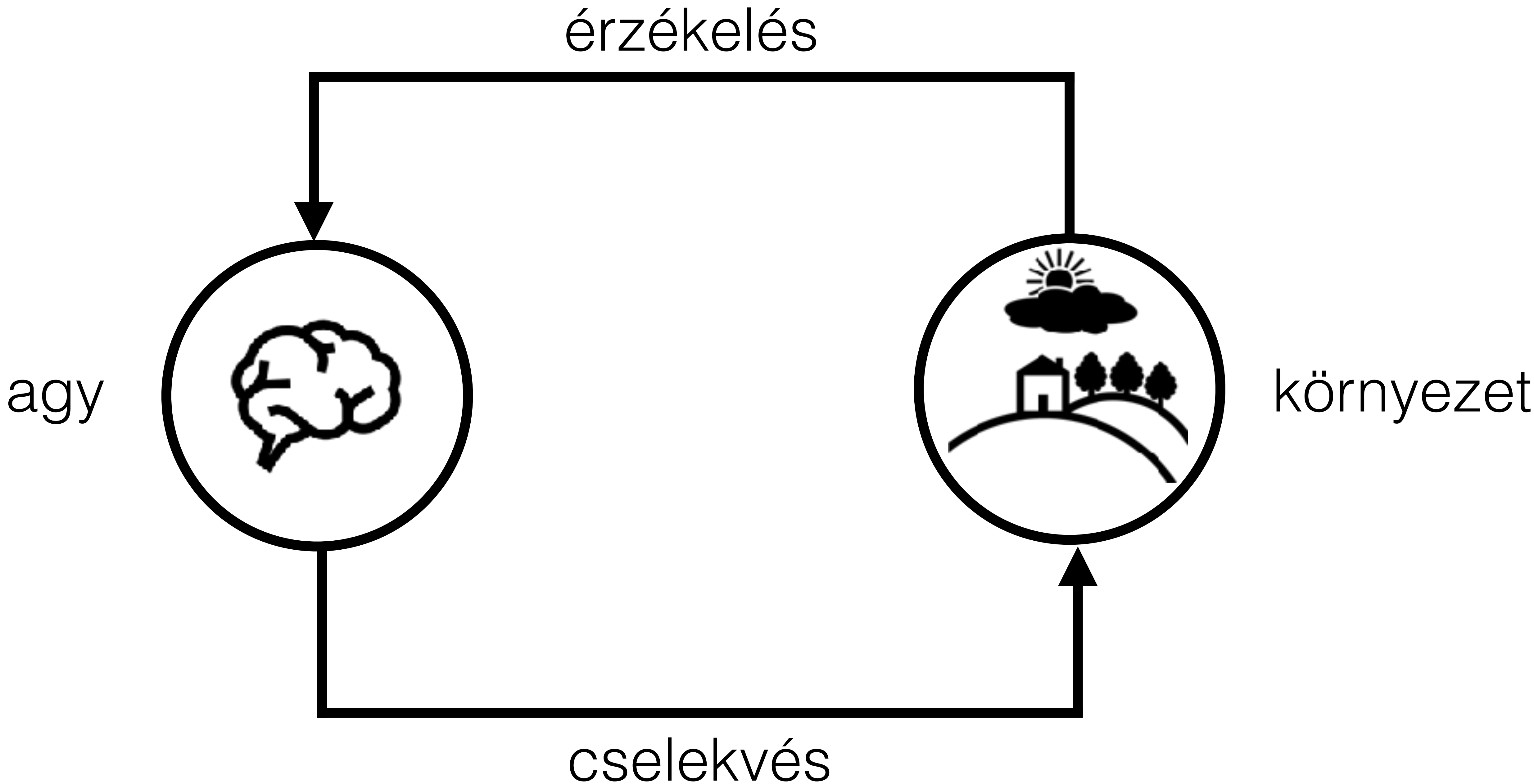
Statisztikus tanulás az idegrendszerben

ORBÁN GERGŐ

golab.wigner.mta.hu

WIGNER RESEARCH CENTRE FOR PHYSICS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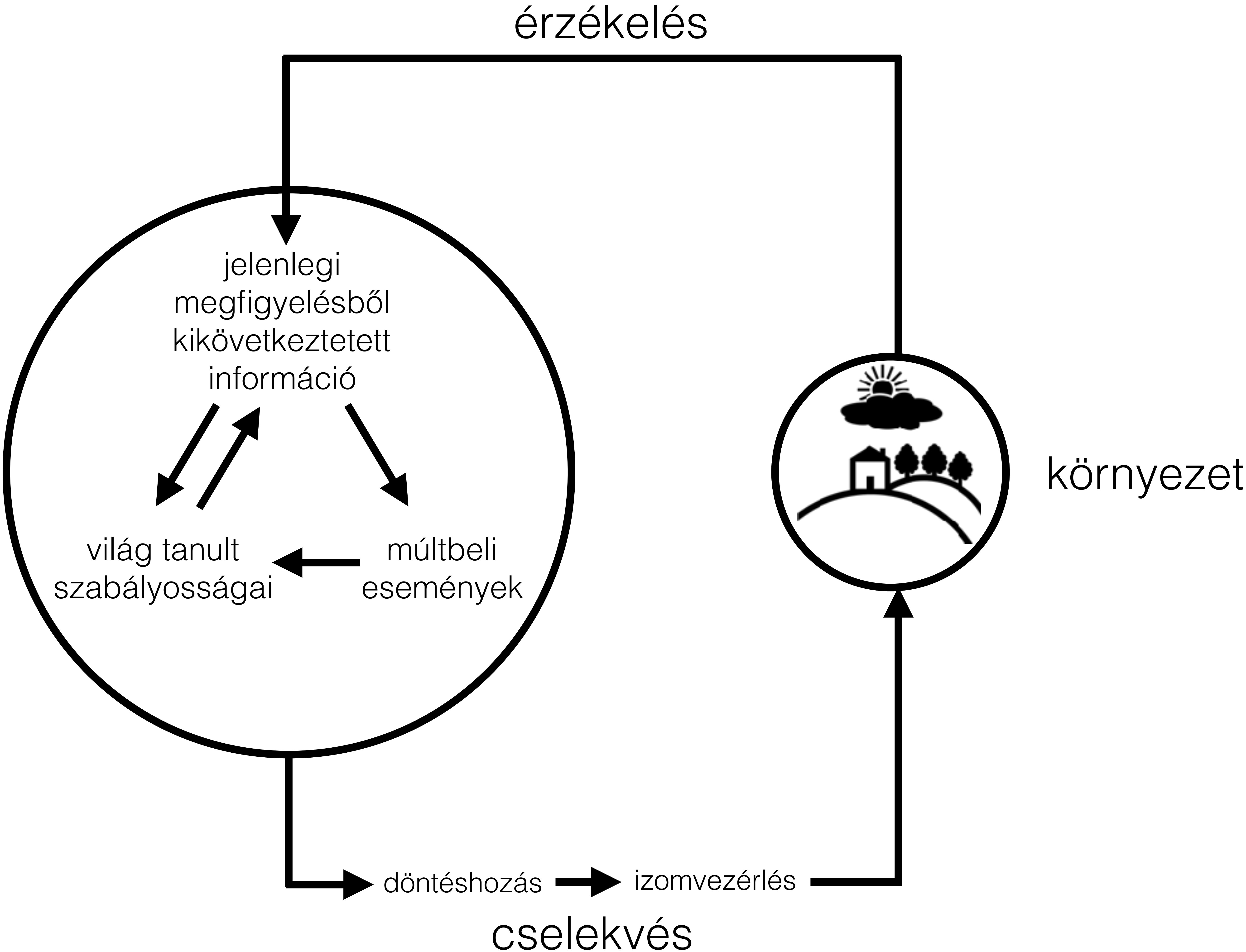
érzékelés
jelenlegi megfigyelésből kikövetkeztetett információ
világ tanult szabályosságai
múltbeli események
környezet
döntéshozás
izomvezérlés
cselekvés

Introduction

Knowledge representation

Probabilistic models

Bayesian behaviour

Approximate inference I (computer lab)

Vision I

Approximate inference II: Sampling

Measuring priors

Neural representation of probabilities

Structure learning

Vision II

Decision making and reinforcement learning

elméleti

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elméleti

kognitív

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elméleti

kognitív

neurális

Bayes inferencia

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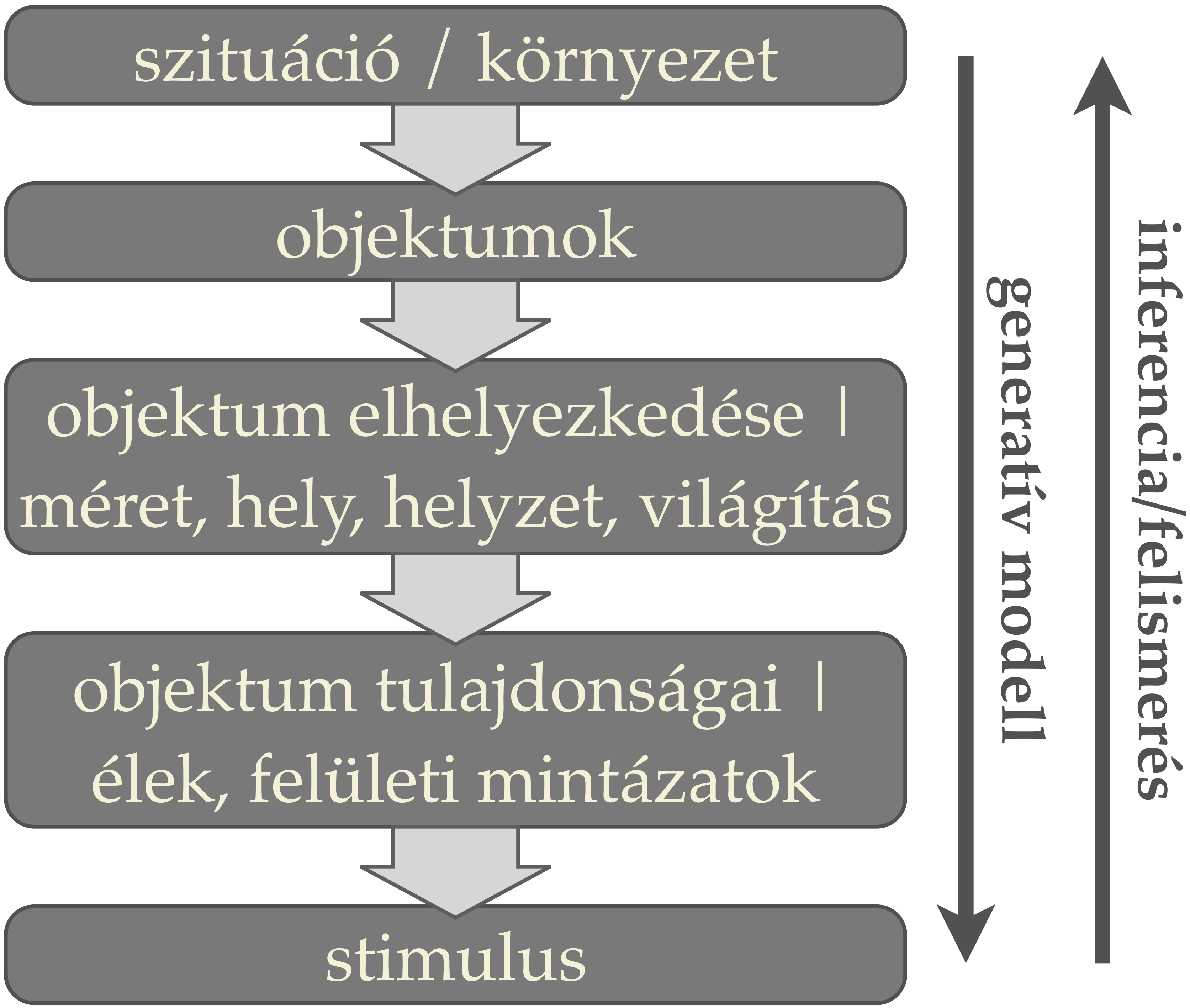

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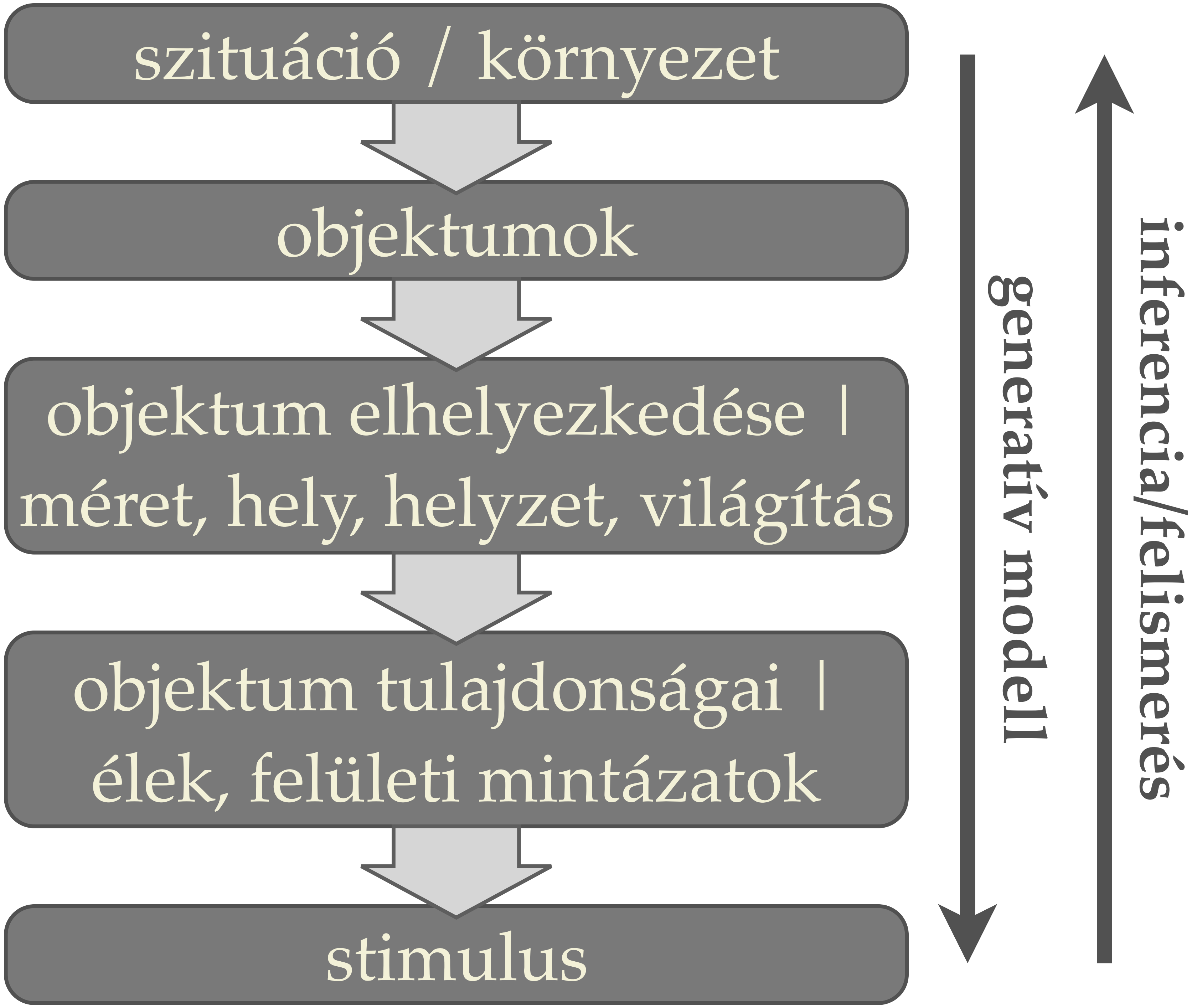

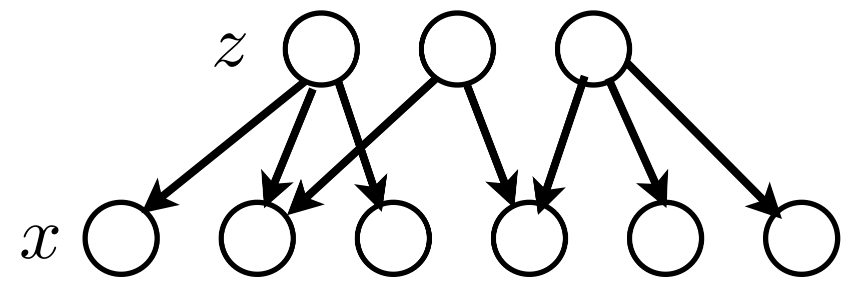

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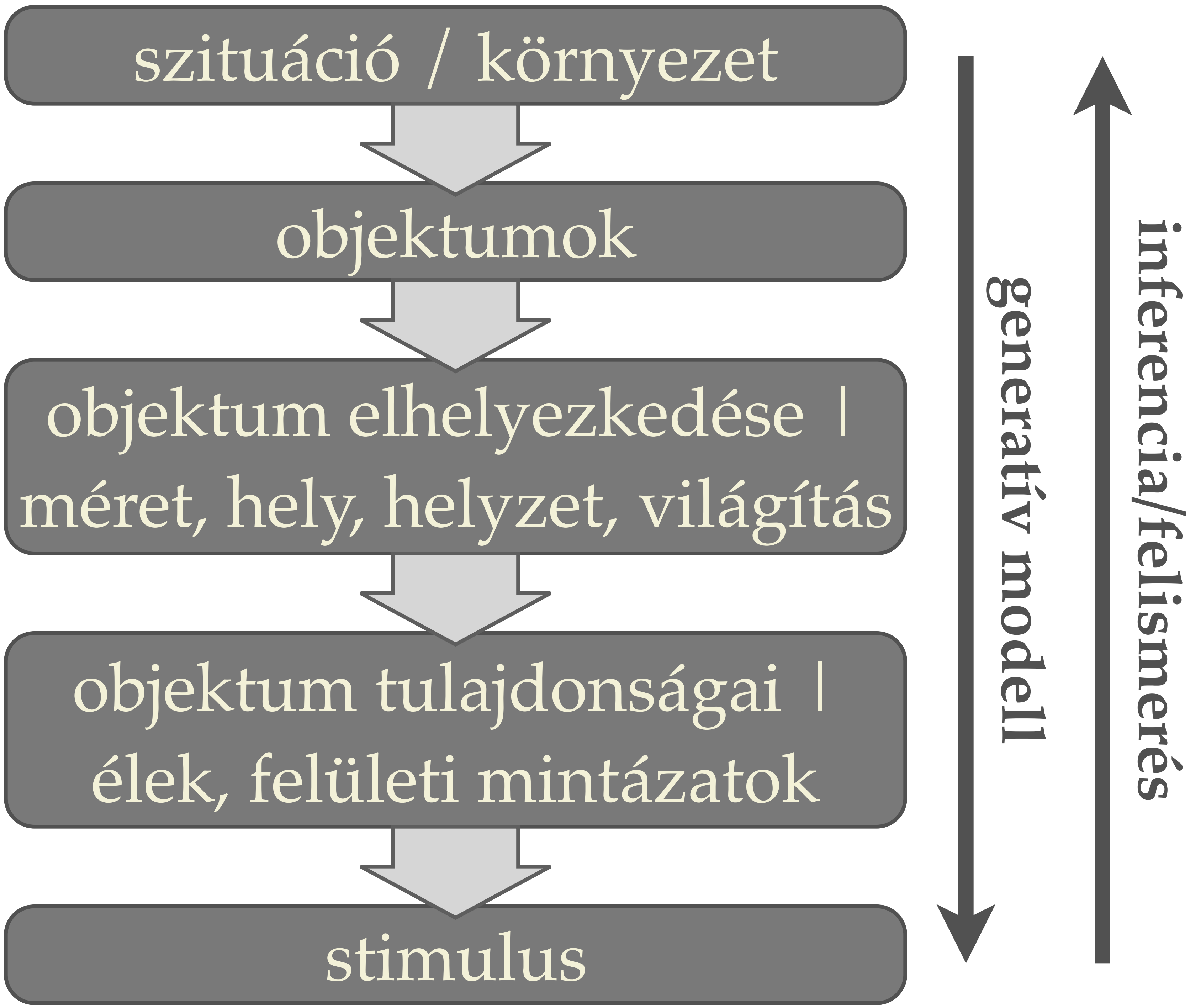
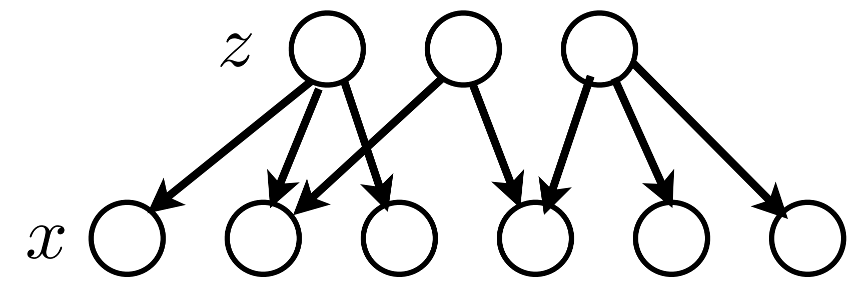




$$\mathrm{P}(\mathbf{z}\,|\,\mathbf{x}) \propto \mathrm{P}(\mathbf{x}\,|\,\mathbf{z})\,\mathrm{P}(\mathbf{z})$$

Bayes inferencia

Miért érdekes a poszterior eloszlás?

Bayes inferencia

Miért érdekes a poszterior eloszlás?

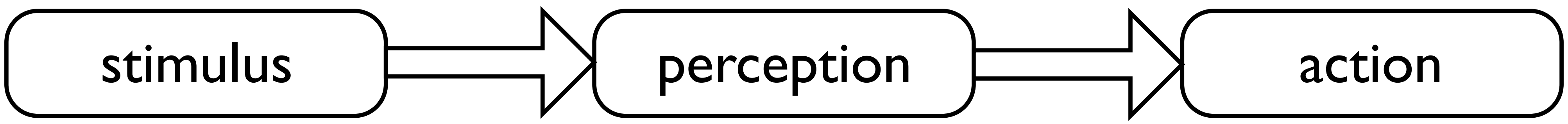
stimulus

perception

action

Bayes inferencia

Miért érdekes a poszterior eloszlás?



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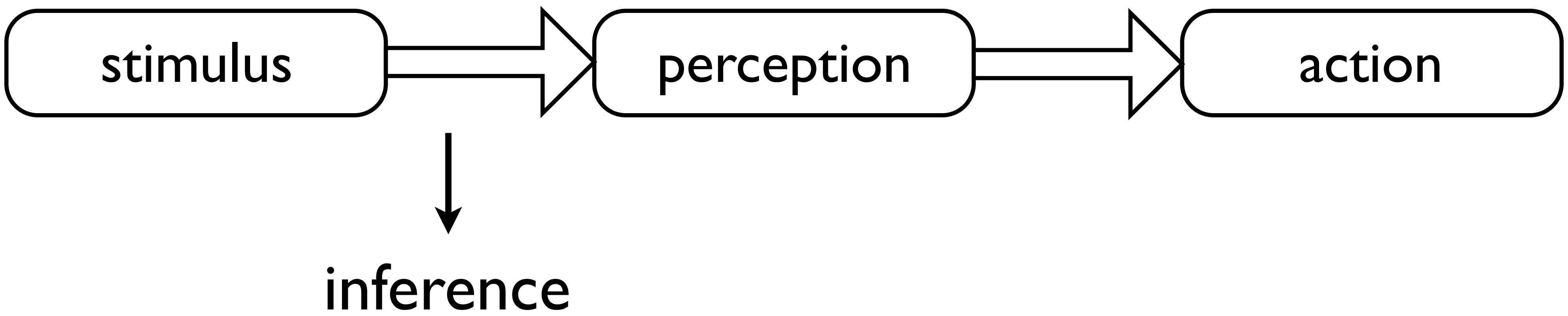

$$P(\mathbf{z} \mid \mathbf{x}) \propto P(\mathbf{x} \mid \mathbf{z})\, P(\mathbf{z})$$

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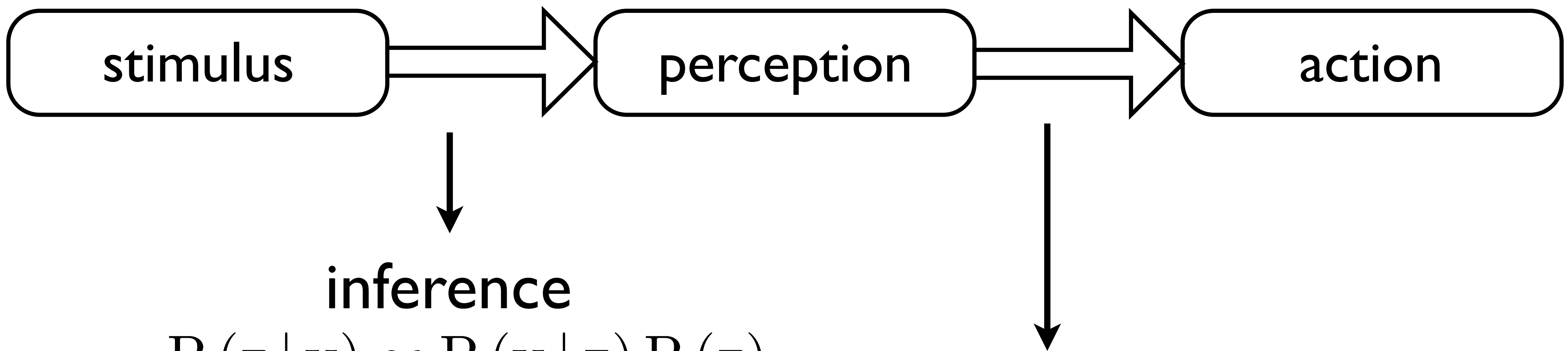


inference

$$\mathrm{P}\left(\mathbf{z}\,|\,\mathbf{x}\right) \propto \mathrm{P}\left(\mathbf{x}\,|\,\mathbf{z}\right)\mathrm{P}\left(\mathbf{z}\right)$$

