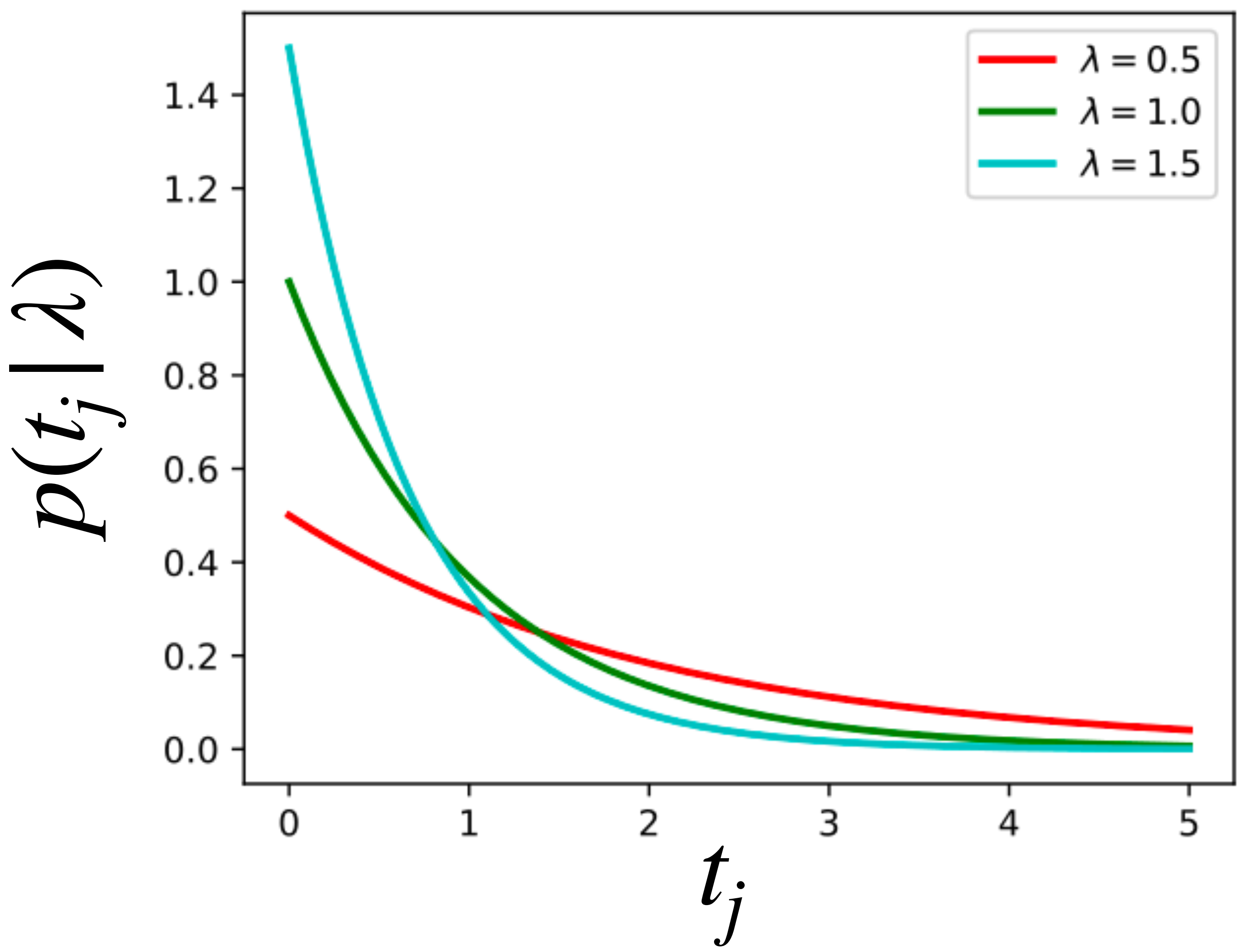
Bayes rule can also be used to fit models