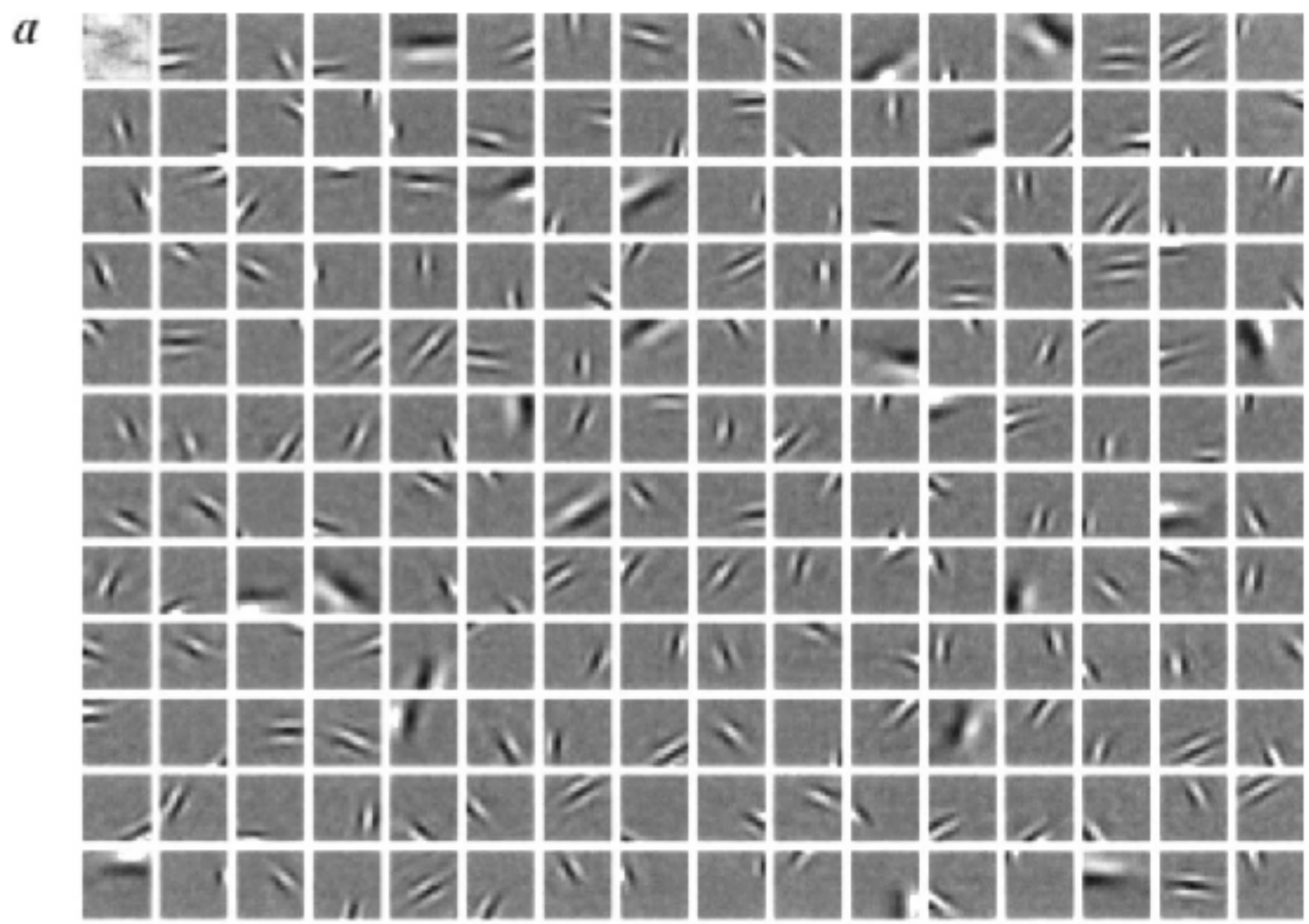
decision making

$$R(a) = \int dz\, U(z,a)\, \mathrm{P}(\mathbf{z}\,|\,\mathbf{x})$$

Independent Component Analysis

$$\mathrm{P}\left(x \mid z\right) = \mathrm{Normal}\left(x; z, \theta\right) = C \exp\left(\left(x - Az\right)^T \Sigma^{-1} \left(x - Az\right)\right)$$

$$P(z) = \mathrm{Laplace}\left(z\right) = \exp\left(|z|/\lambda\right)$$



Olshausen & Field

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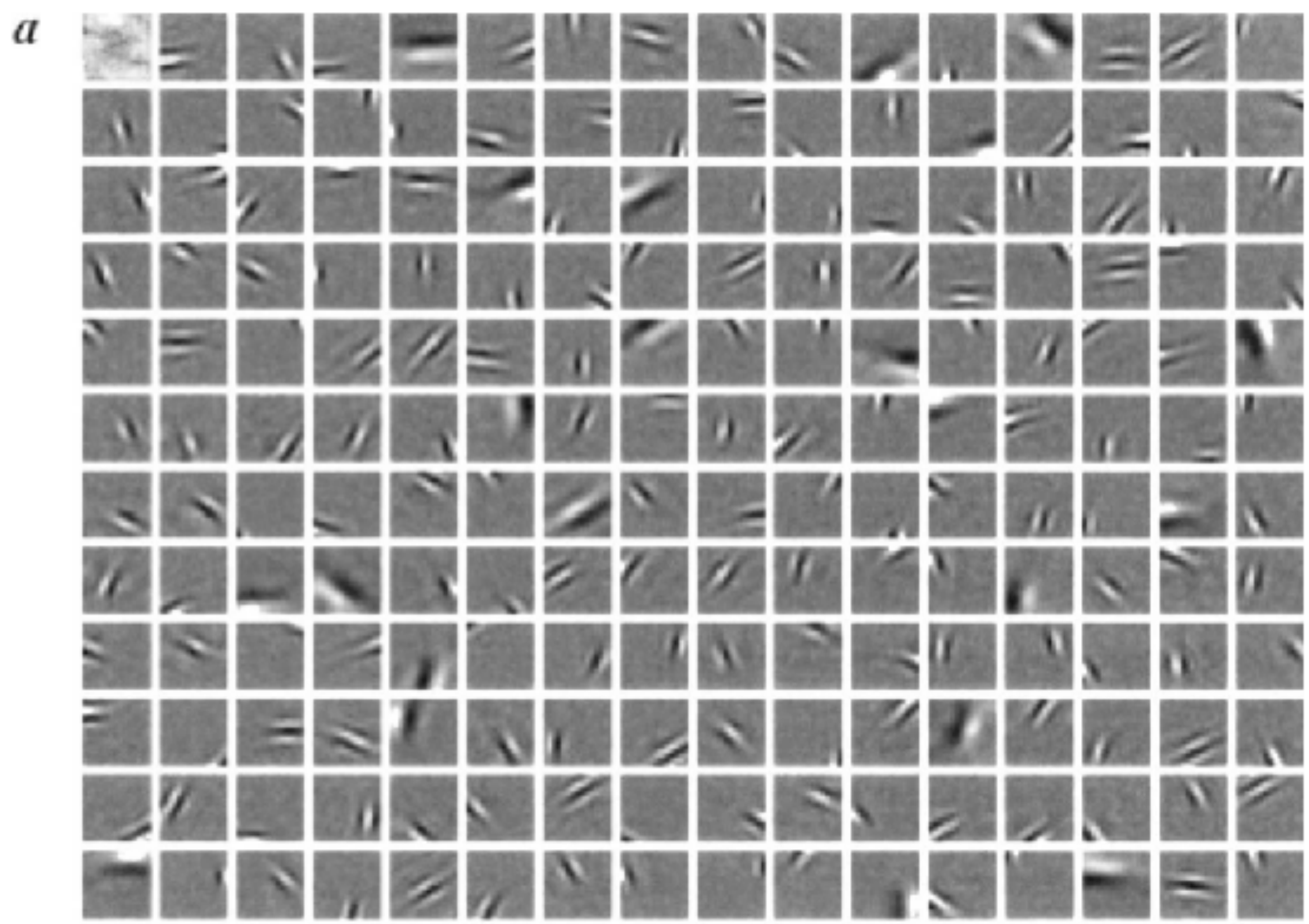
$$x = \mathbf{A} \cdot z + \epsilon$$



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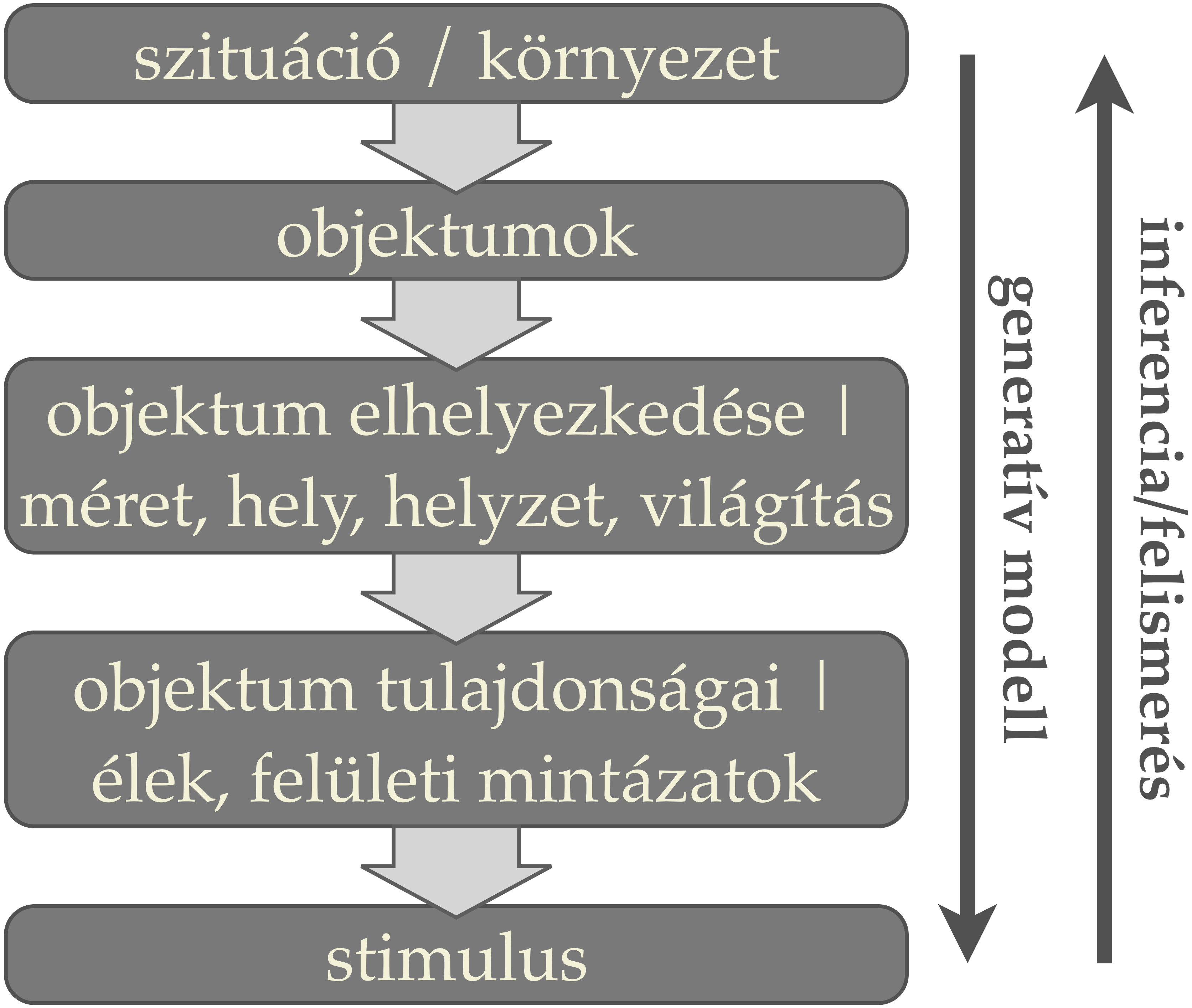

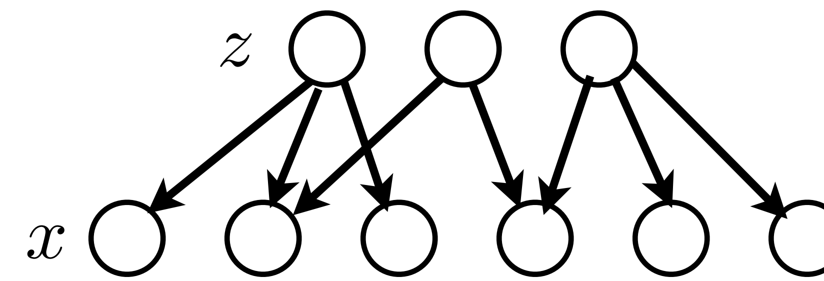

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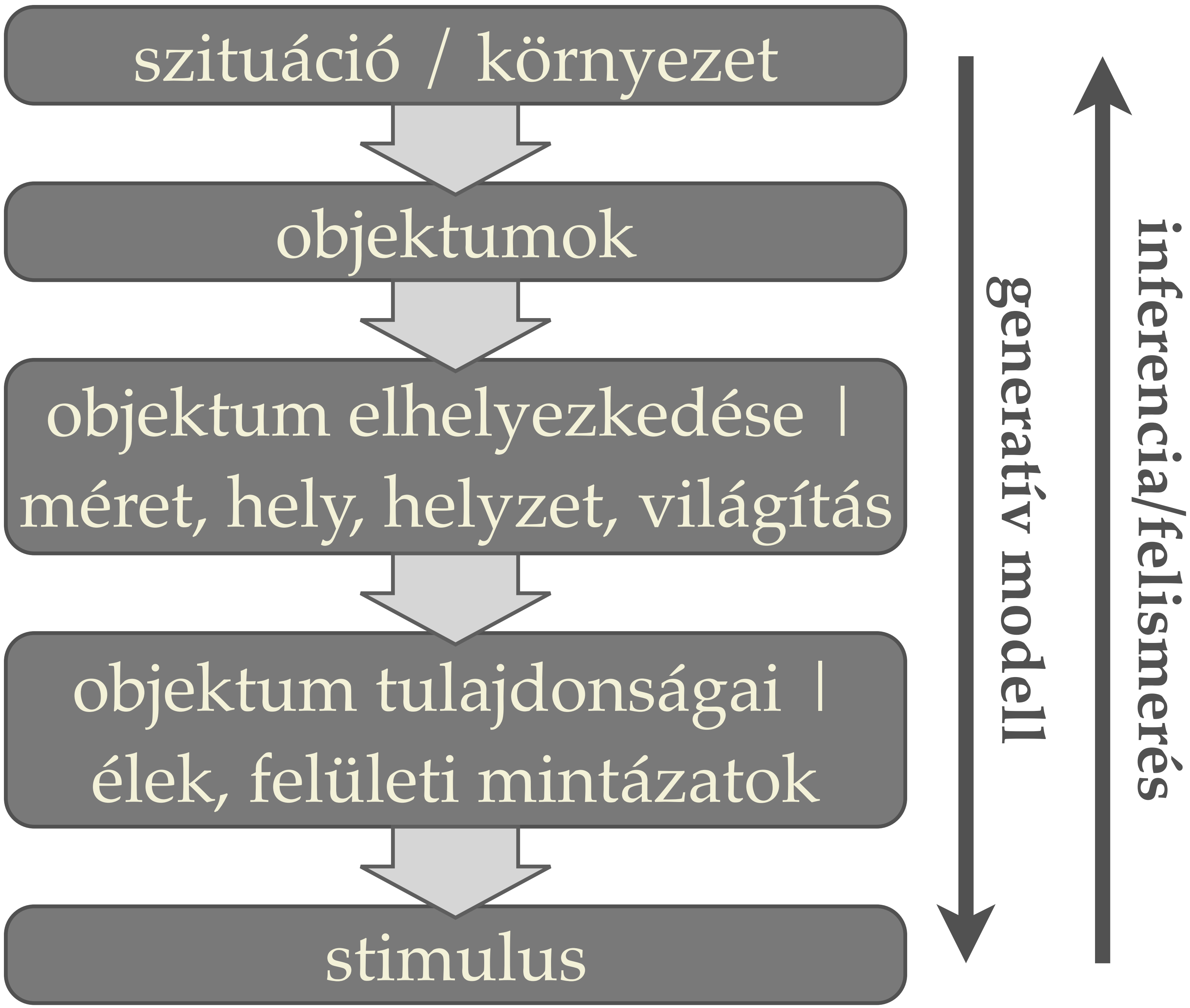

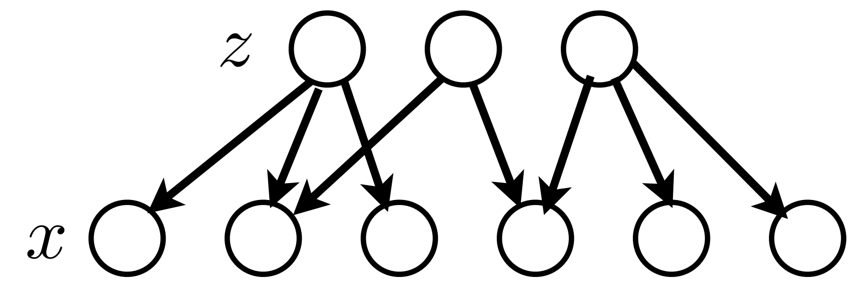

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Eddig arra koncentráltunk, hogy mi a legvalószínűbb aktivitás

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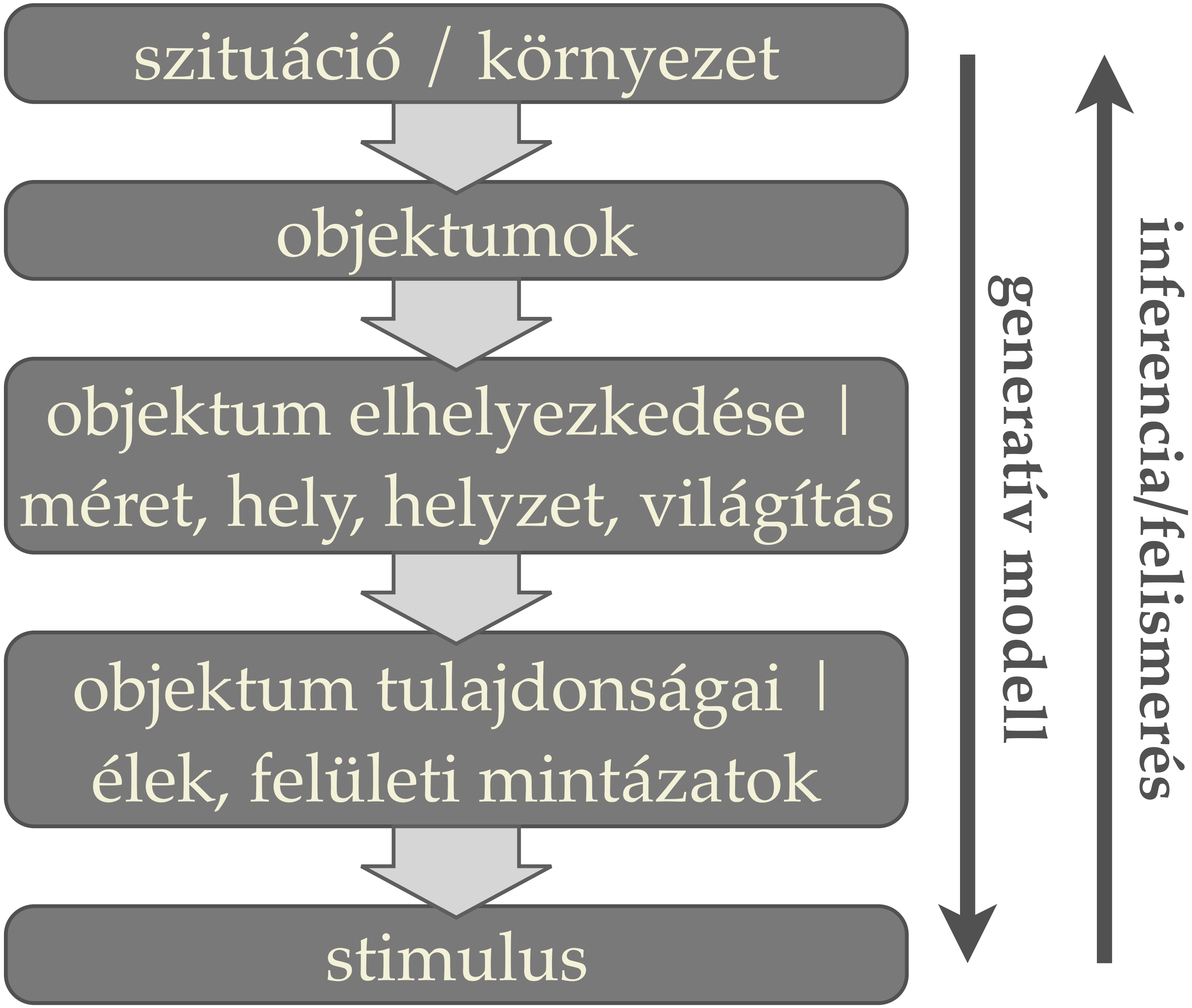

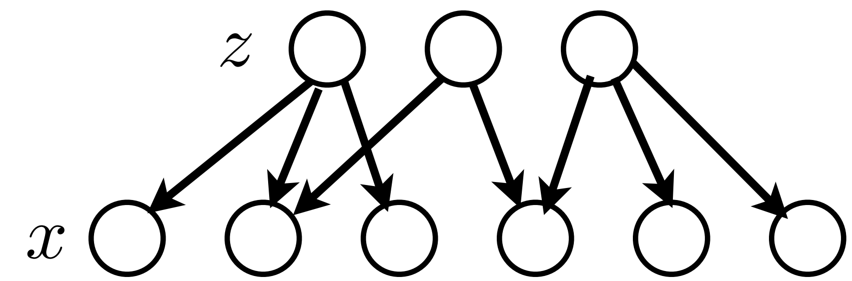

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Ez a maximum a posteriori becslés (MAP)

Neurális válaszok

$$s \sim r$$

Encoding:

$$P\left[r \mid s\right]$$

Decoding:

$$P\left[s \mid r\right] = \frac{P\left[r \mid s\right] P\left[s\right]}{P\left[r\right]}$$

For binary discrimination:

$$P\left[s_1 \mid r\right] = \frac{P\left[r \mid s_1\right] P\left[s_1\right]}{P\left[r\right]} =$$

$$\frac{P\left[r \mid s_1\right] P\left[s_1\right]}{P\left[r \mid s_1\right] P\left[s_1\right] + P\left[r \mid s_2\right] P\left[s_2\right]}$$

Lineáris dekódolás

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$$P[r \mid s_1] = \mathcal{N}(r; \mu_1, \Sigma)$$

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Discrimination is linear:

$$P[s_1 \mid r] = \sigma(\mathbf{w}^\mathsf{T} r + w_0)$$

$$\mathbf{w} = \Sigma^{-1}(\mu_1 - \mu_2)$$

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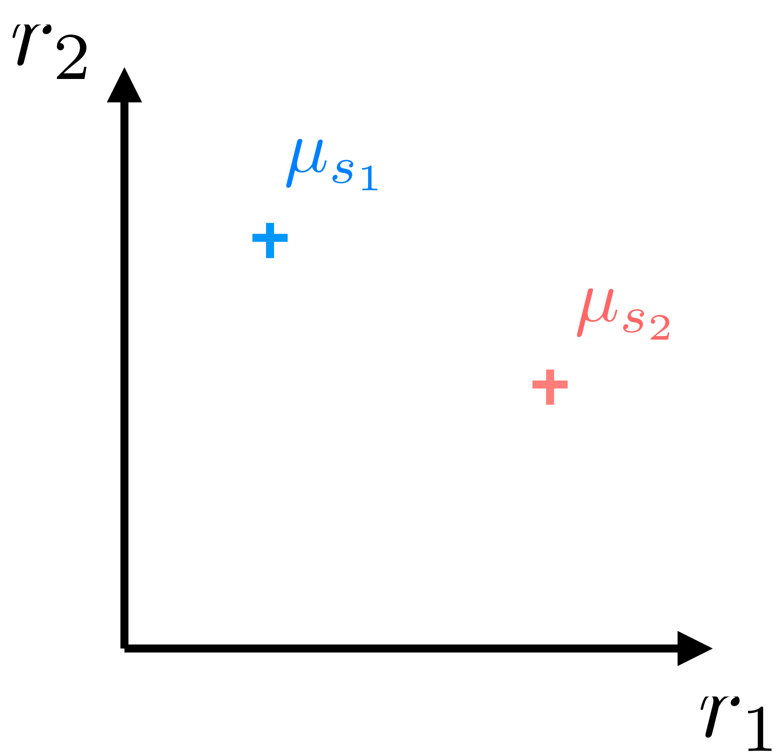

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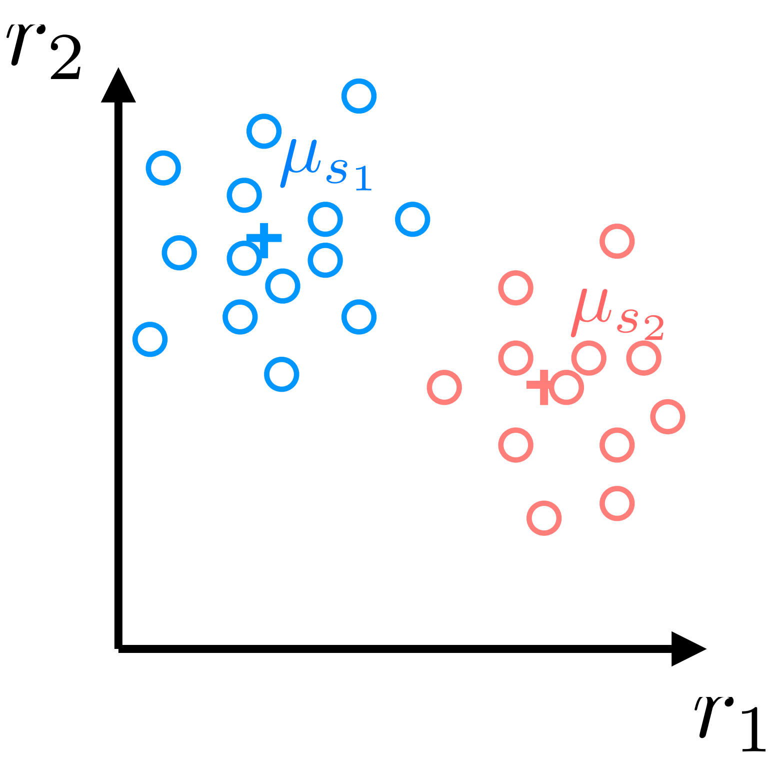

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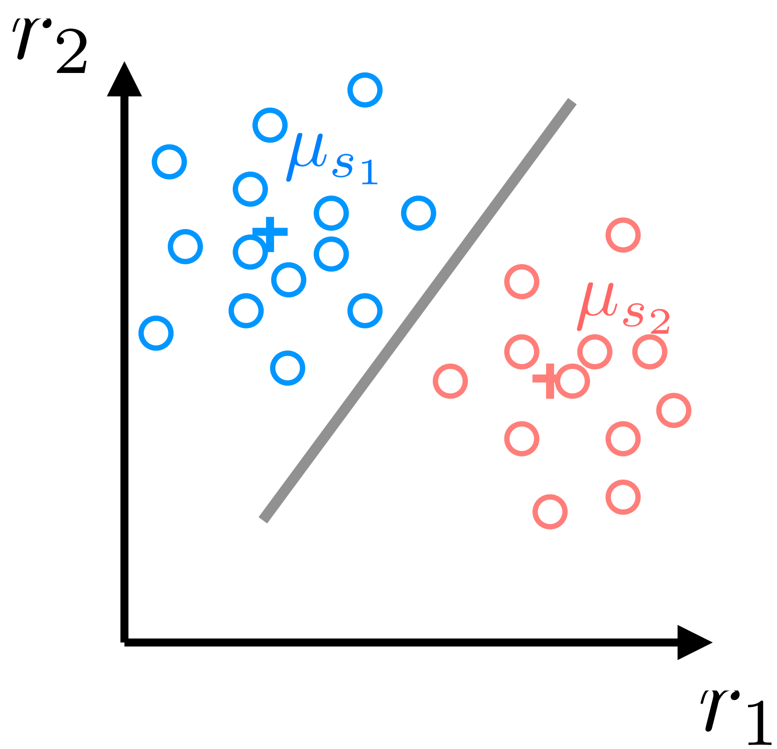

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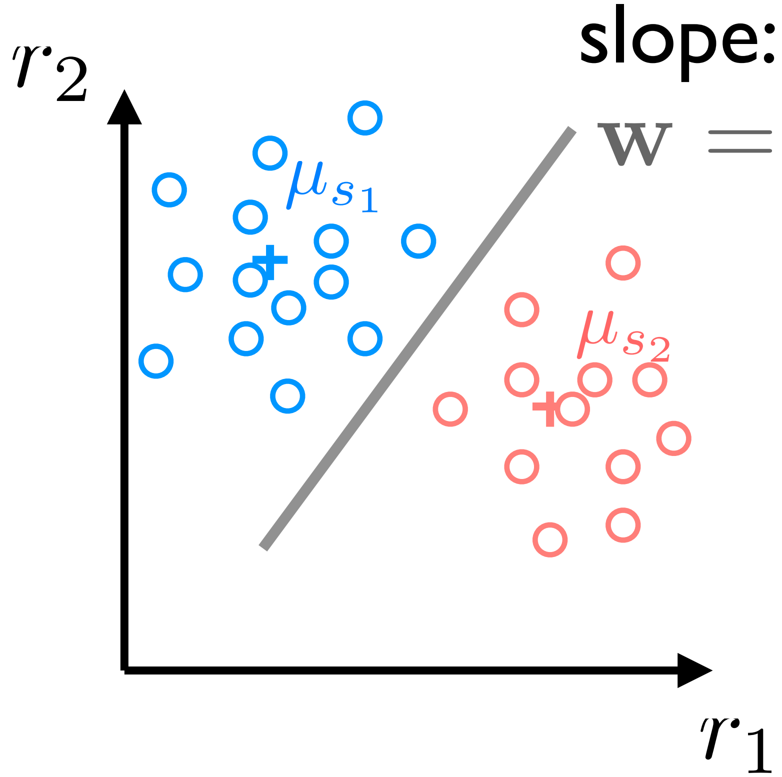
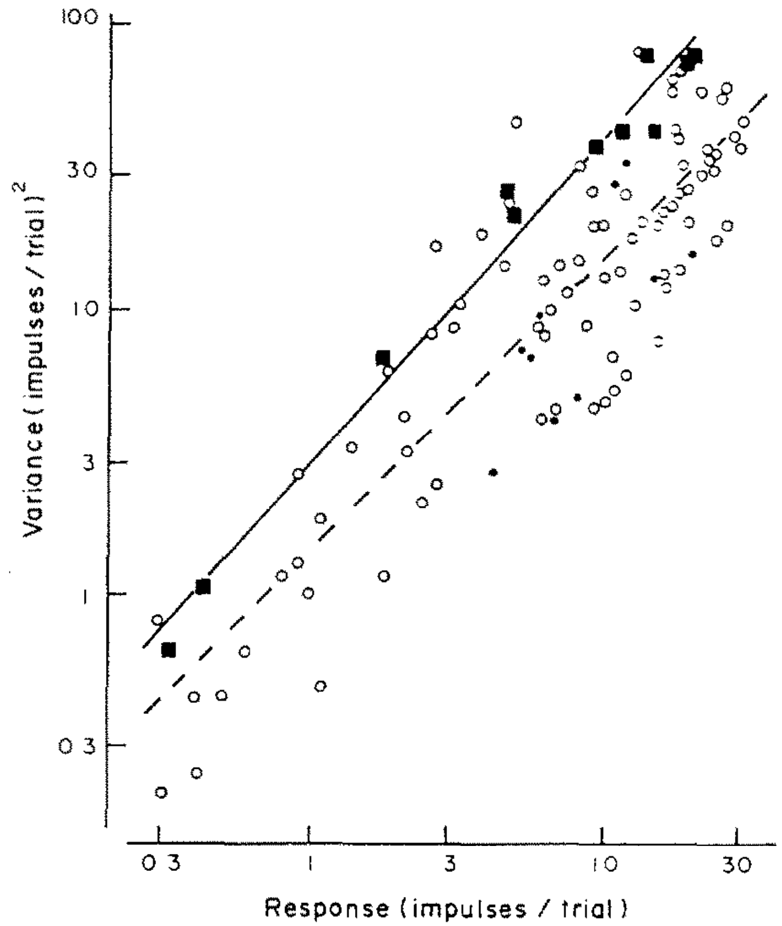


slope:

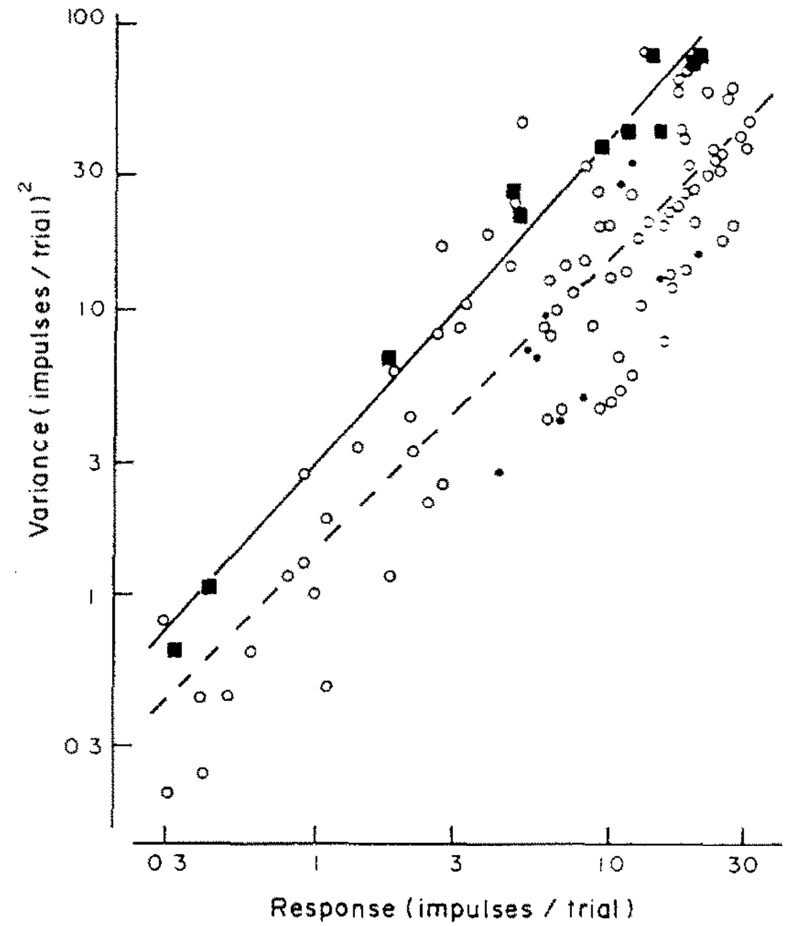
$$\mathbf{w} = \Sigma^{-1}(\mu_1 - \mu_2)$$

Neurális zaj



Tolhurst et al (1983) Vision Res

Neurális zaj



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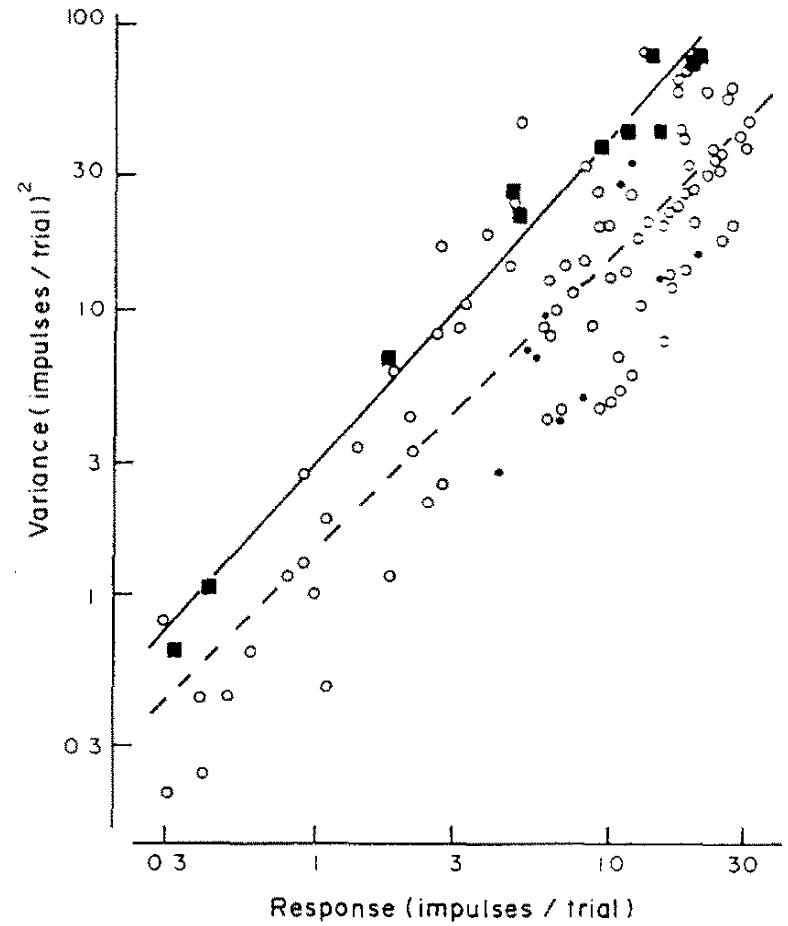
Poisson process: In any given time window λ the probability of firing is determined by the firing rate

Neurális zaj



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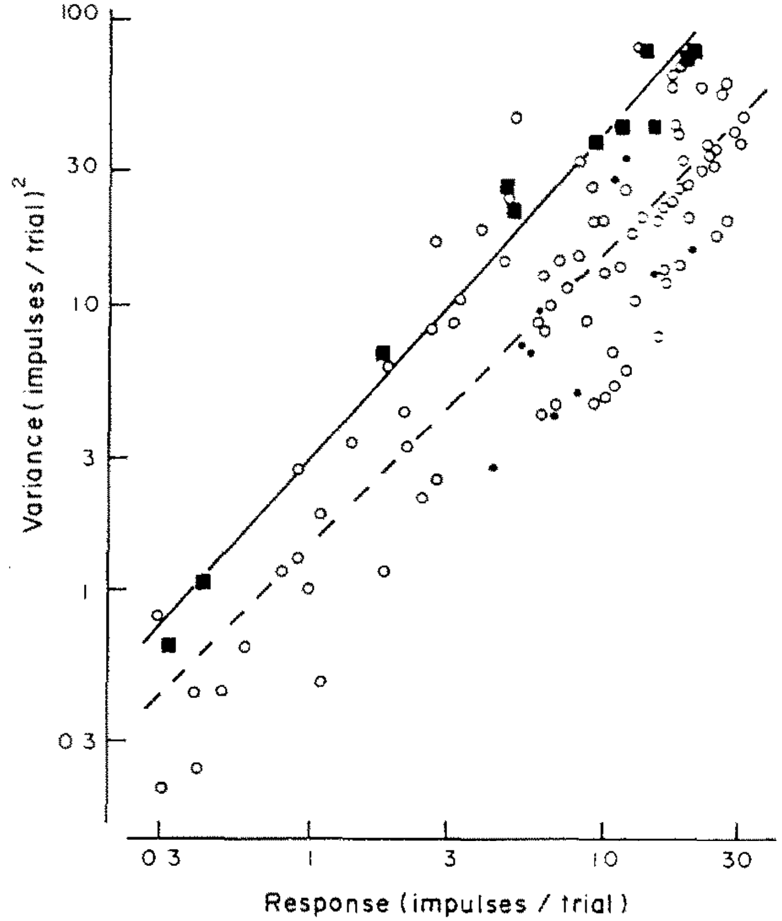
$$P\left[N \mid s\right] = \lambda^N \frac{\exp(-\lambda)}{k!}$$

Neurális zaj



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$$\mathrm{mean}[P\left[N \mid s\right]] = \lambda$$

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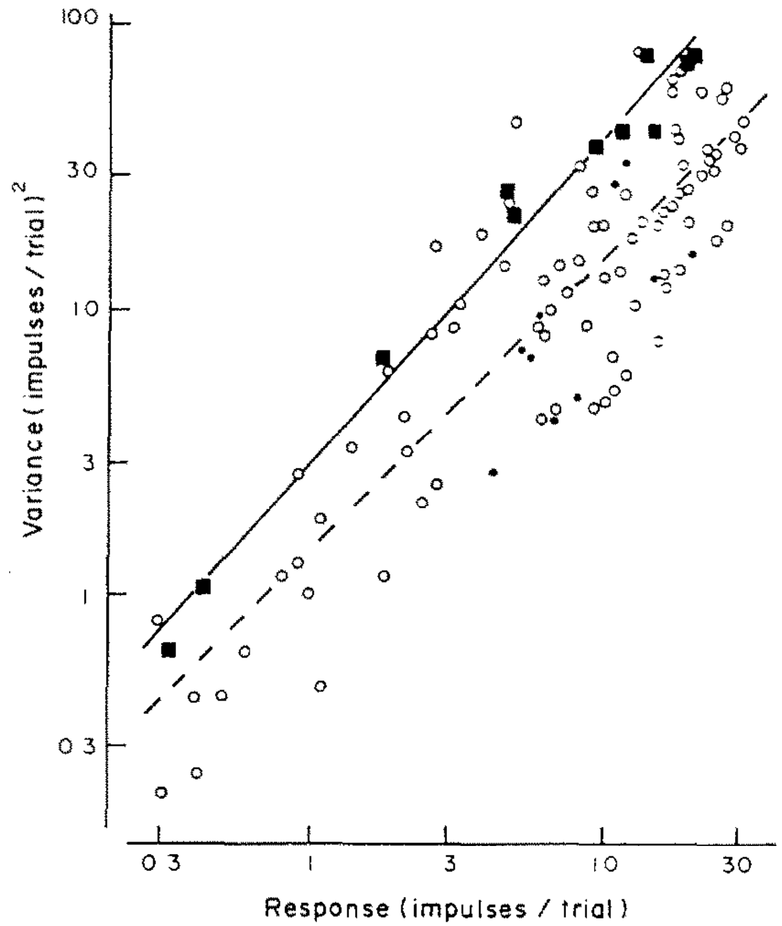

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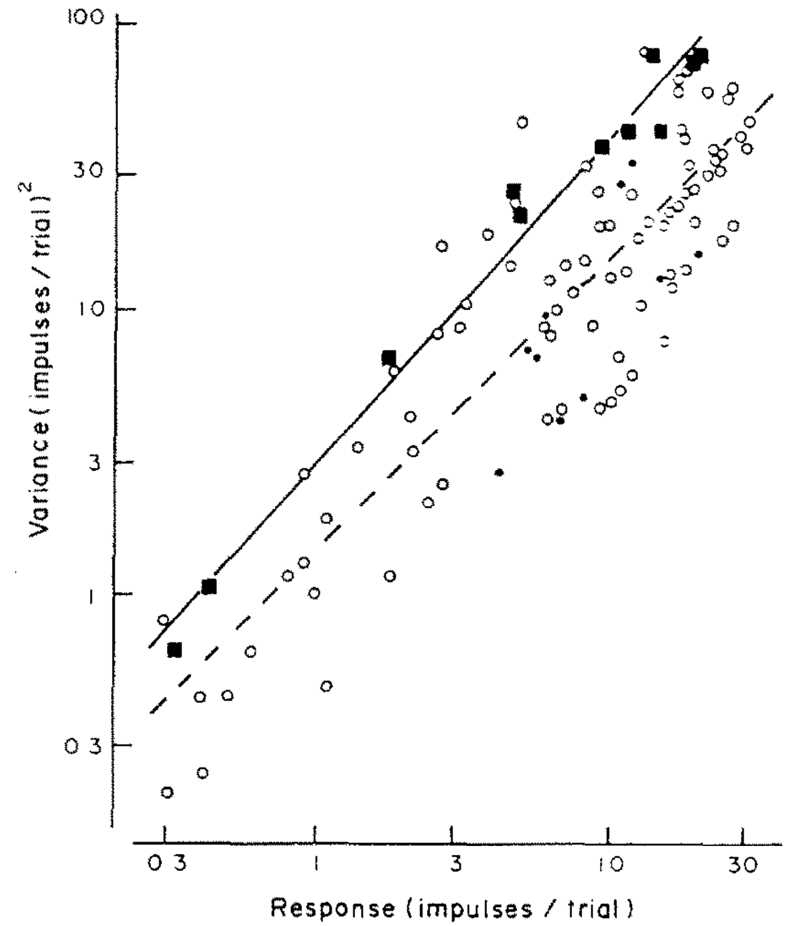

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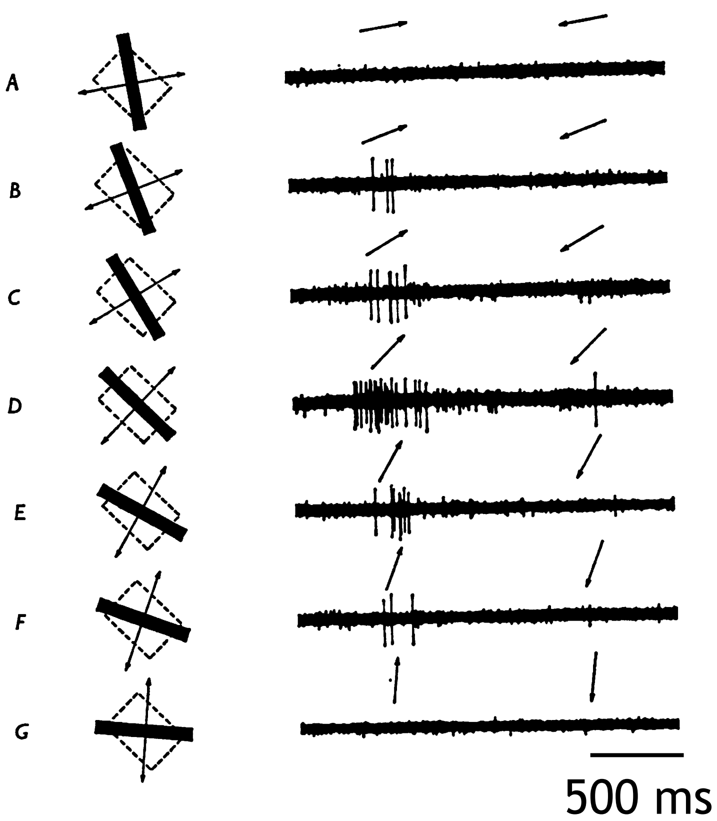
$$\mathrm{Var}[P[N \mid s]] = \lambda$$

Homework: prove that we will obtain a linear decoder if the response noise is Poisson

Neurális válaszok

V1 characteristic response



Hubel & Wiesel, J Physiol 1968

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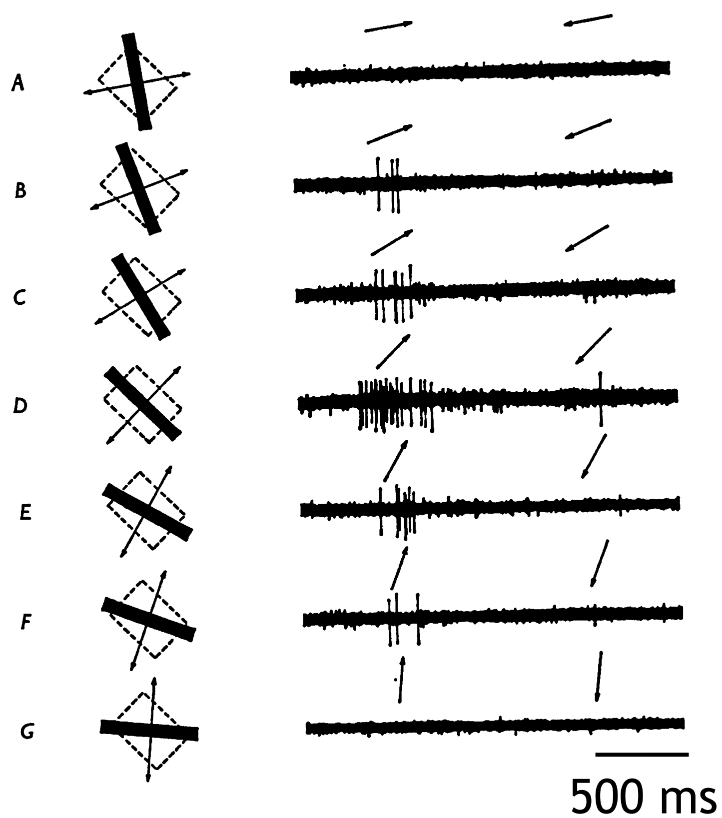

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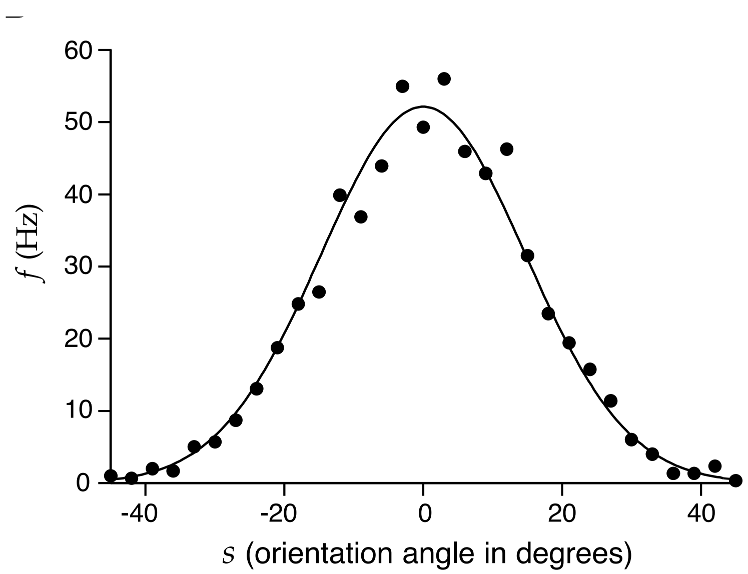

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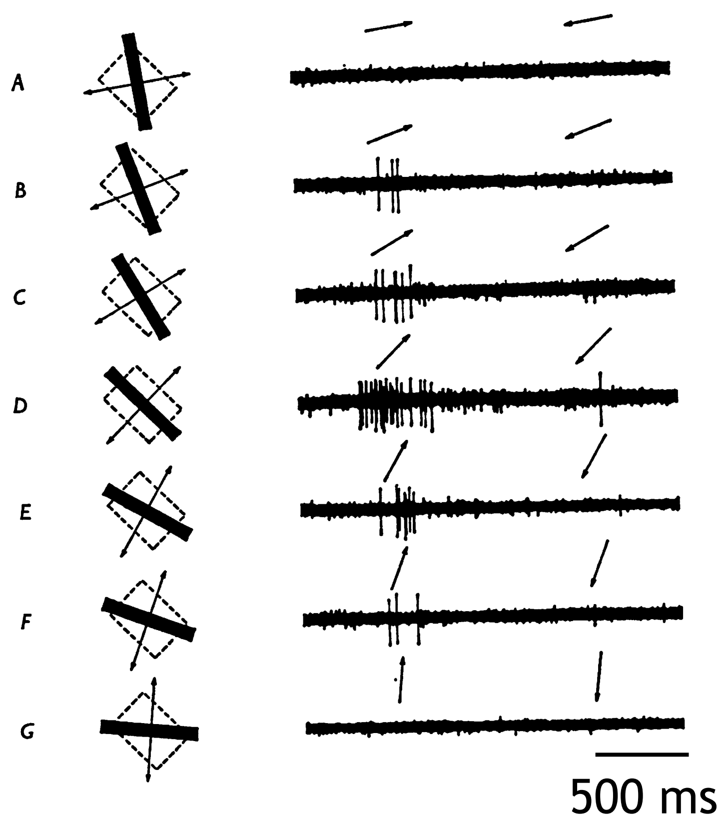
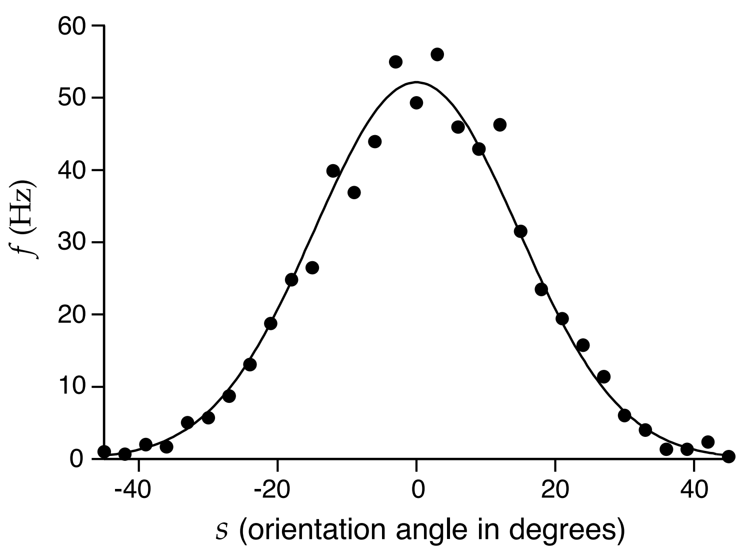
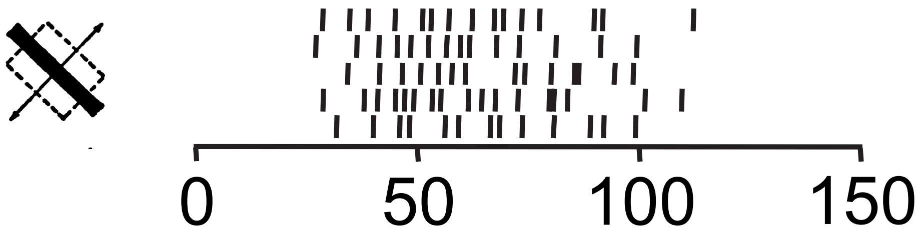