consider a Poisson neuron model with rate parameter λ

interspike intervals are exponentially distributed

$$p(t_j \mid \lambda) = \lambda e^{-\lambda t_j}$$



Poisson model assumes independence of consecutive spike time intervals

$$p(t_{1:N} \mid \lambda) = p(t_1 \mid \lambda) p(t_2 \mid \lambda) \cdots p(t_N \mid \lambda)$$

assume λ is not known; we can use Bayes rule to invert the above to find it

$$p(\lambda \mid t_{1:N}) \propto p(t_1 \mid \lambda) p(t_2 \mid \lambda) \cdots p(t_N \mid \lambda) p(\lambda)$$

might use flat "improper" $p(\lambda) = c$ or something simple $p(\lambda) = e^{-\lambda t_0}$

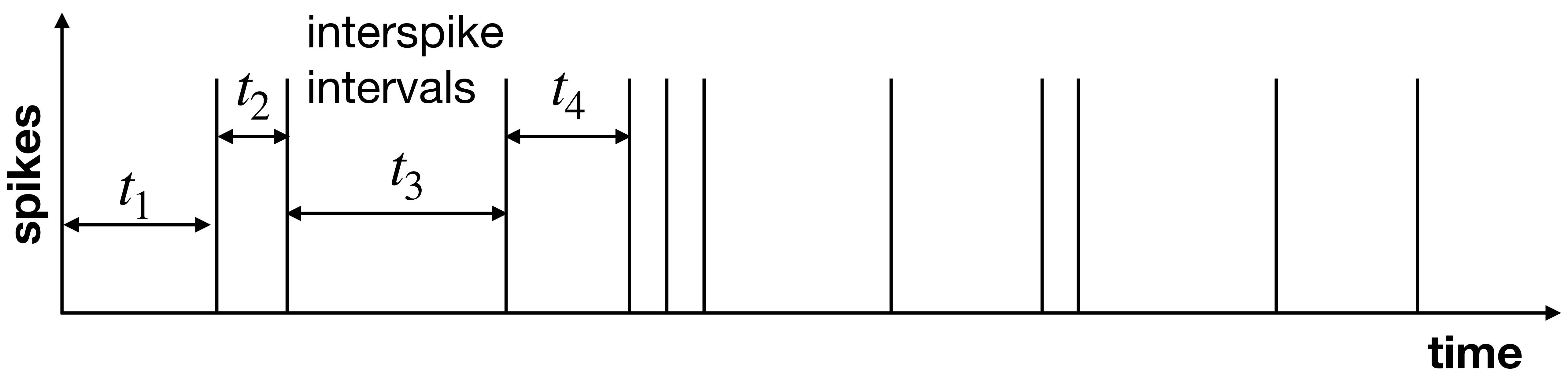
a major advantage of Bayesian parameter fitting is each observation can be incorporated sequentially to update estimate

$$p(\lambda \mid t_{1:N}) \propto p(t_N \mid \lambda) \cdot p(\lambda \mid t_{1:N-1})$$

<u>example with exponential waiting times</u>

$$p(\lambda \mid t_{1:N}) \propto \lambda e^{-\lambda t_1} \lambda e^{-\lambda t_2} \ldots \lambda e^{-\lambda t_N} e^{-\lambda t_0} = \lambda^N e^{-\lambda \sum_{n=0}^{N} t_n}$$

Bayesian model selection



what if we are deciding between two types of model?

let's say intervals are maybe exponentially or perhaps Gamma distributed: let's see which model is more likely!

$$p(t_j|\lambda) = \lambda e^{-\lambda t_j}$$

exponential

$$p(\lambda) = e^{-\lambda}$$

presumed prior

$$p(t_j|\lambda) = \frac{\beta^{\alpha+1}}{\alpha!}\lambda^\alpha e^{-\beta\lambda}$$

Gamma

$$p(\alpha,\beta) = e^{-\alpha-\beta}$$

presumed prior

OK, now make a few observations from spikes and compute the observation/data (not parametric) posterior for either model

exponential $$p(t_{1:N}|\lambda) = C_e \lambda^N e^{-\lambda \sum_{n=1}^N t_n}$$

Gamma $$p(t_{1:N}|\alpha,\beta) = C_g \left(\prod_{n=1}^N t_n\right)^\alpha e^{-\beta\cdot \sum_{n=1}^N t_n}$$

<u>Bayes factor:</u> integrate observation posterior against prior to obtain total model likelihood and compare between models

$$\mathrm{BF} = \frac{\sum_{\alpha=0}^\infty \int_0^\infty p(t_{1:N}|\alpha,\beta)p(\alpha,\beta)d\beta}{\int_0^\infty p(t_{1:N}|\lambda)p(\lambda)d\lambda}$$

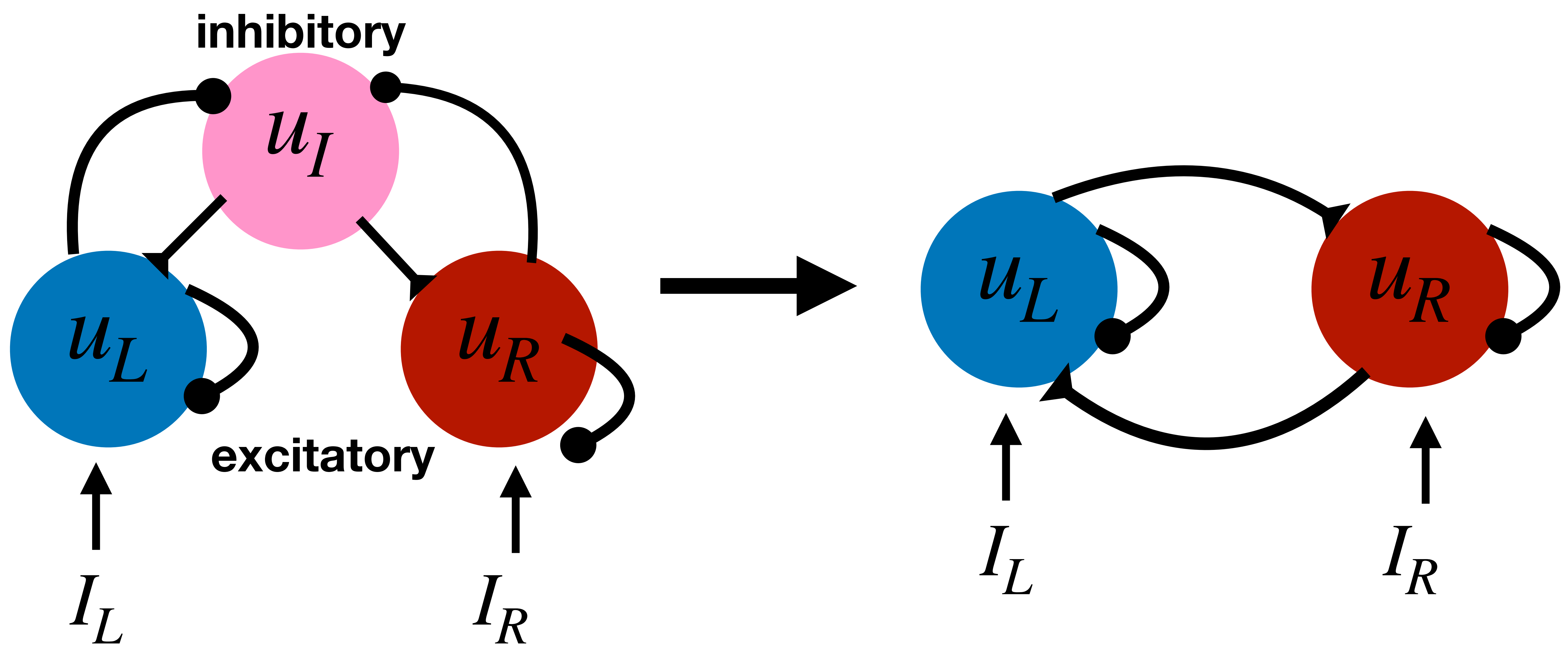
if BF>1, then top model is more likely

if BF<1, then bottom model is more likely

jupyter notebook

Mutual inhibition and winner take all circuits

How can decisions be implemented in a neural circuit? One classic proposed and observed mechanism is mutual inhibition.