Hubel & Wiesel, J Physiol 1968

V1 spike train variability



Gur & Snodderly, Cereb Cortex 2006

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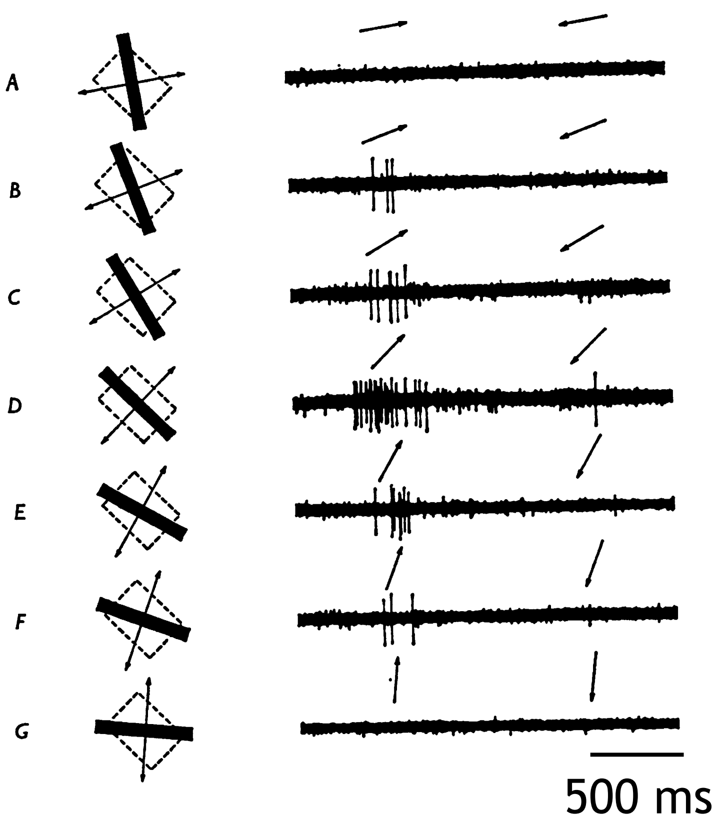

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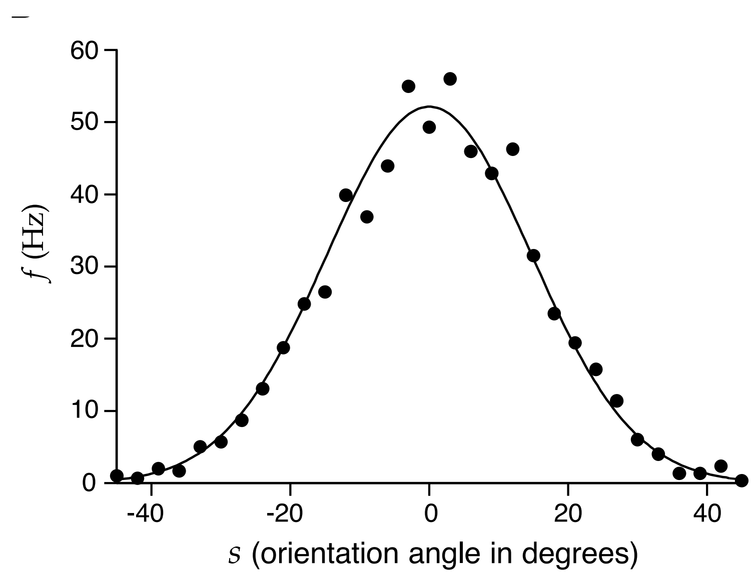
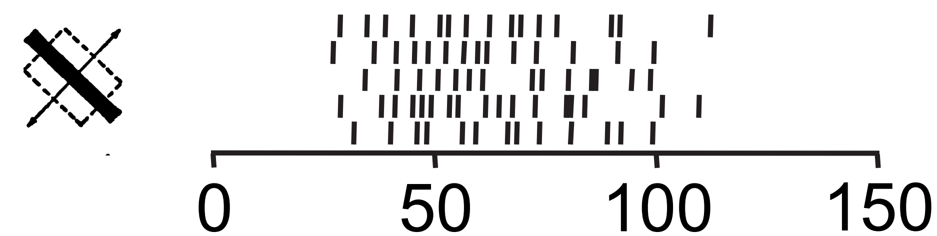


$$E[P(r|s)] = f(s)$$

V1 spike train variability



Gur & Snodderly, Cereb Cortex 2006

Bayes inferencia neuronhálózatokkal: PPC

V1 orientáció-szelektív neuronok

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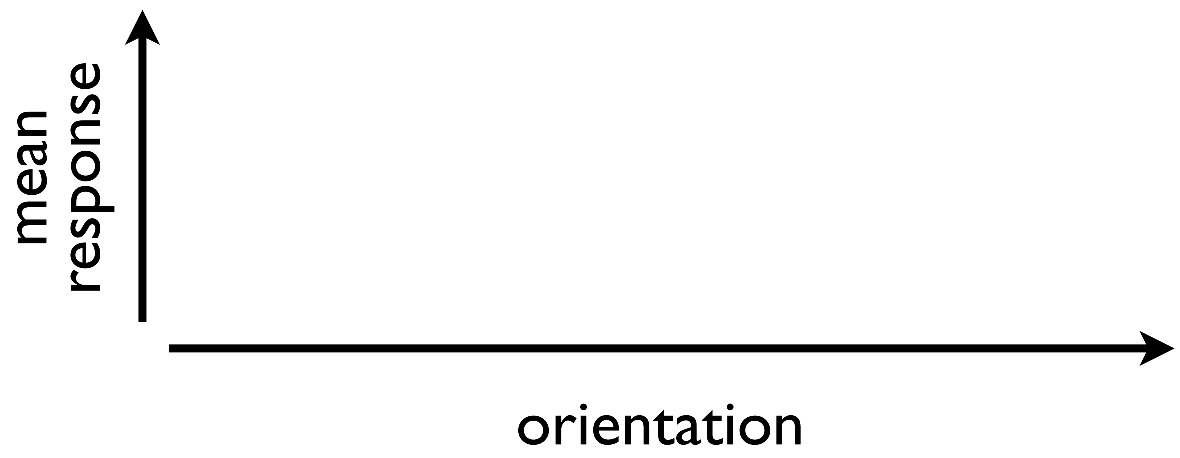
V1 orientáció-szelektív neuronok



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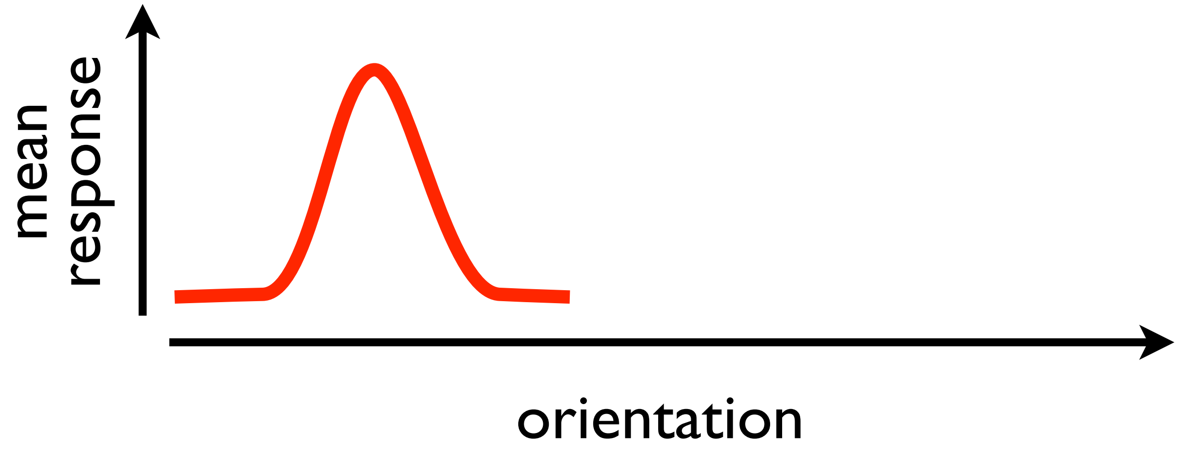

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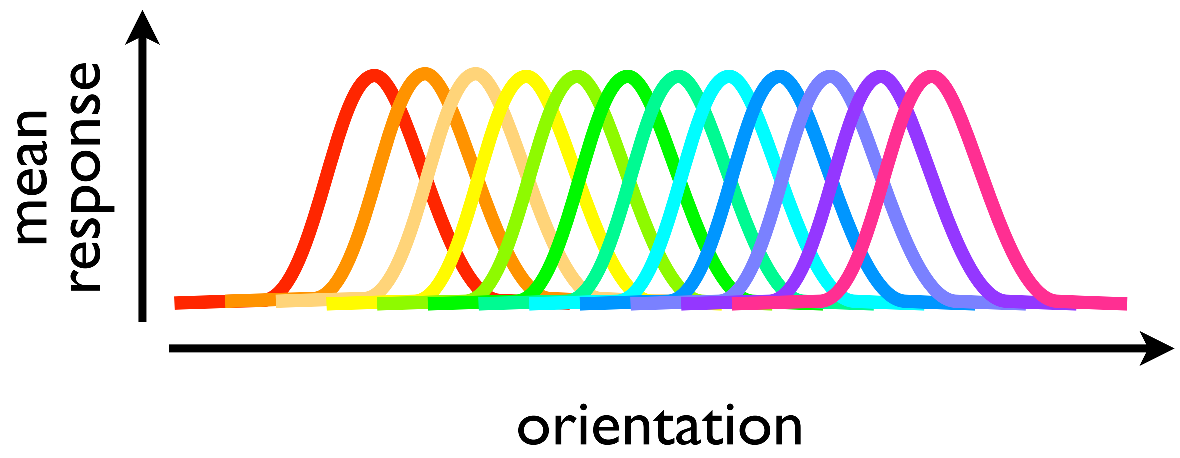

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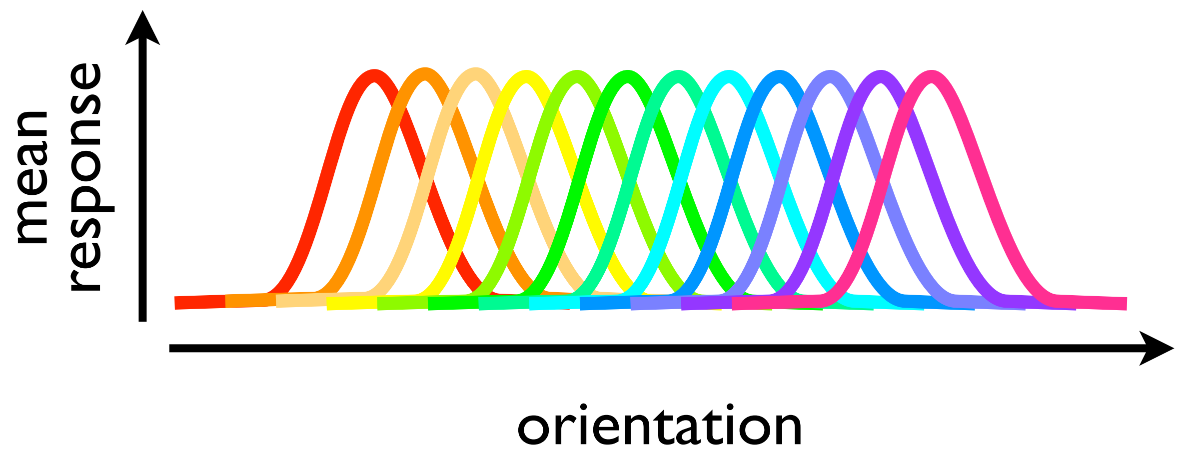

a neuronok azonban zajosak:
az átlag körül az átlaggal
arányos variabilitás van jelen

Bayes inferencia neuronhálózatokkal: PPC

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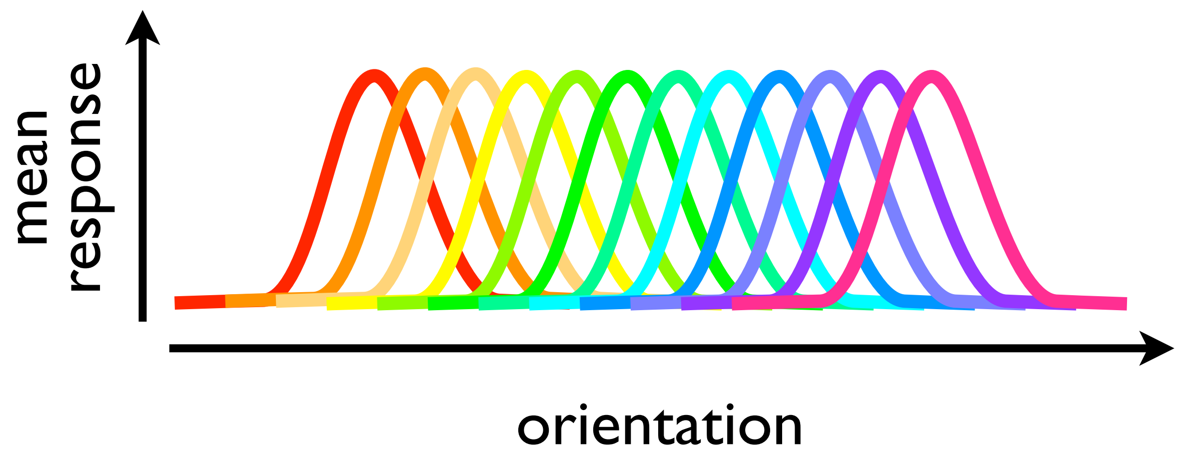

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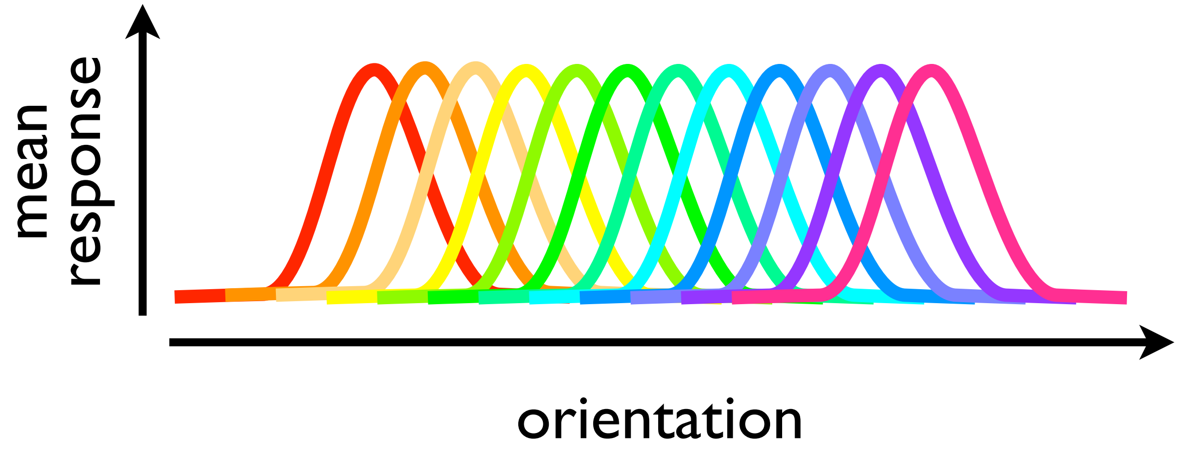

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megfigyelt változók: $\mathrm{r} = \{r_1, r_2, \ldots r_N\}$

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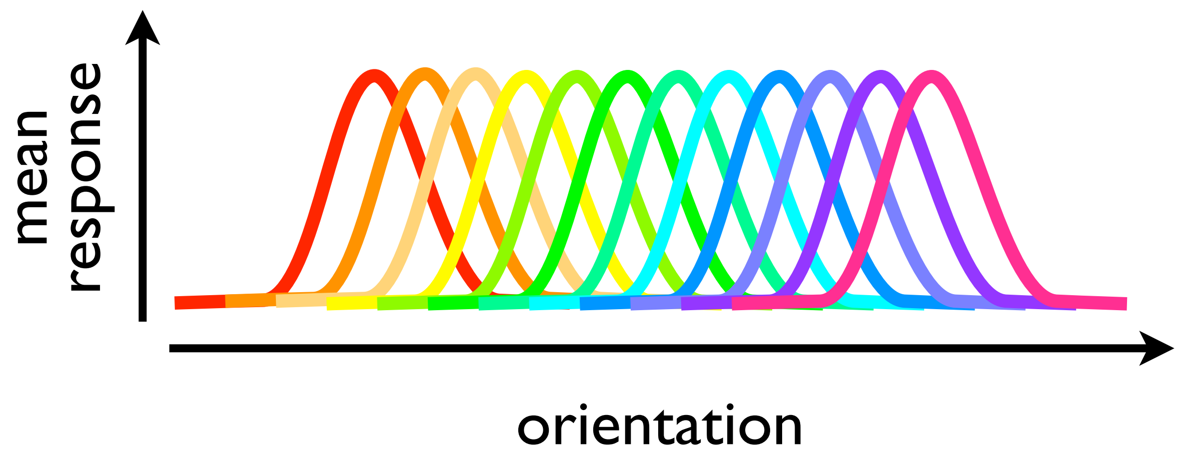

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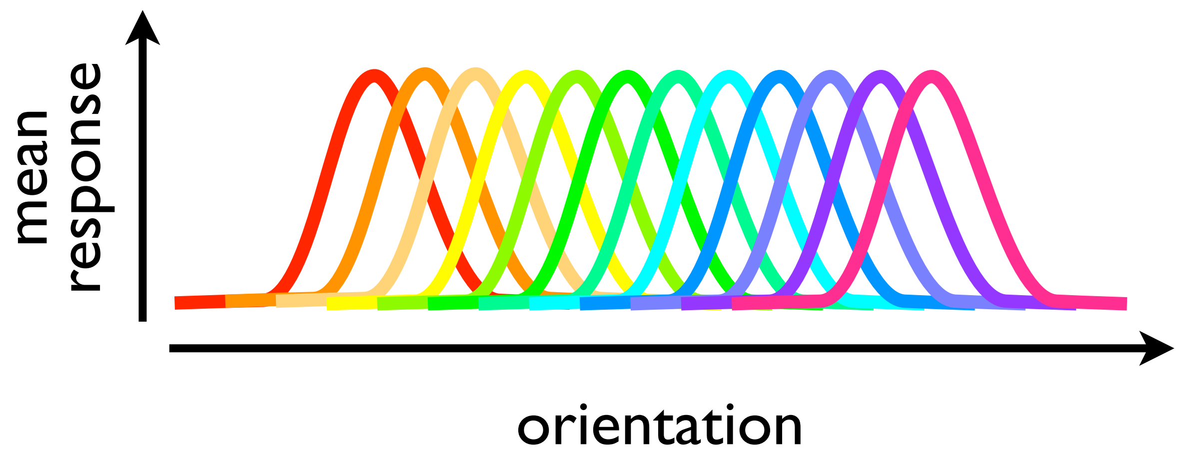

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Bayes: $P(s \,|\, \mathbf{r}) \propto P(\mathbf{r} \,|\, s)\, P(s)$

Probabilistic Population Codes

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- Neurális zaj varianciája arányos az átlagos aktivitással: Poisson zaj

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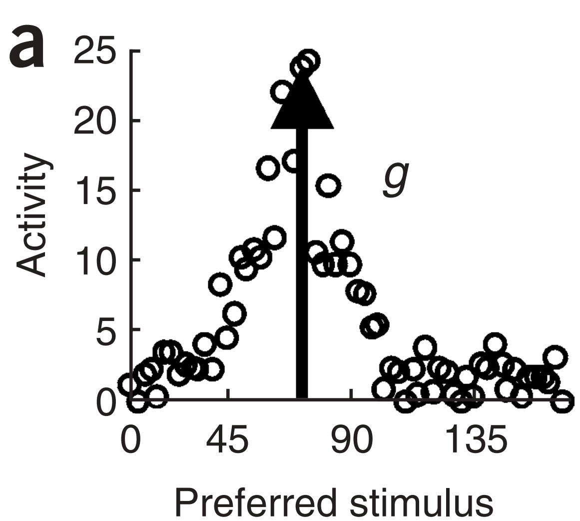

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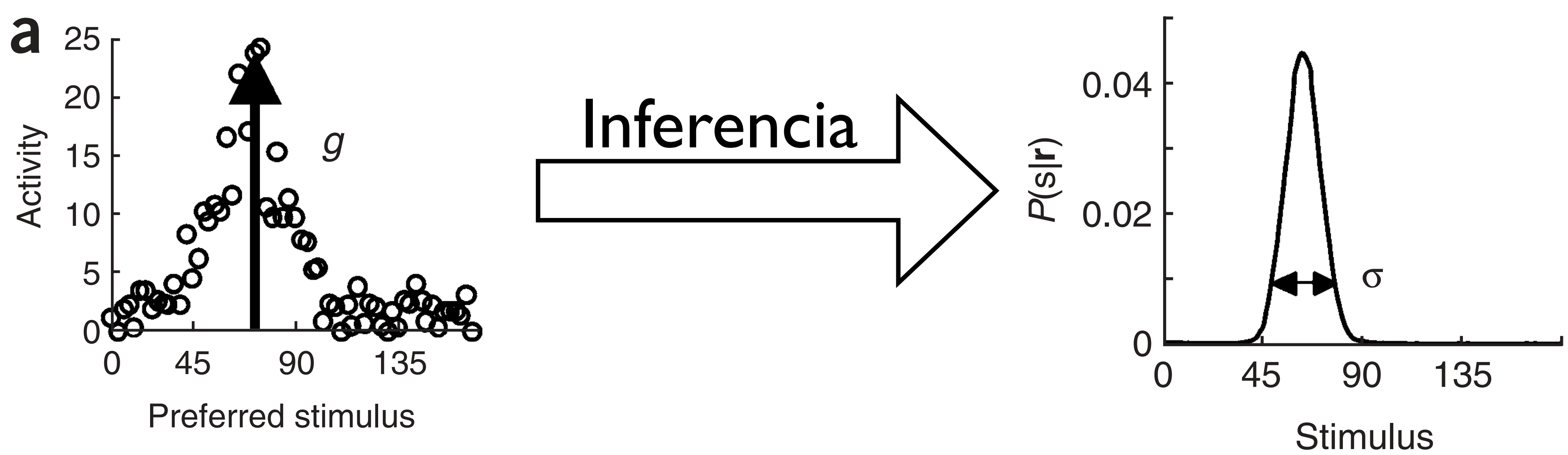