$$\frac{du_L}{dt} = -u_L + f(I_L + \alpha u_L - \beta u_R)$$

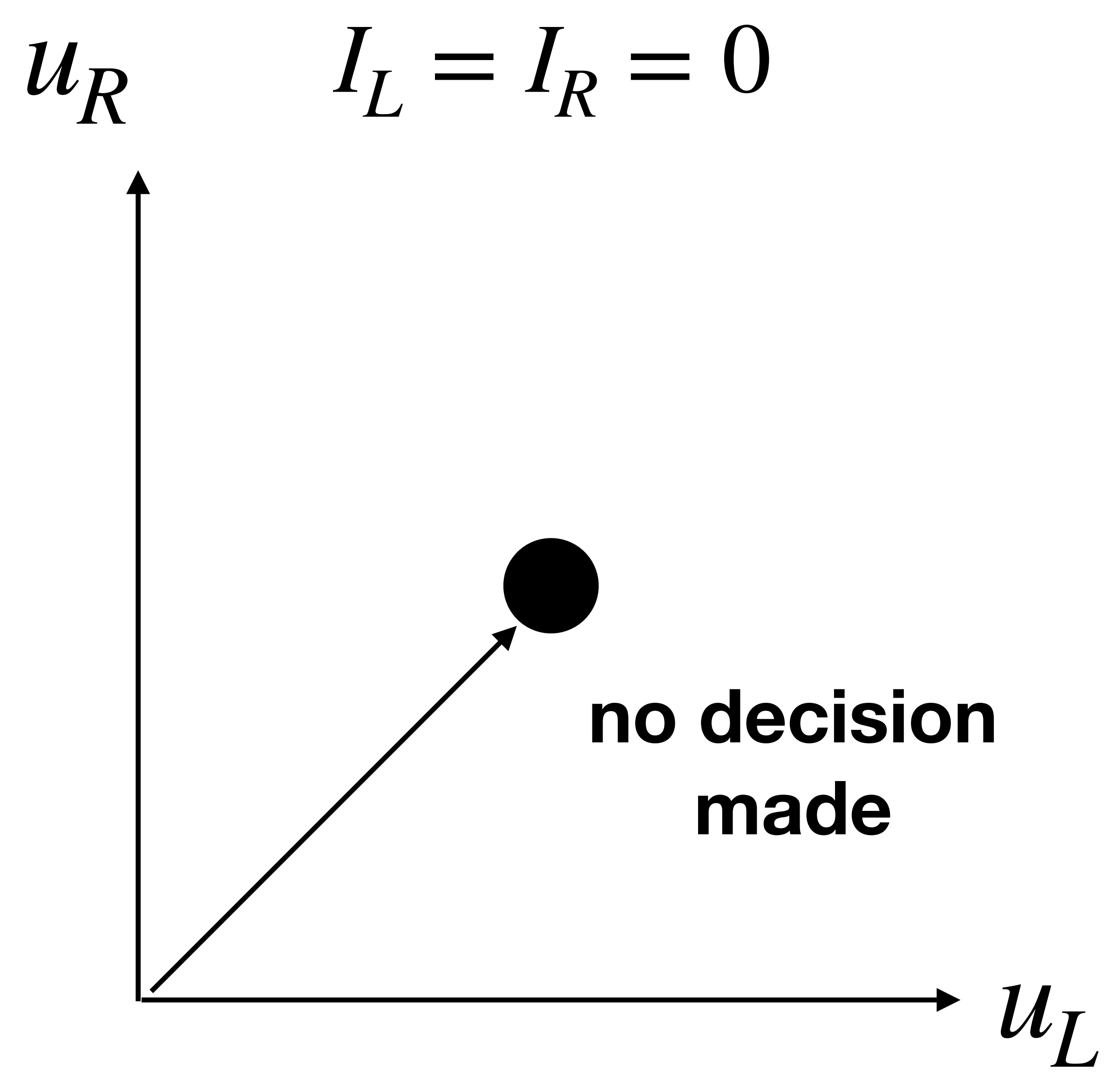