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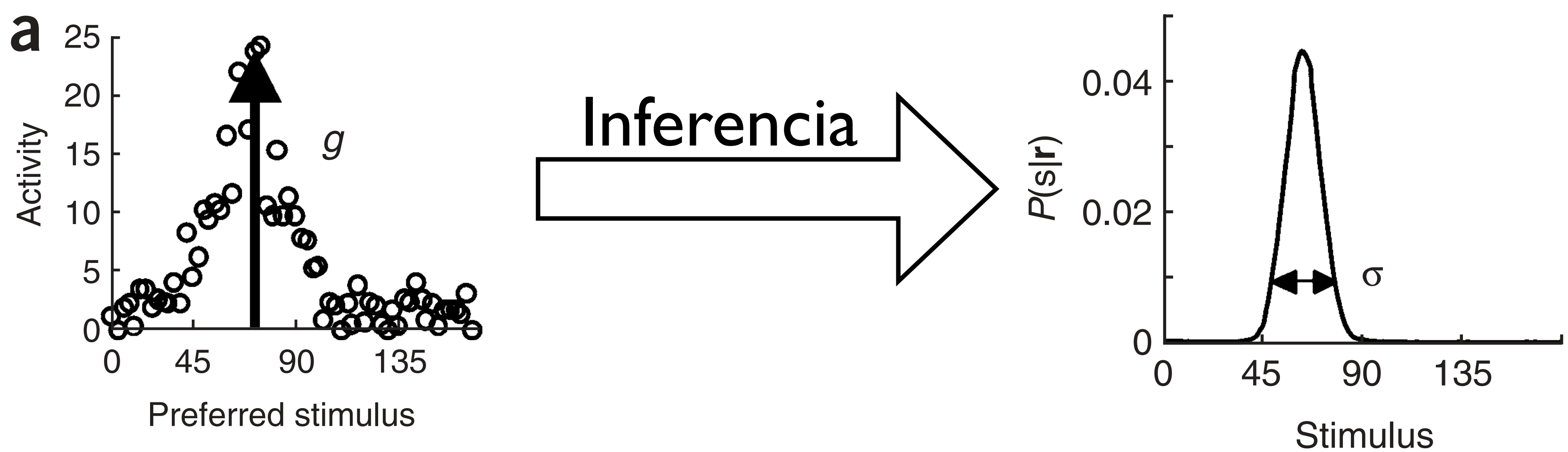

az aktivitás-intenzítás arányos a precizióval

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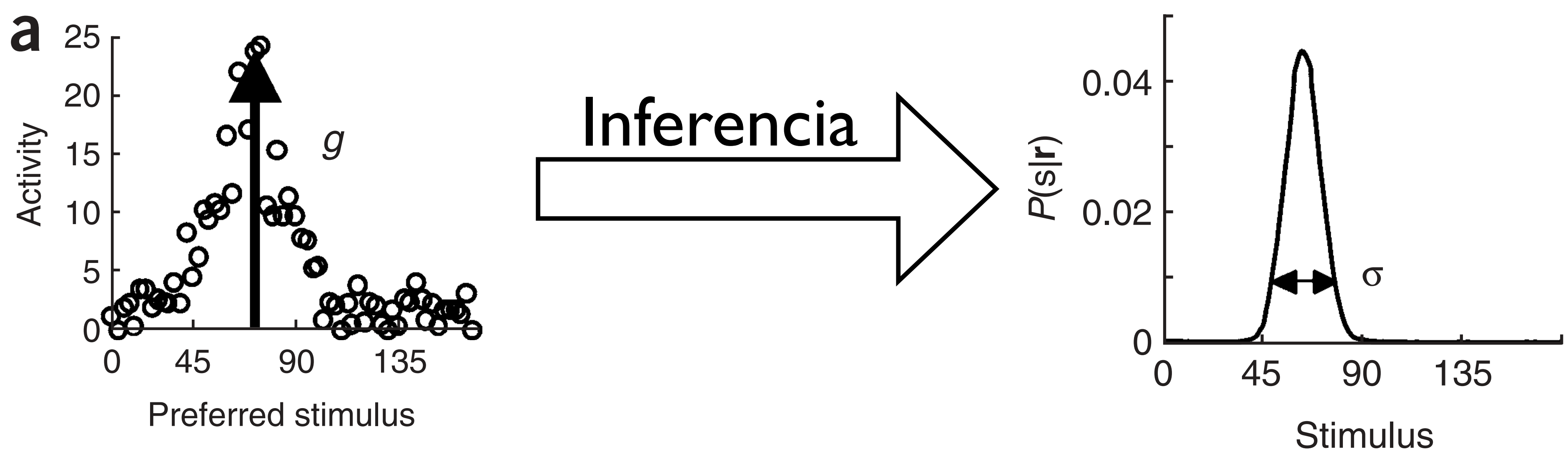
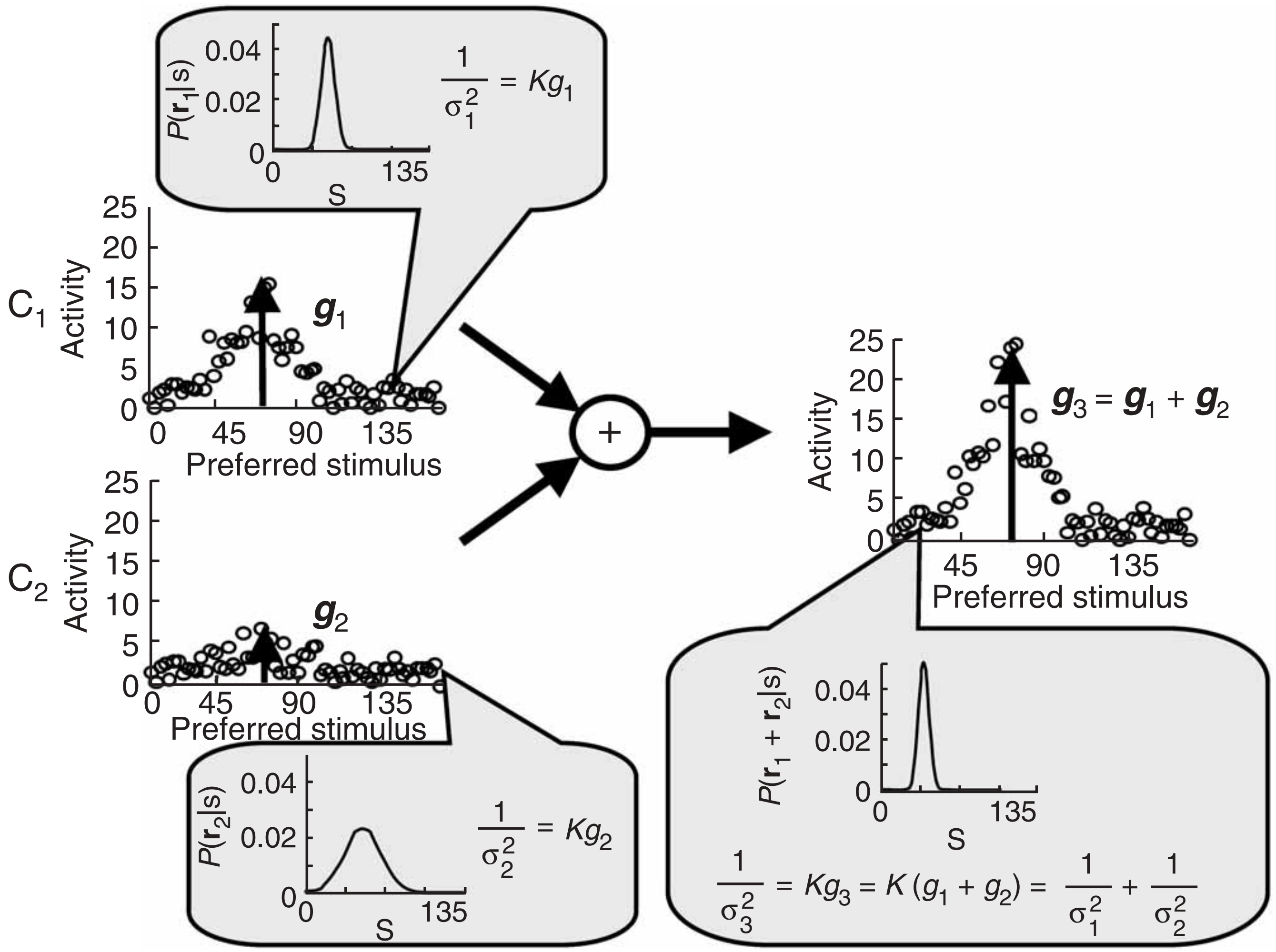


az aktivitás-intenzítás arányos a precizióval

$$g \propto \frac{1}{\sigma^2}$$

PPC: Multiszenzoros integráció



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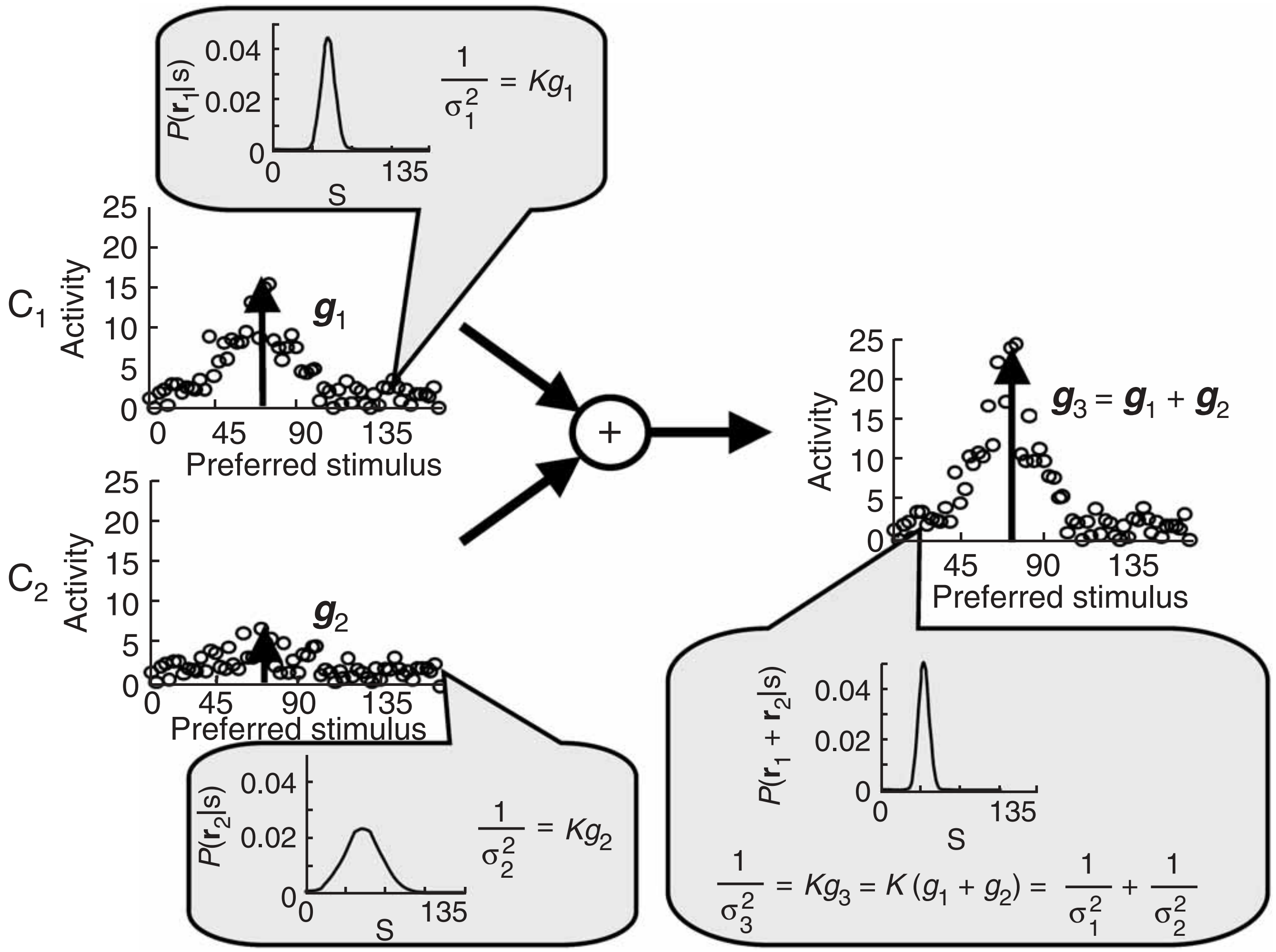

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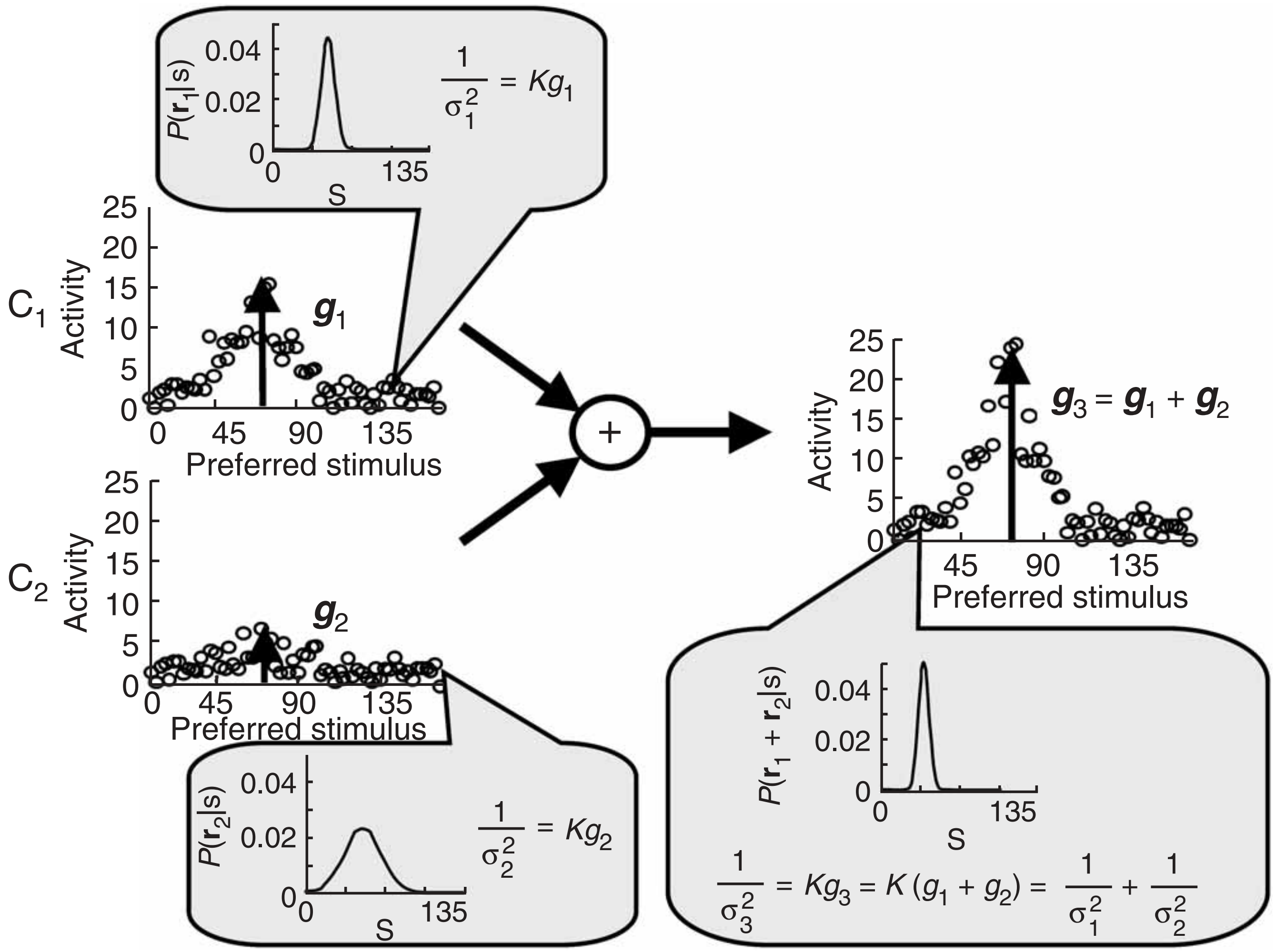

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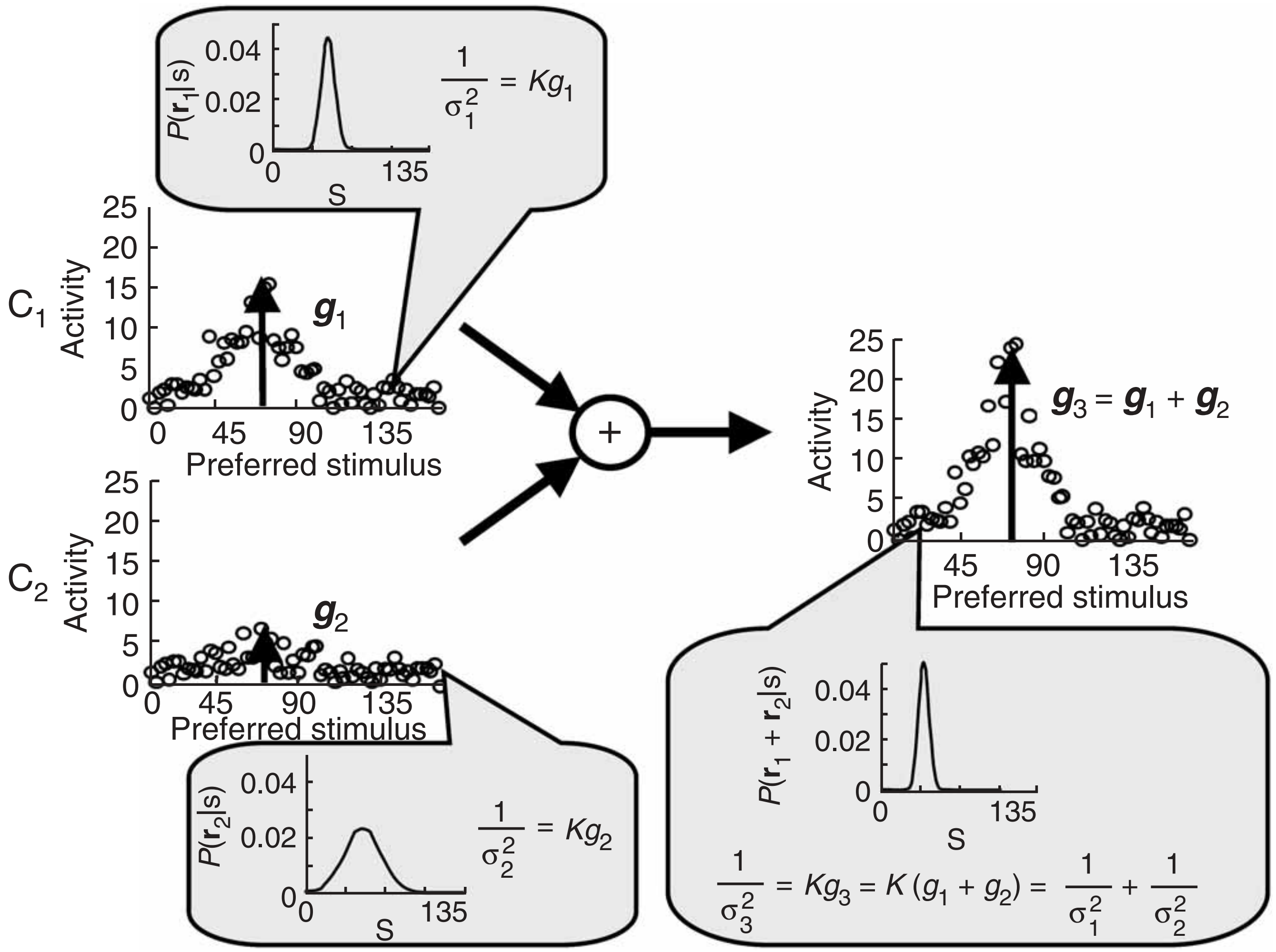

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$$\frac{1}{\sigma_3^2} = \frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2}$$

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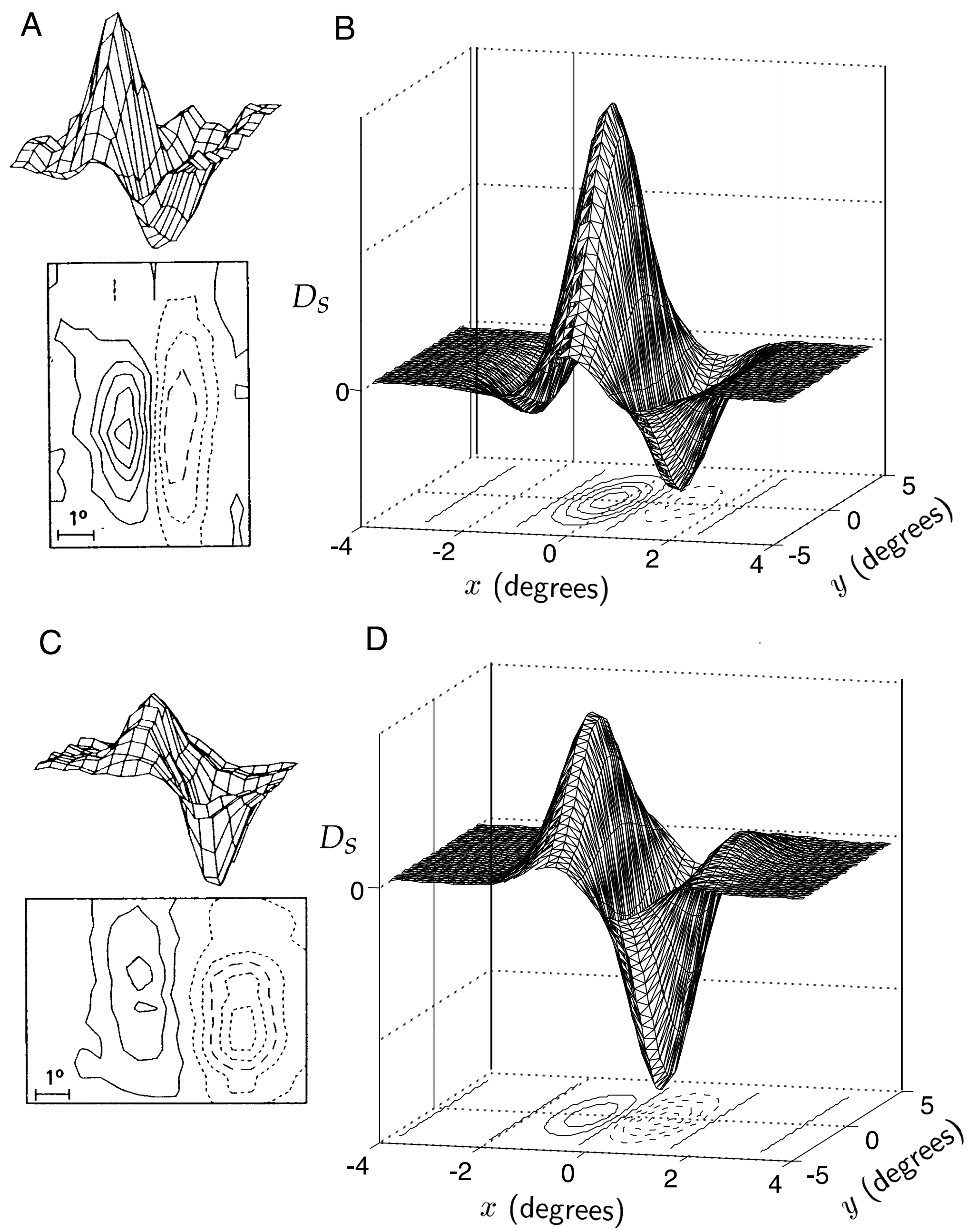
Receptív mezők

Stimulus is not orientation or any other simple stimulus feature , rather a 2D image (sequence)



Dayan & Abbott (2000) Theoretical

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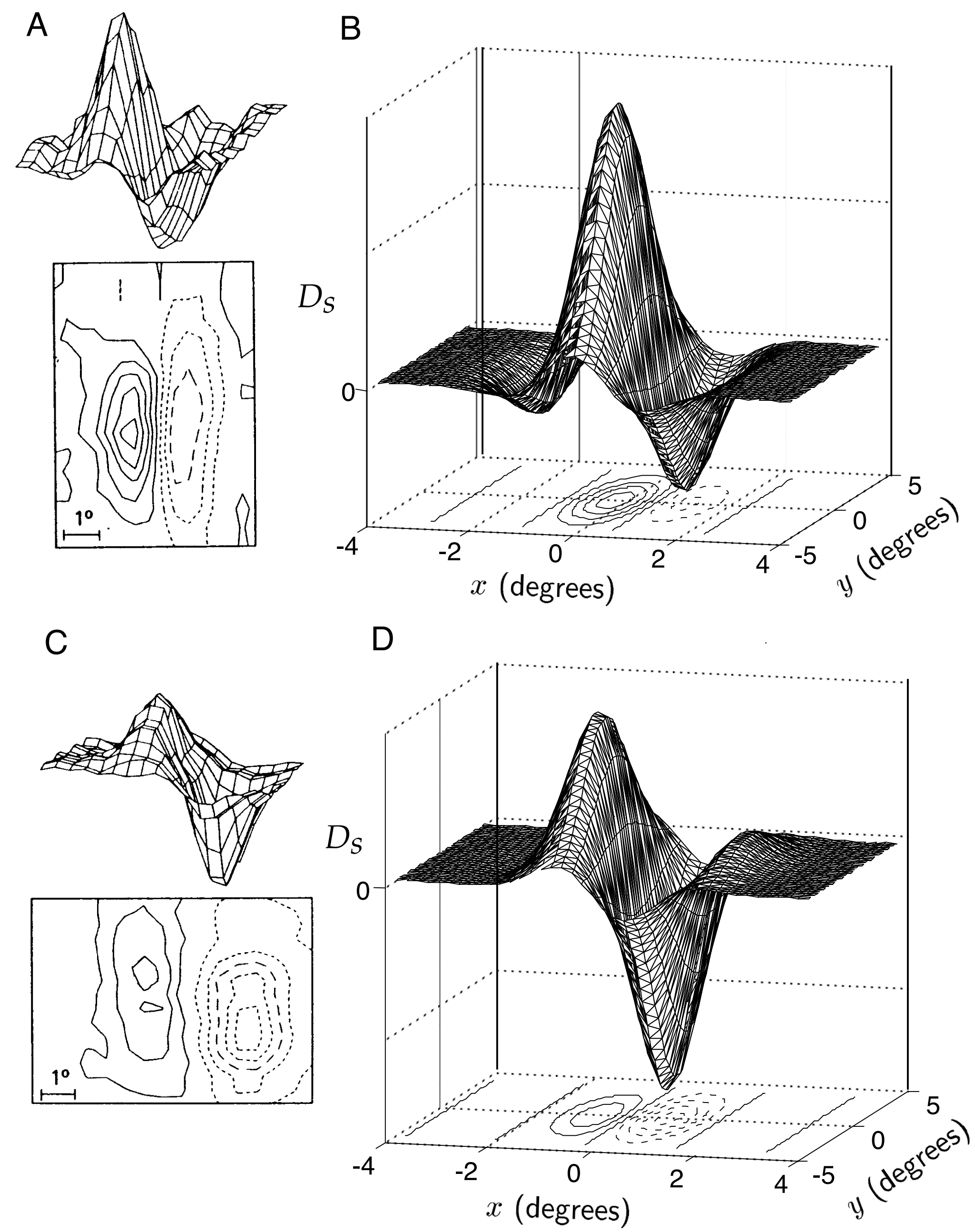

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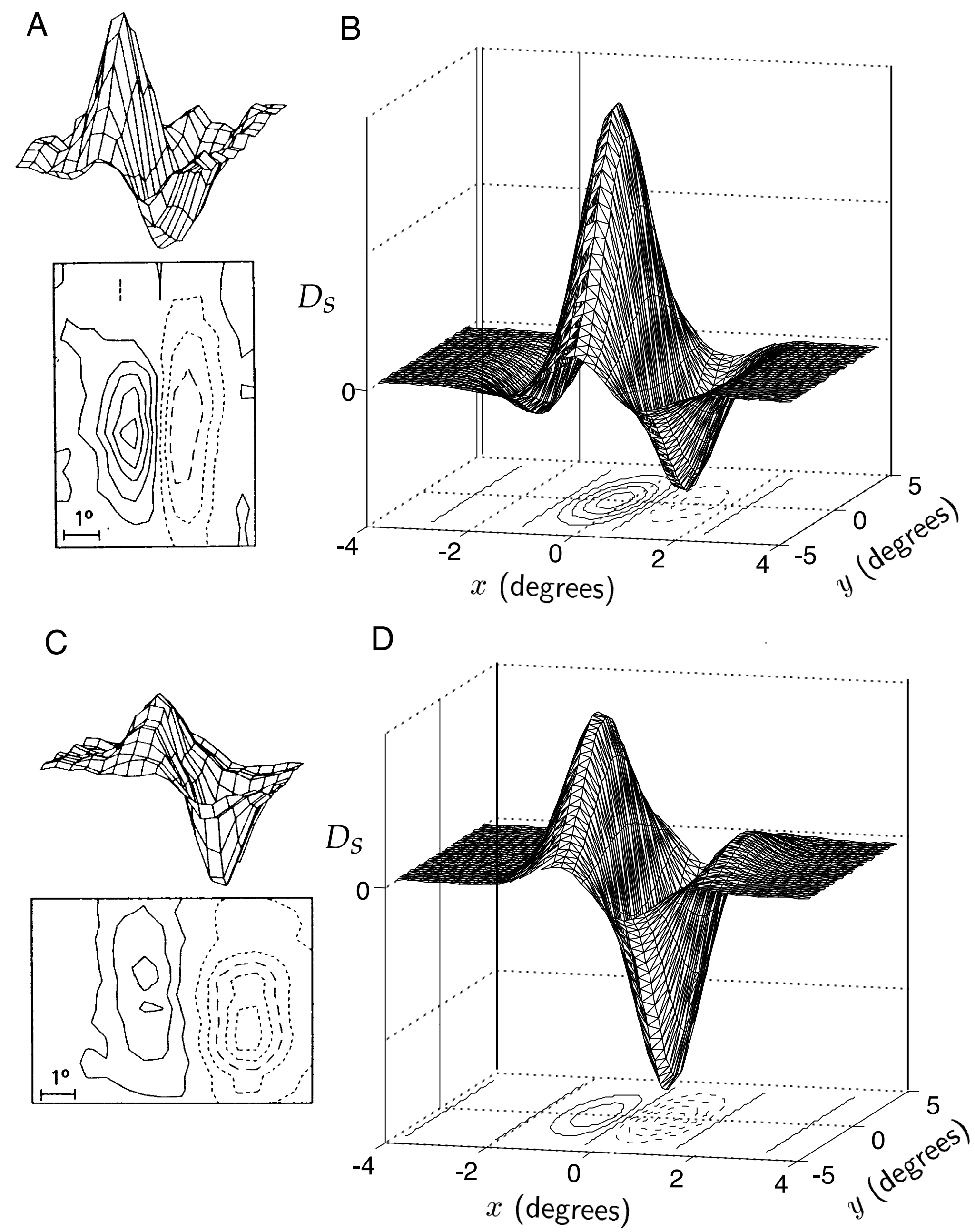

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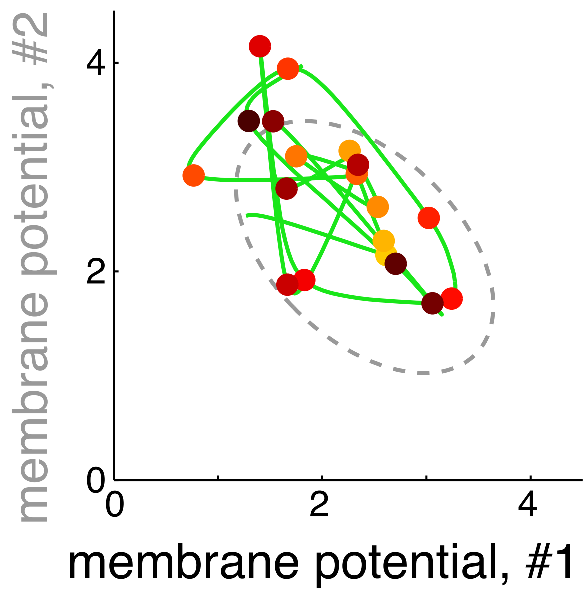
maximum likelihood fitting?

stochastic sampling



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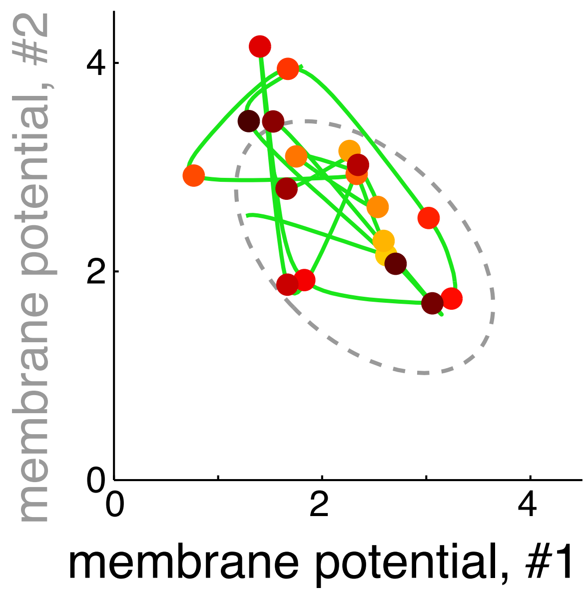

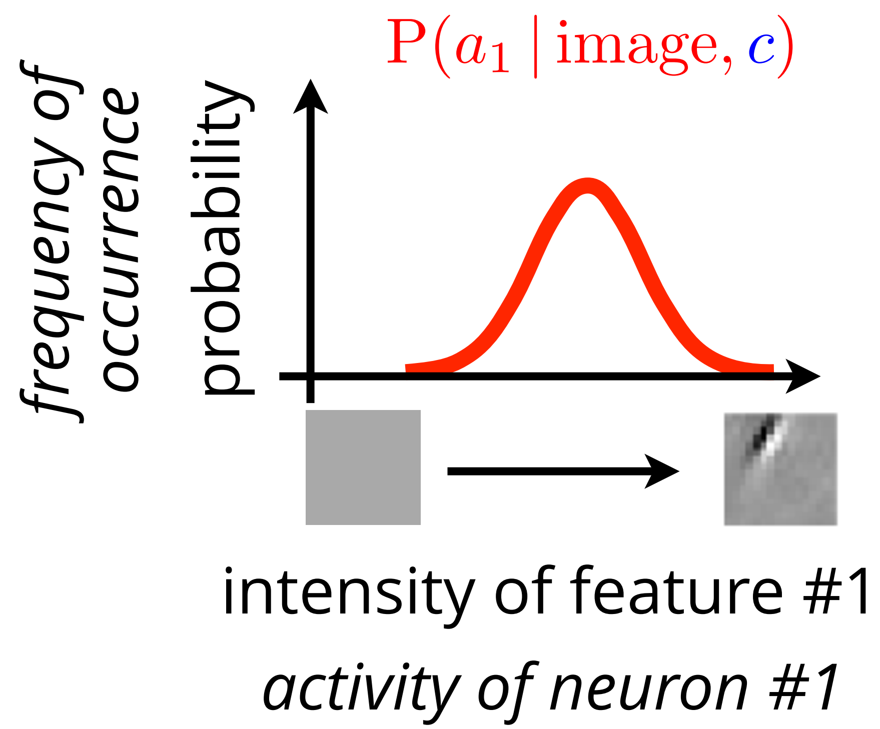

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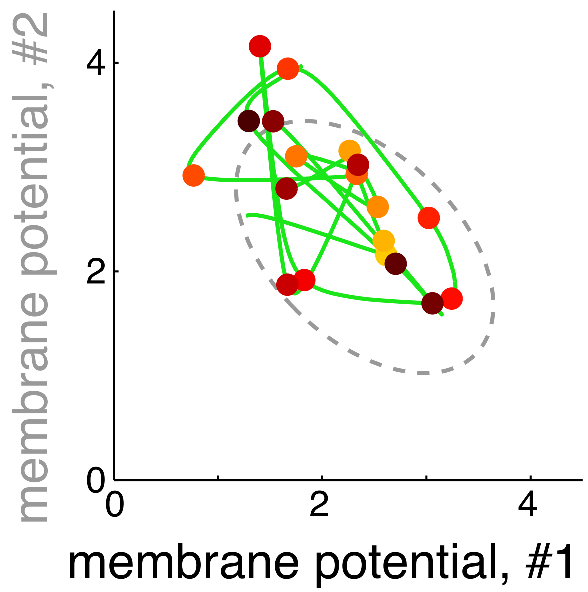

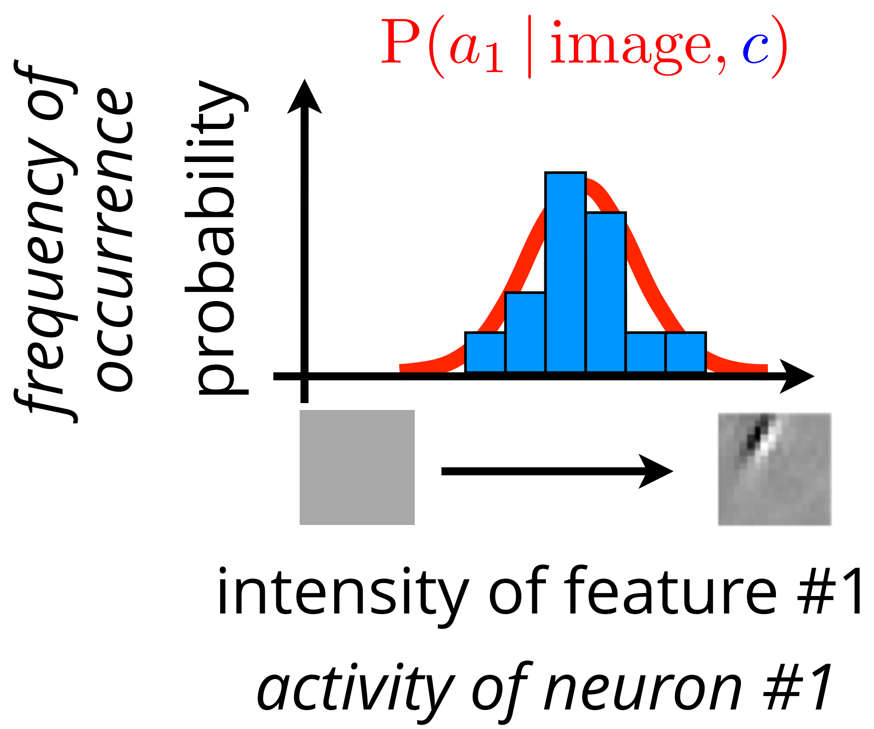

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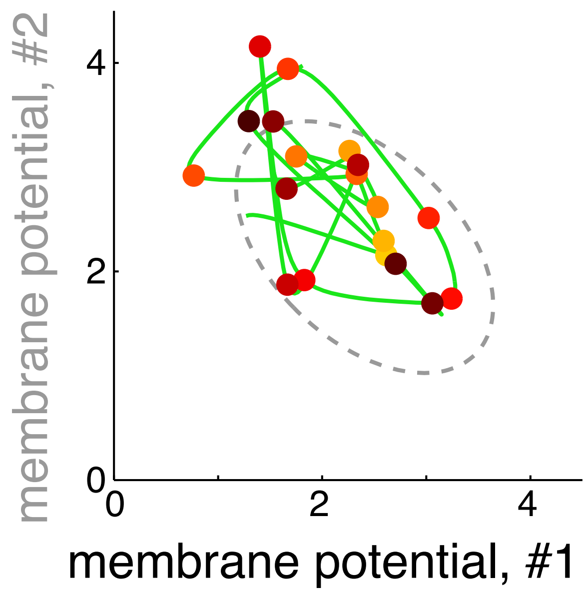

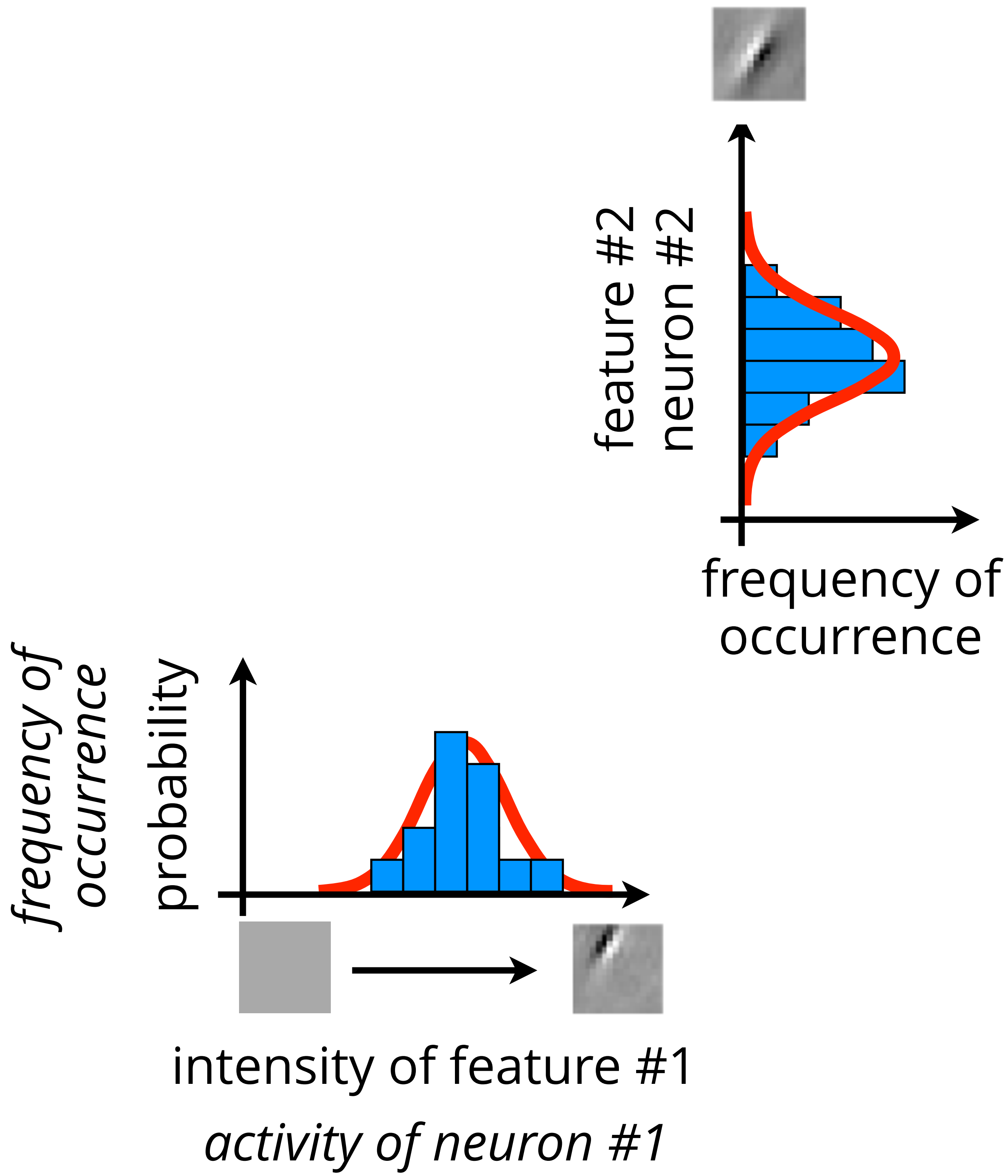

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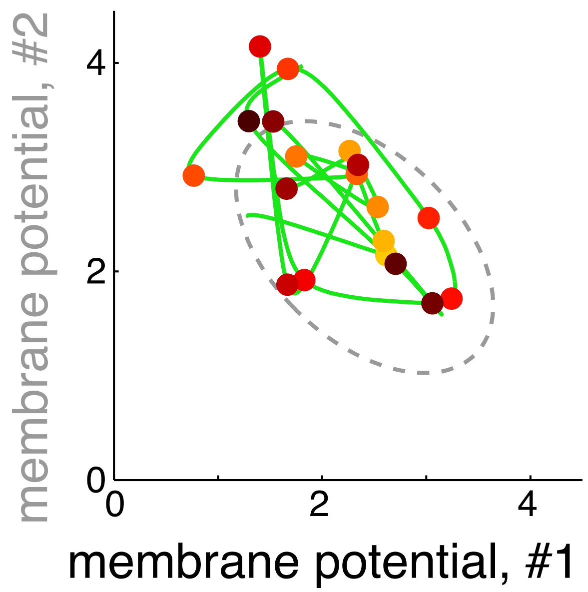

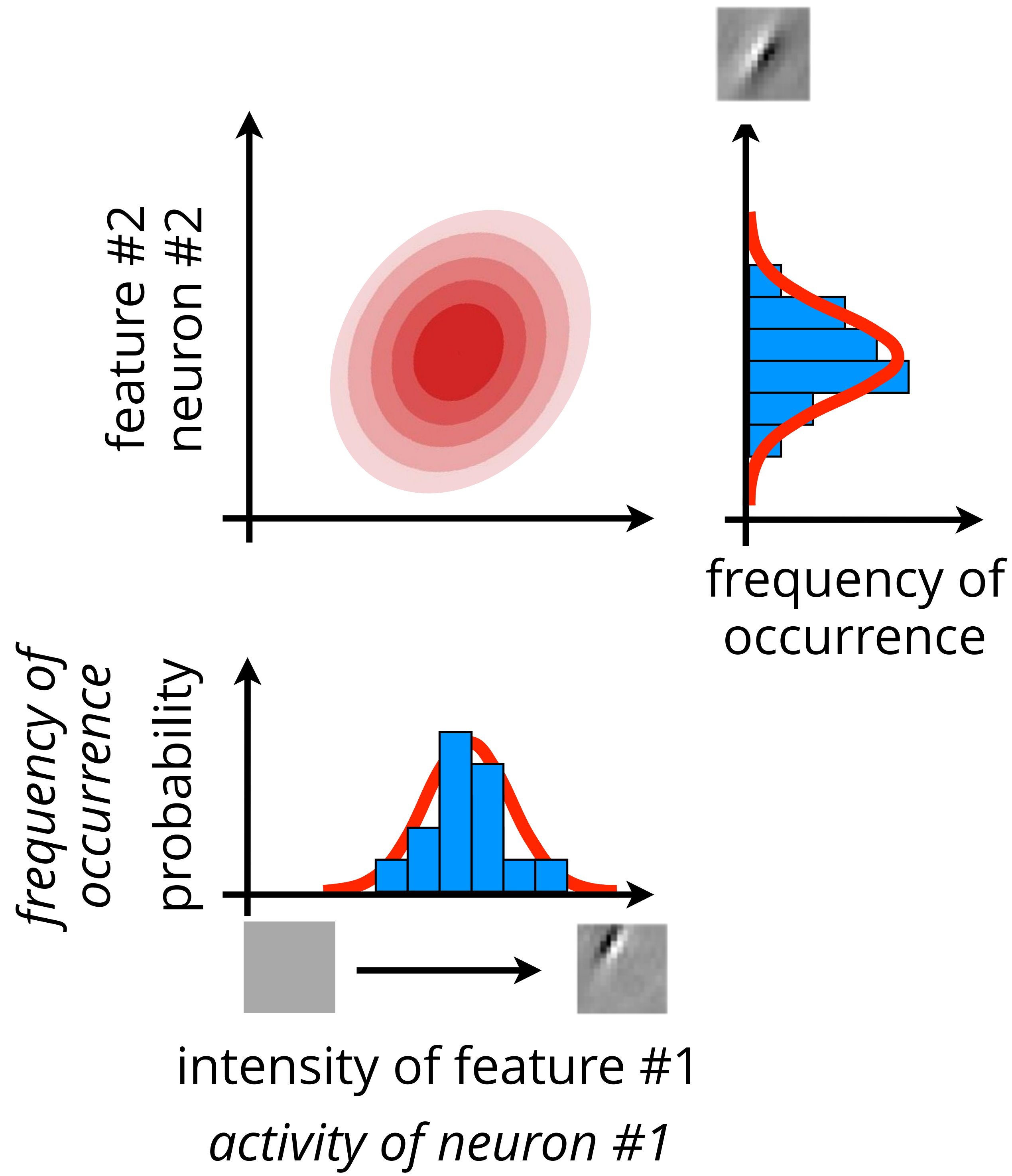

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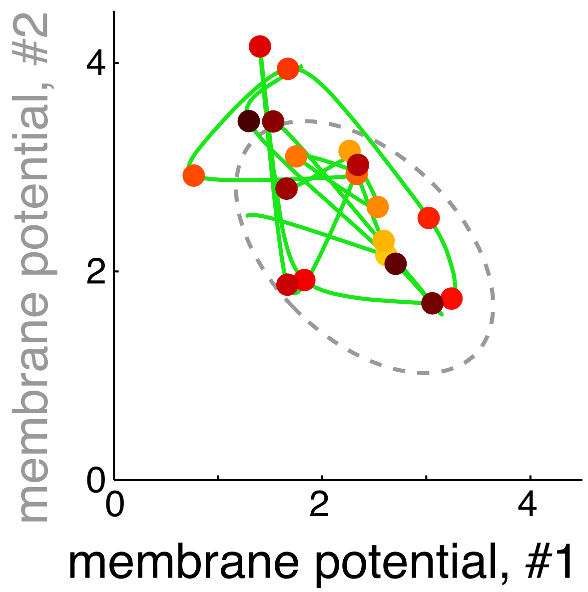