left pop differential equation

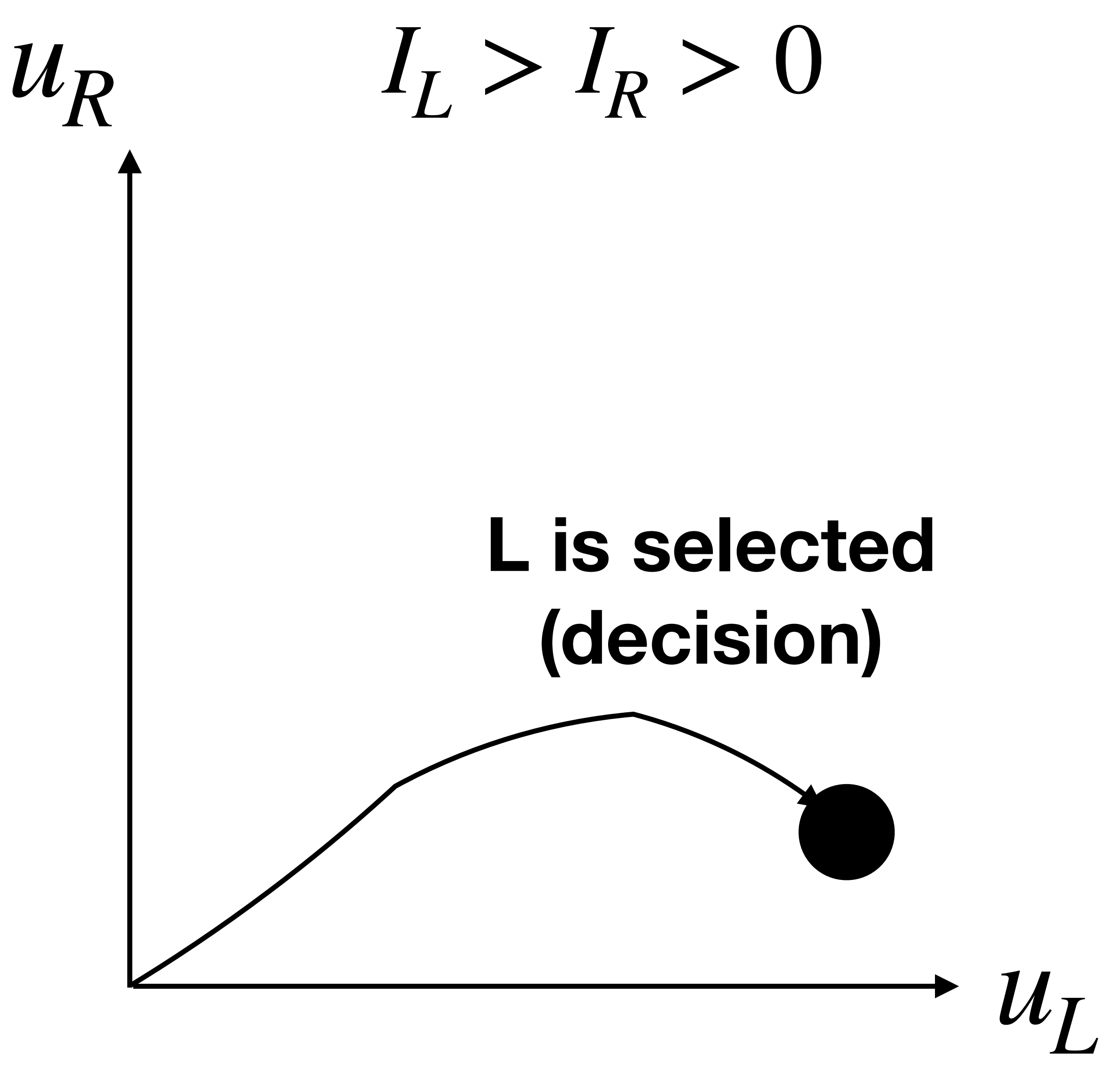
$$\frac{du_R}{dt} = -u_R + f(I_R + \alpha u_R - \beta u_L)$$