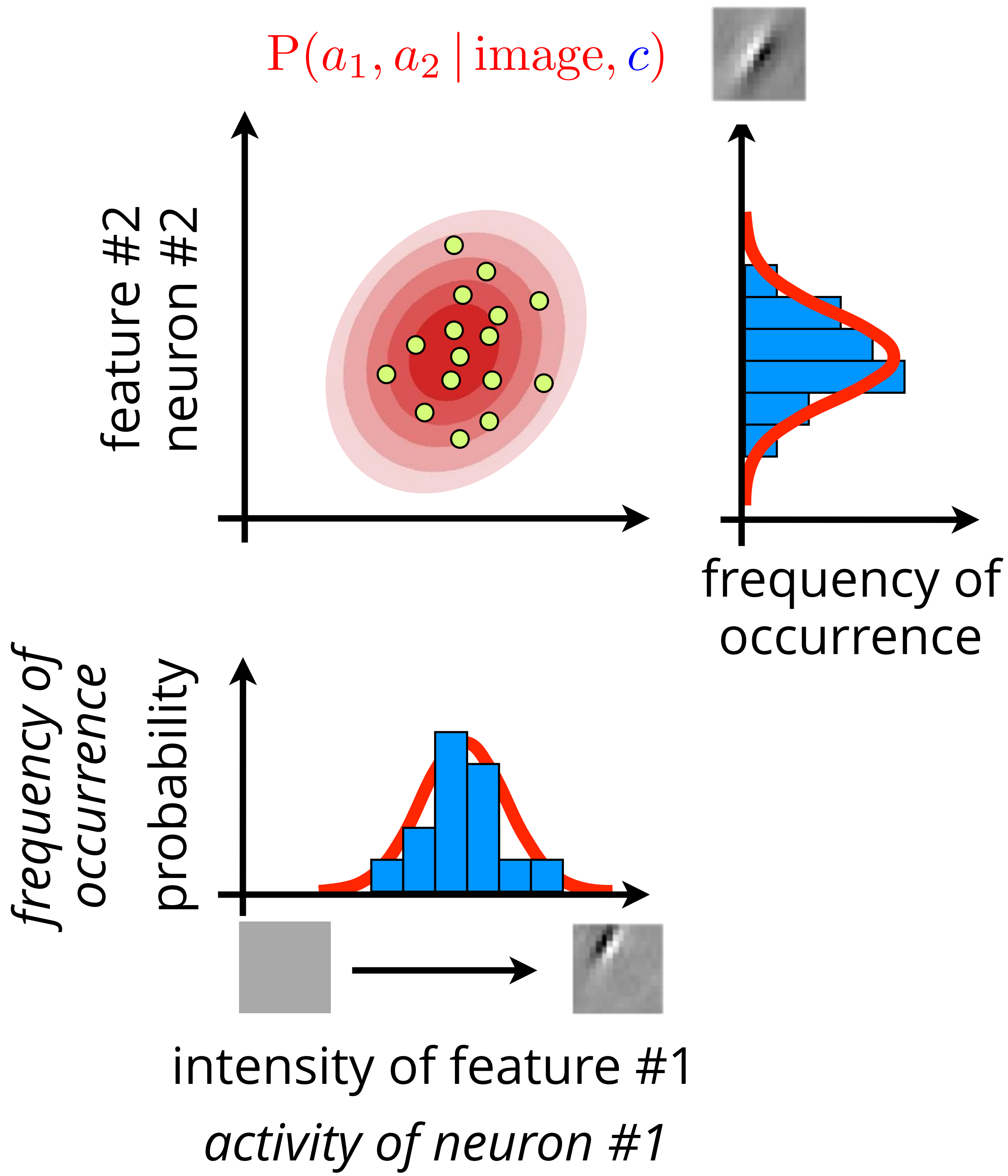

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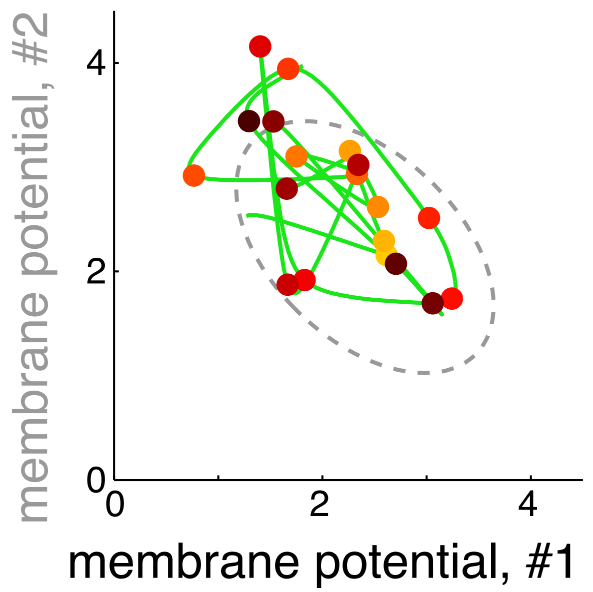
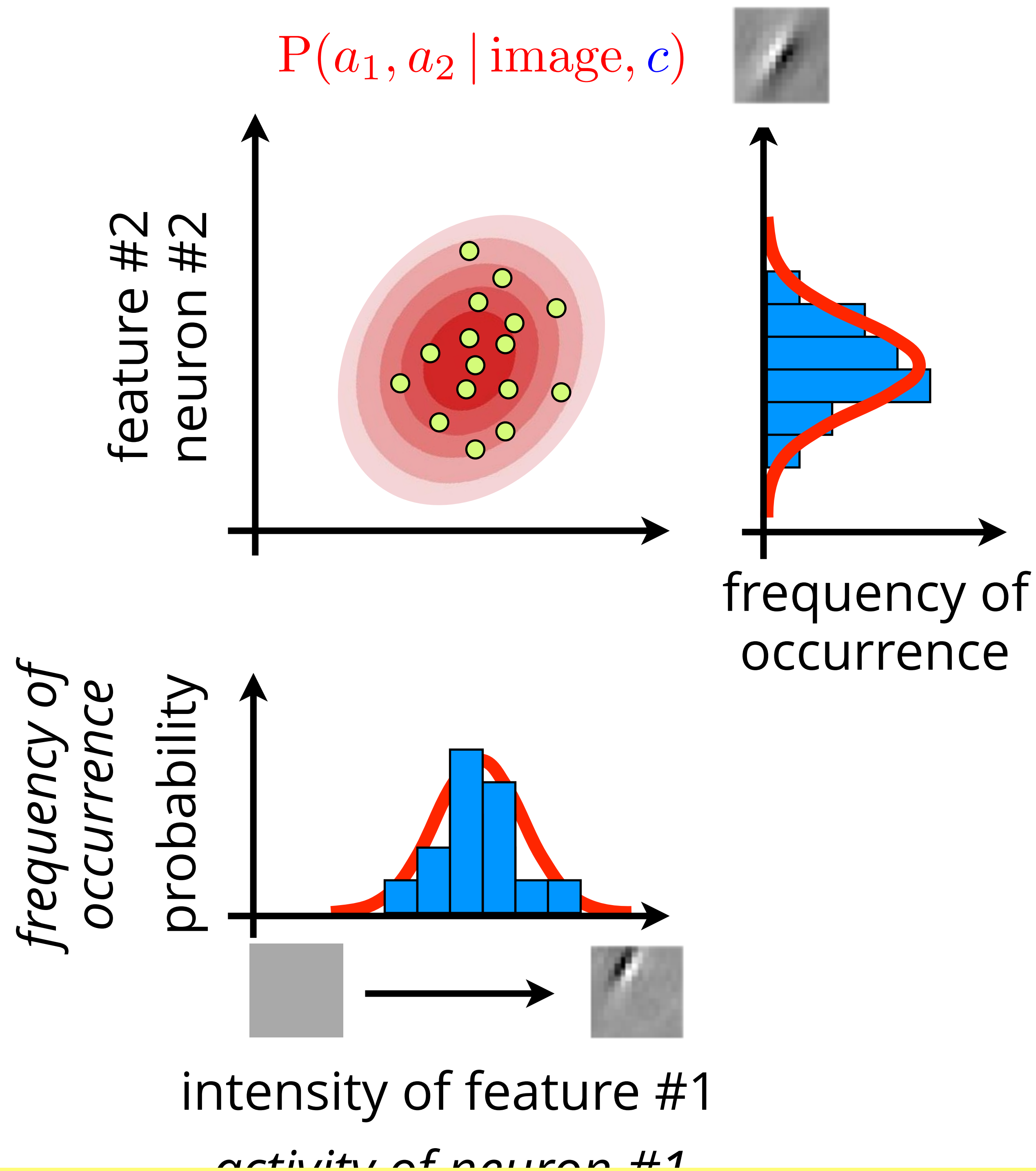
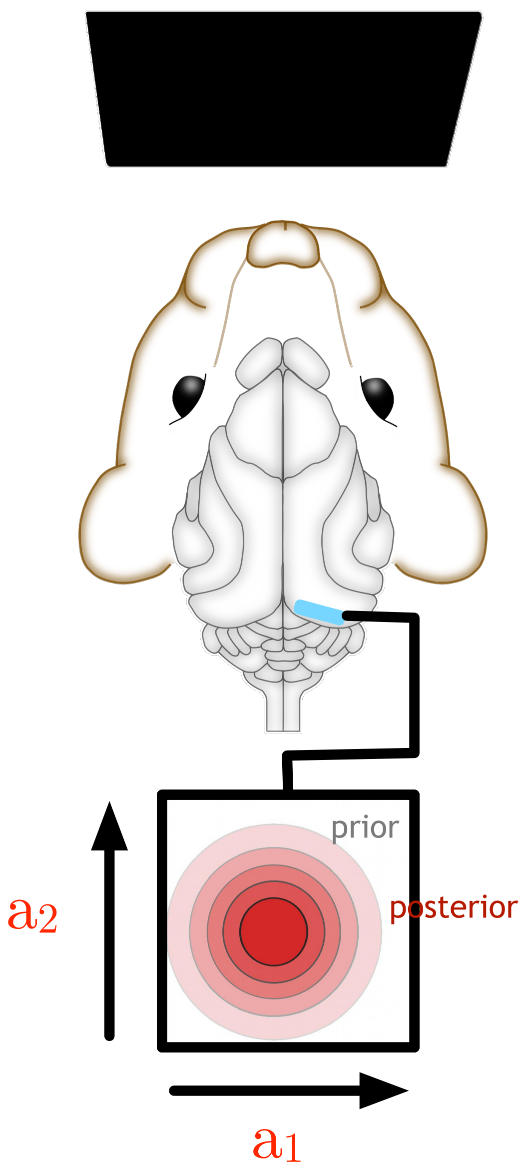




changes in inferences need to be reflected in the response statistics

Full response statistics

prior expectations



Full response statistics

prior expectations

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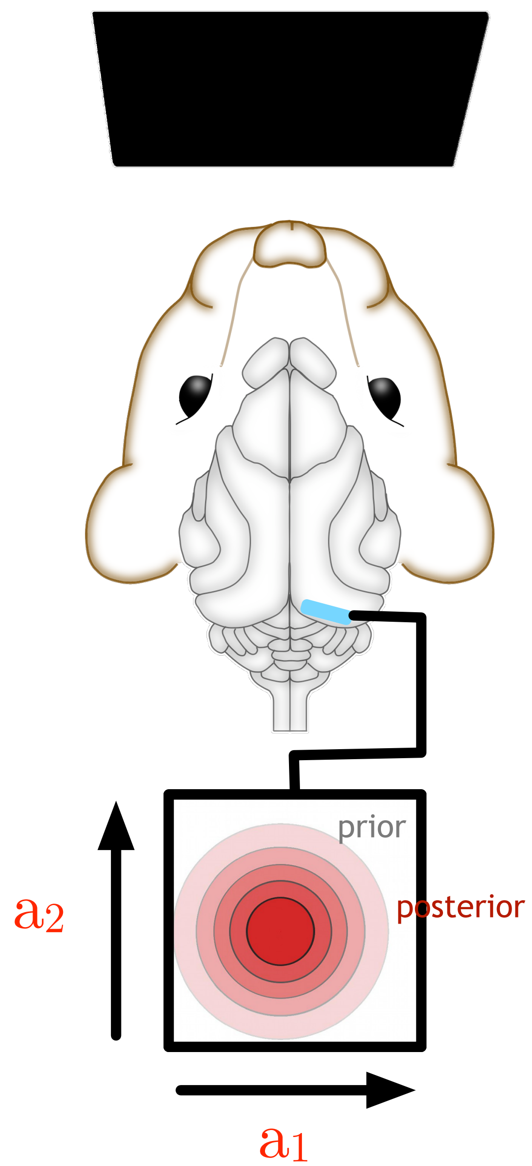

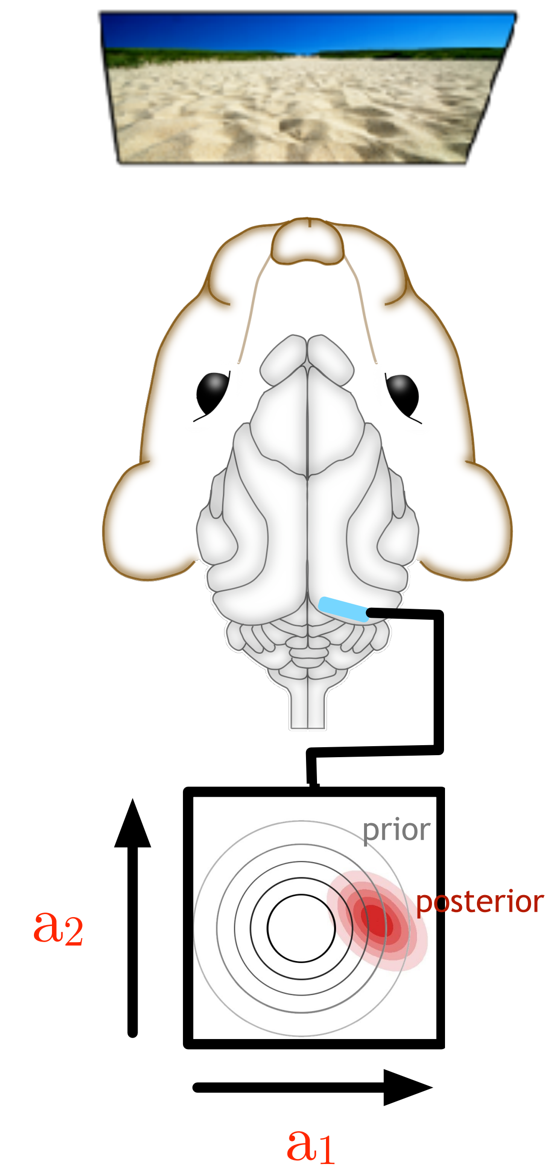

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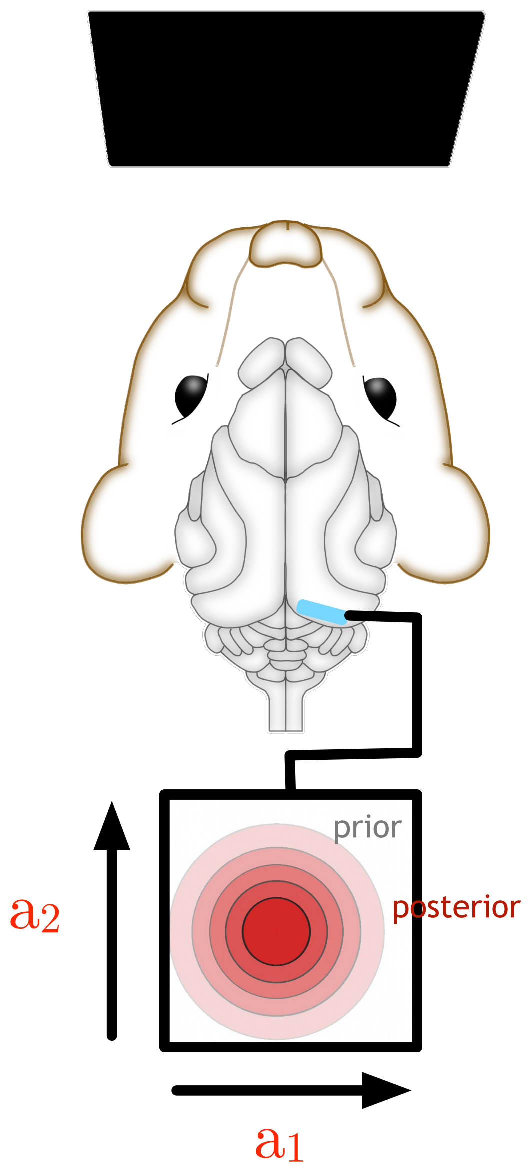

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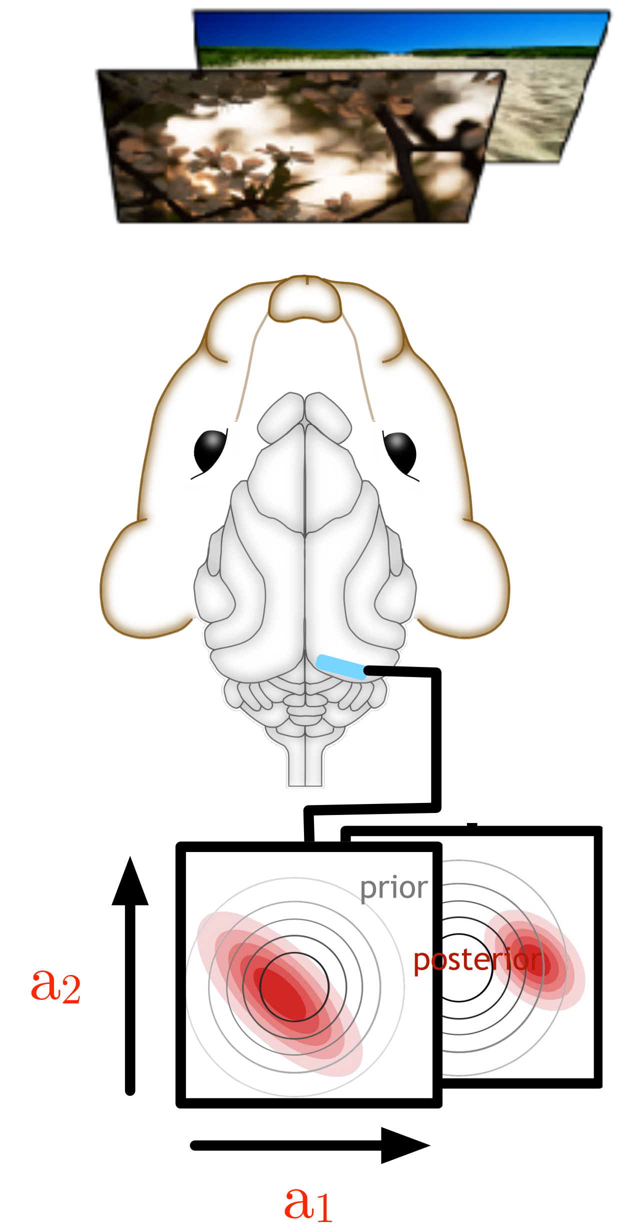

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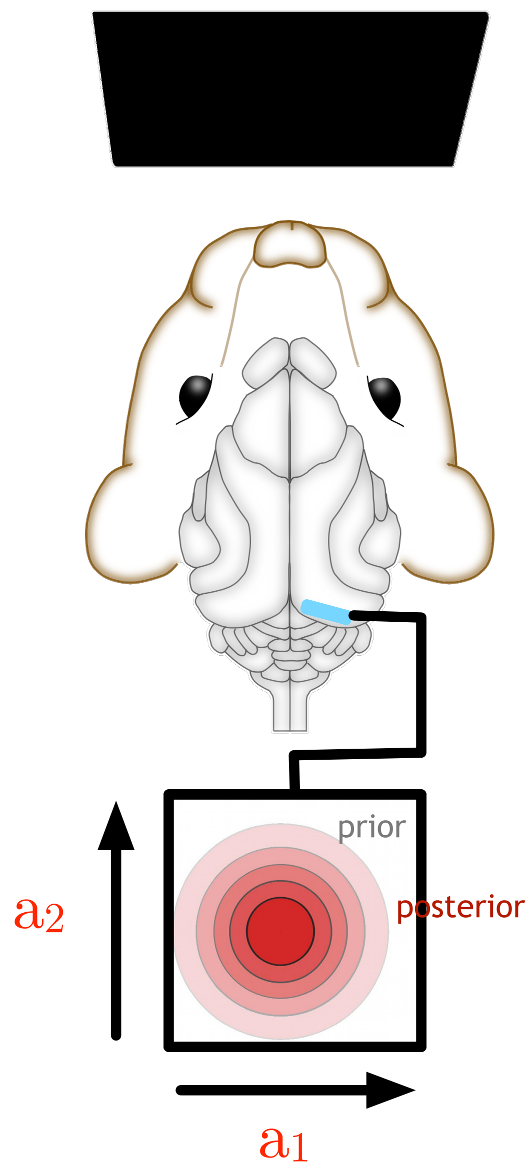

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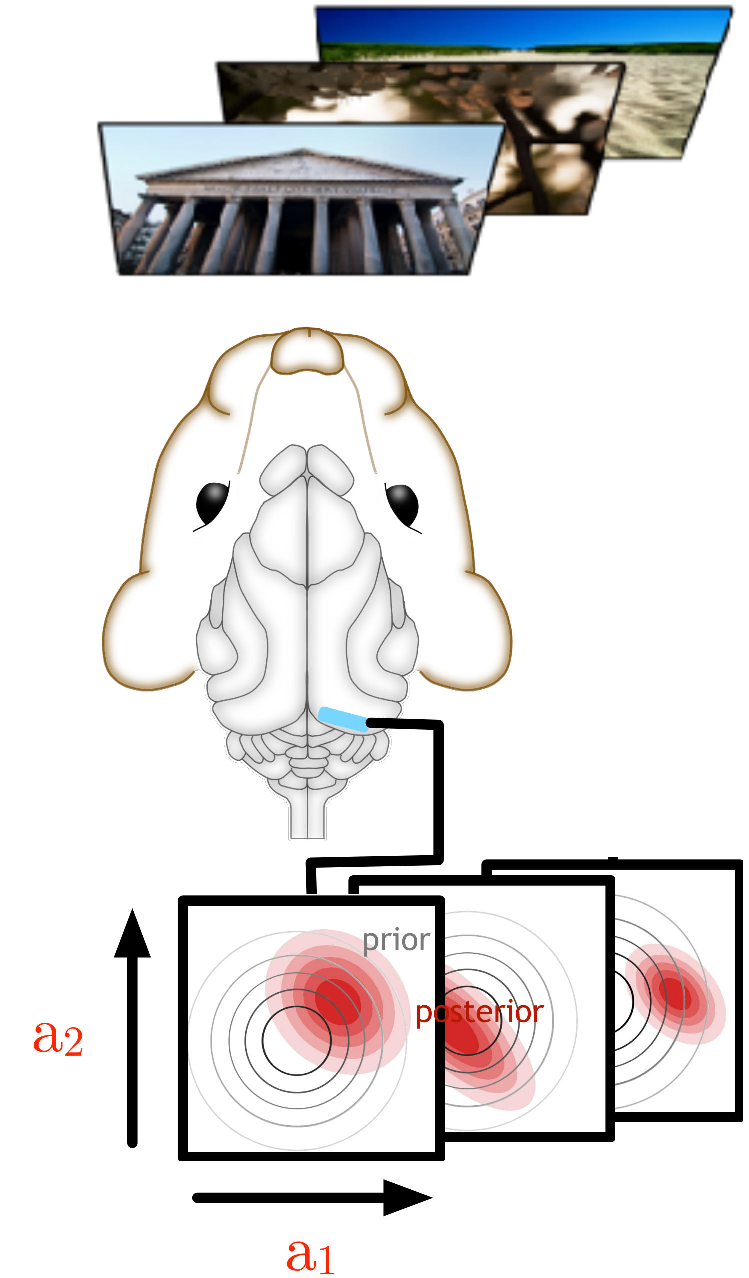

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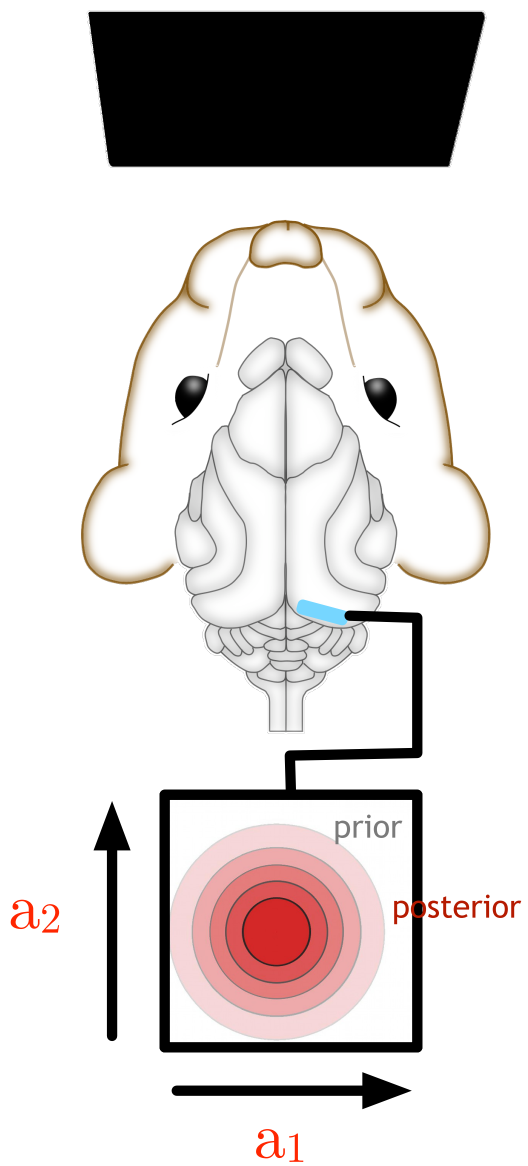

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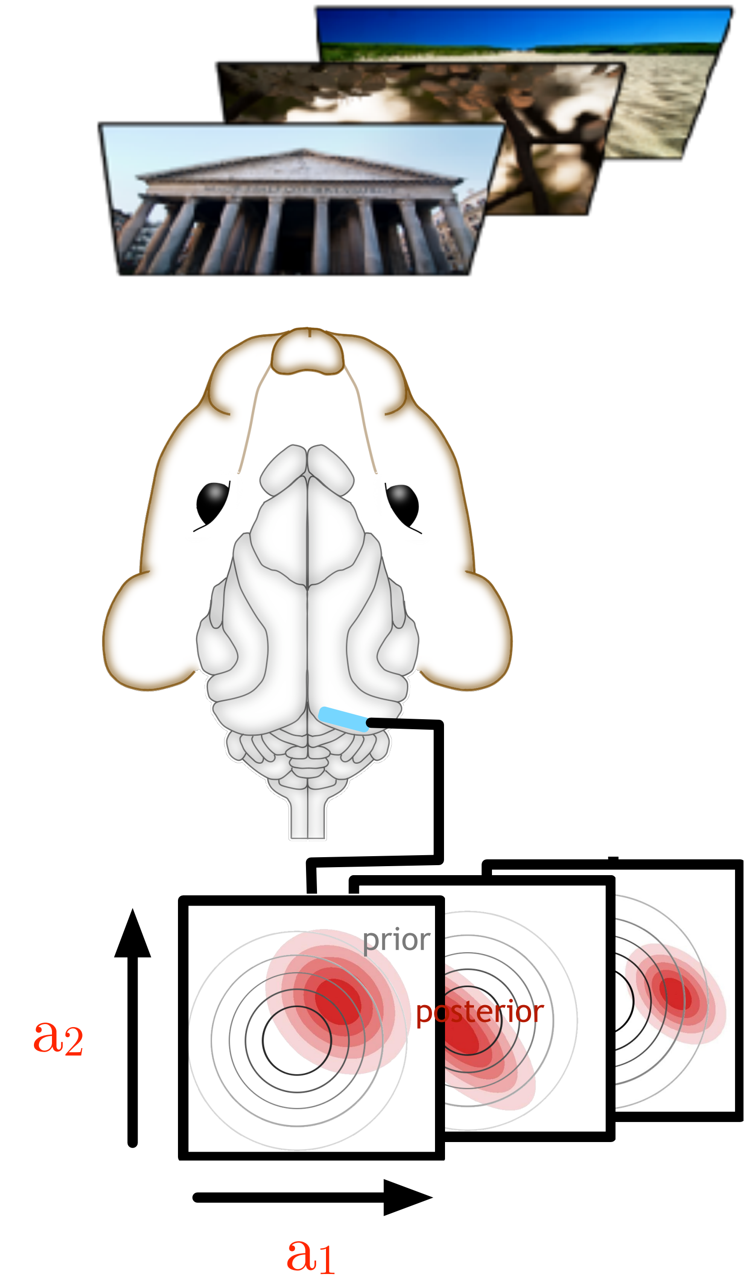