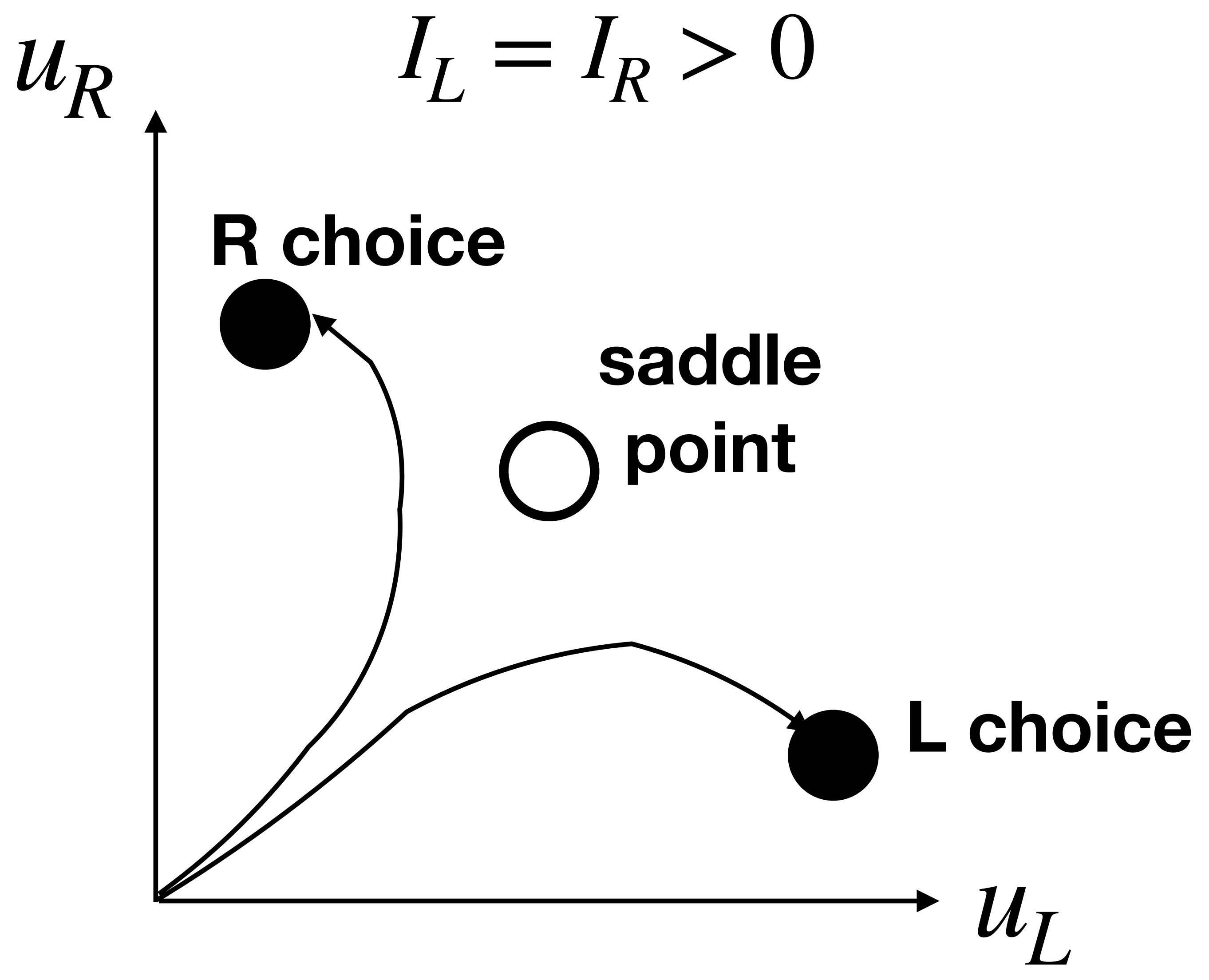
right pop differential equation

$$f(x) = \frac{1}{1 + e^{-\gamma x}}$$

firing rate function







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