spontaneous activity

$$P(\mathbf{a})$$

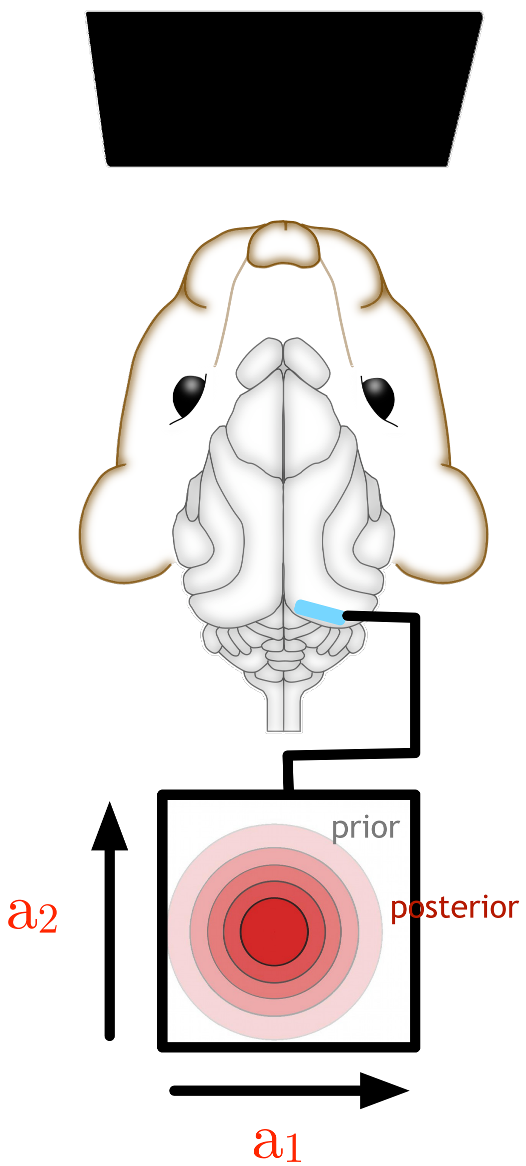
evoked activity

$$P(\mathbf{a} \mid \mathbf{x})$$

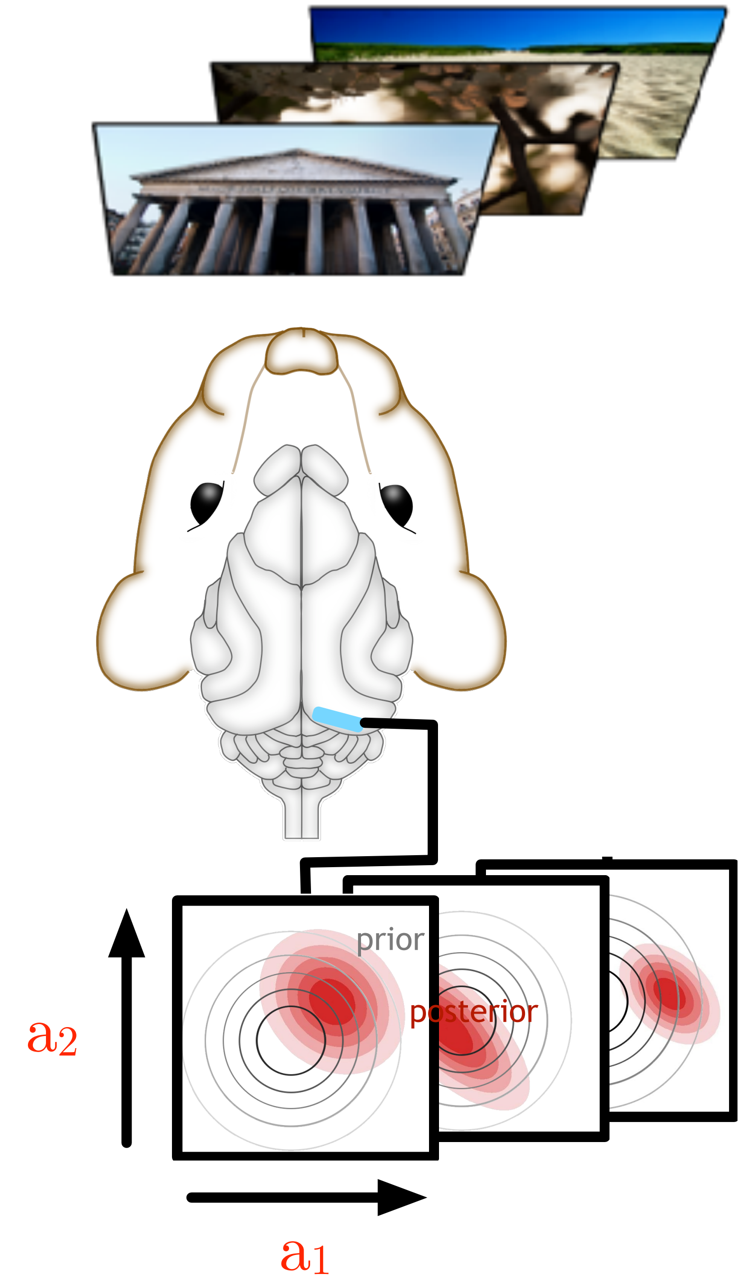
Full response statistics

prior expectations

inferences



$$P(\mathbf{a}) = \int dx \, P(\mathbf{a} \,|\, \mathbf{x}) \, P(\mathbf{x})$$



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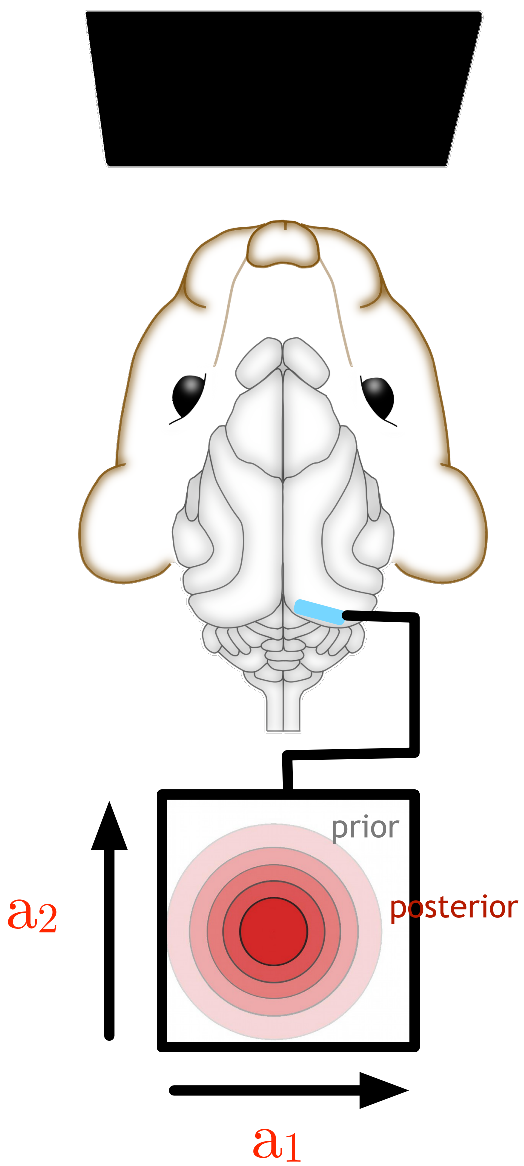
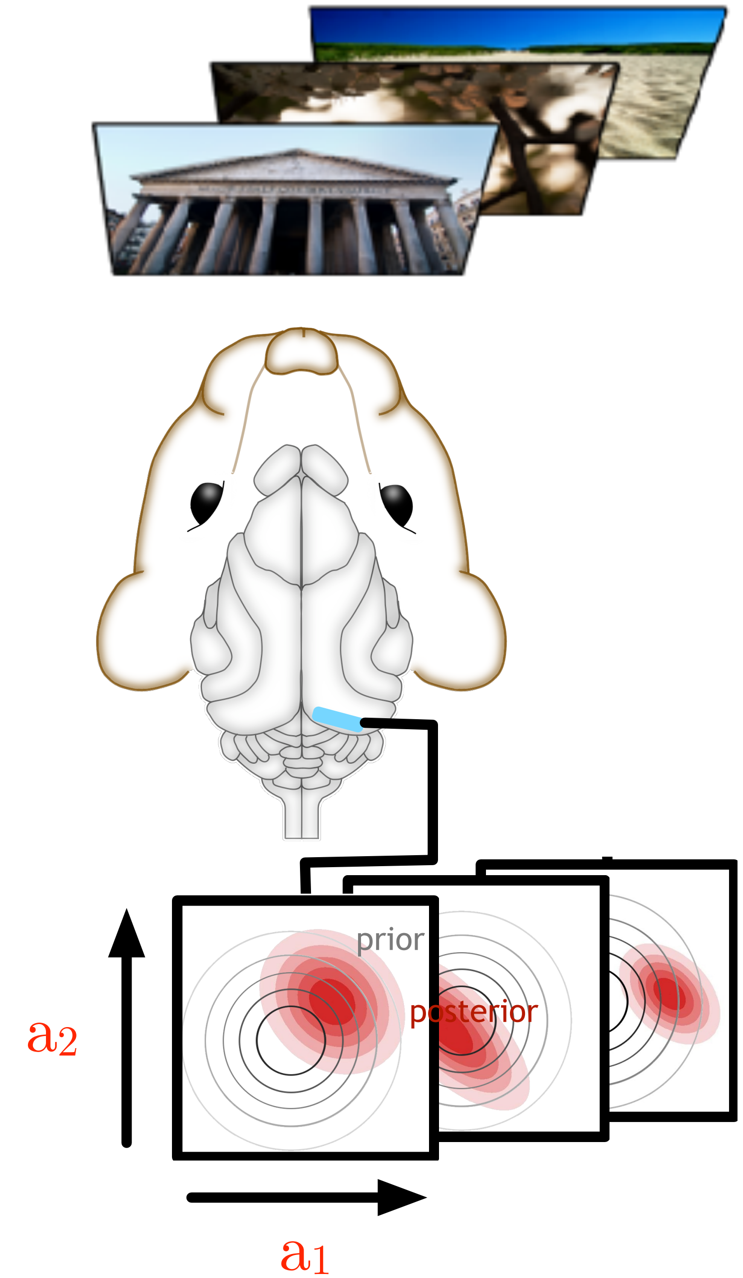


inferences



expectations

$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

spontaneous activity

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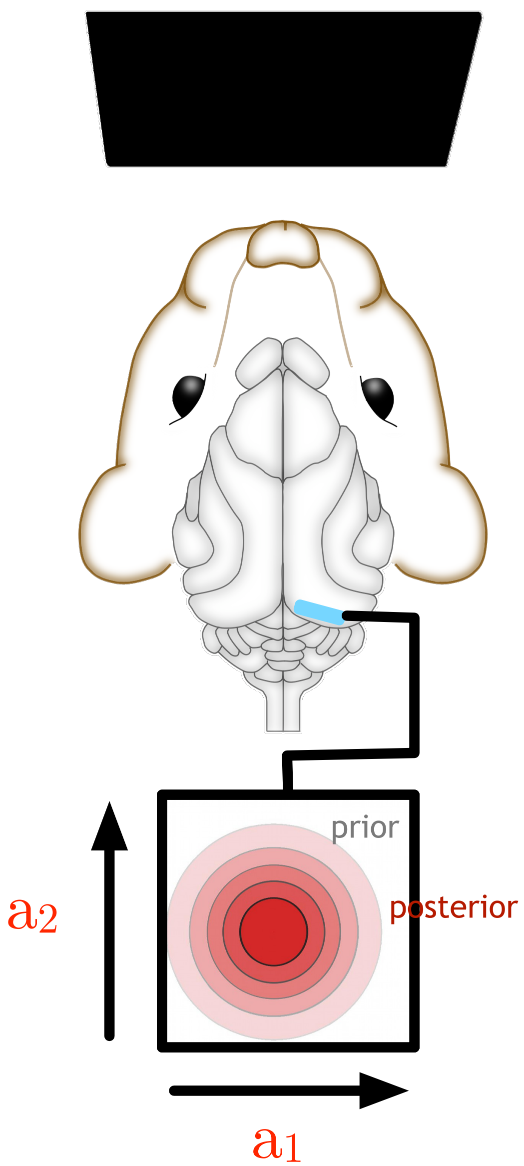

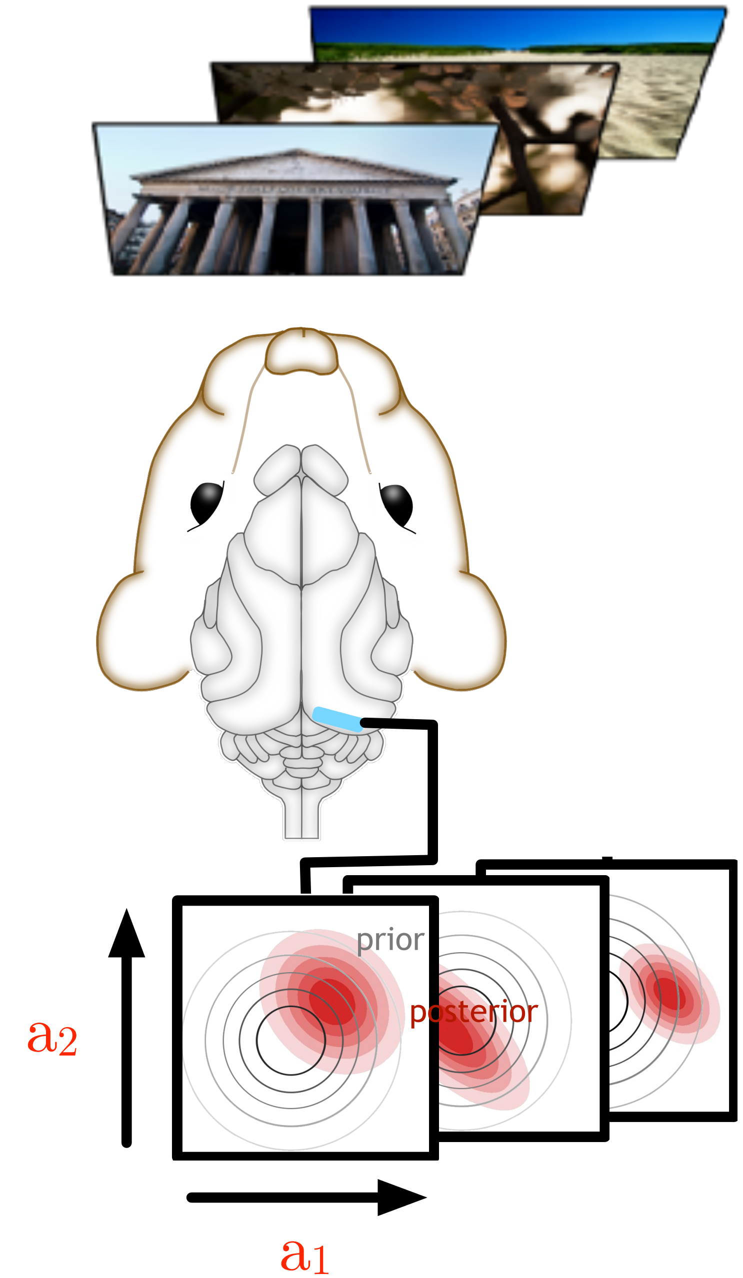

expectations *inference*

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spontaneous activity

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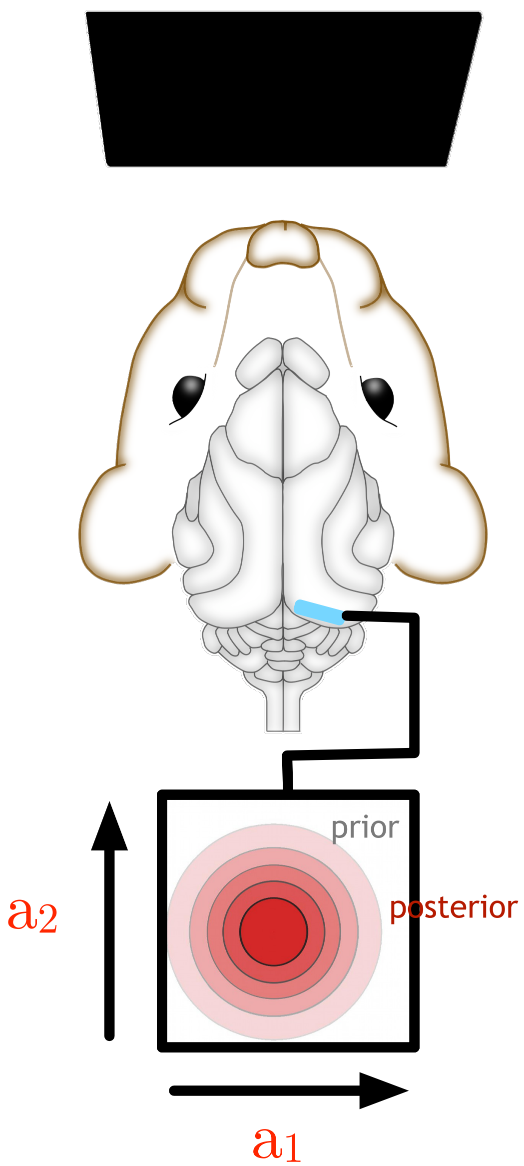
Full response statistics

prior expectations



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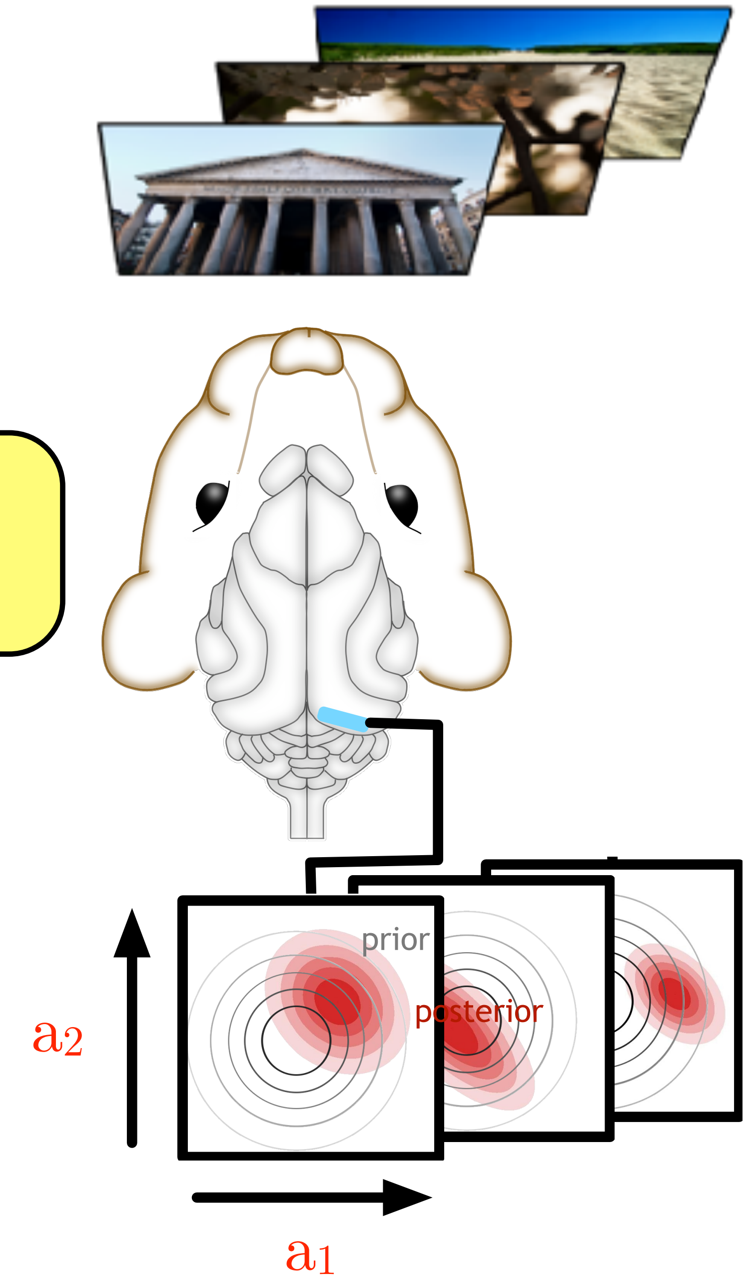


expectations

inference

stimulus statistics

$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

spontaneous activity

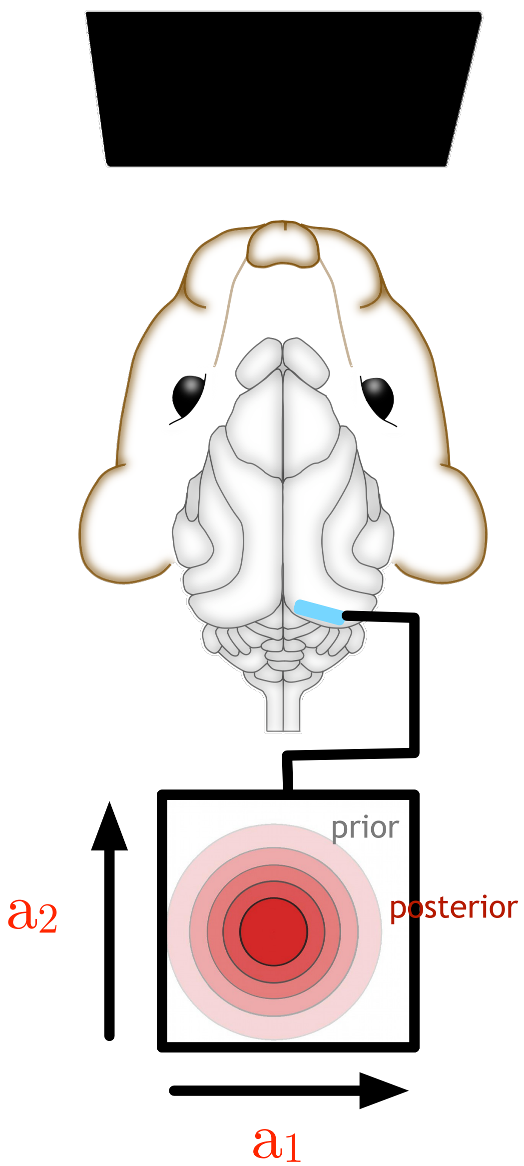
$P(\mathbf{a})$

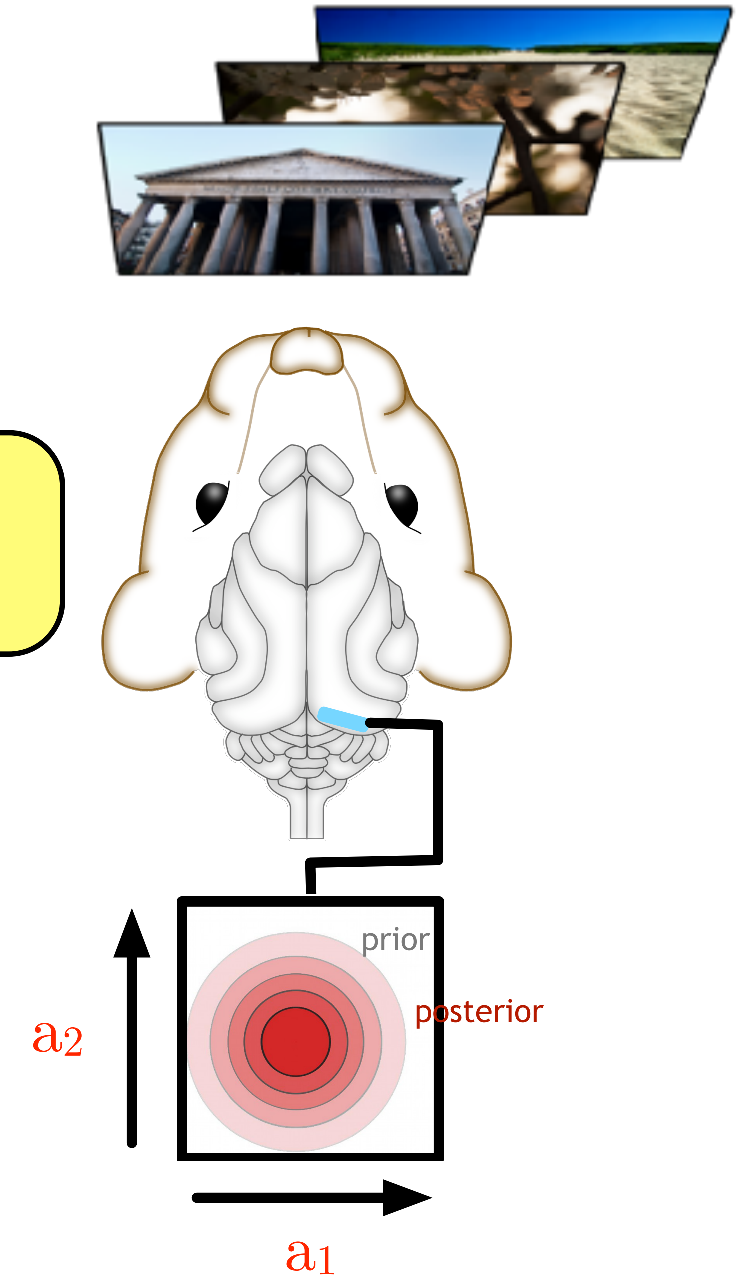
evoked activity

$P(\mathbf{a}\,|\,\mathbf{x})$

Full response statistics

prior expectations *average inferences*





expectations *inference* stimulus statistics

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spontaneous activity

$P(\mathbf{a})$

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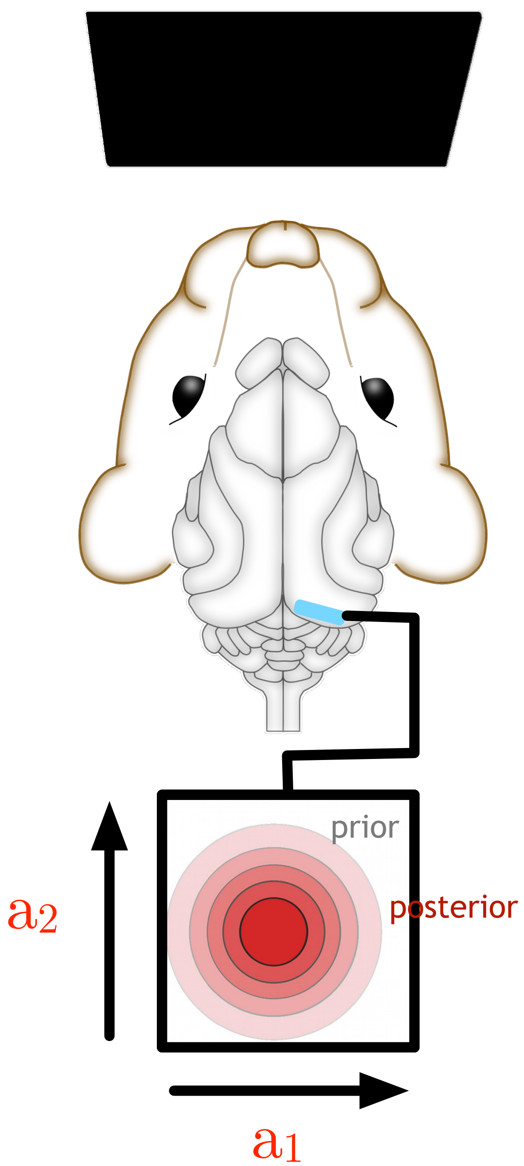
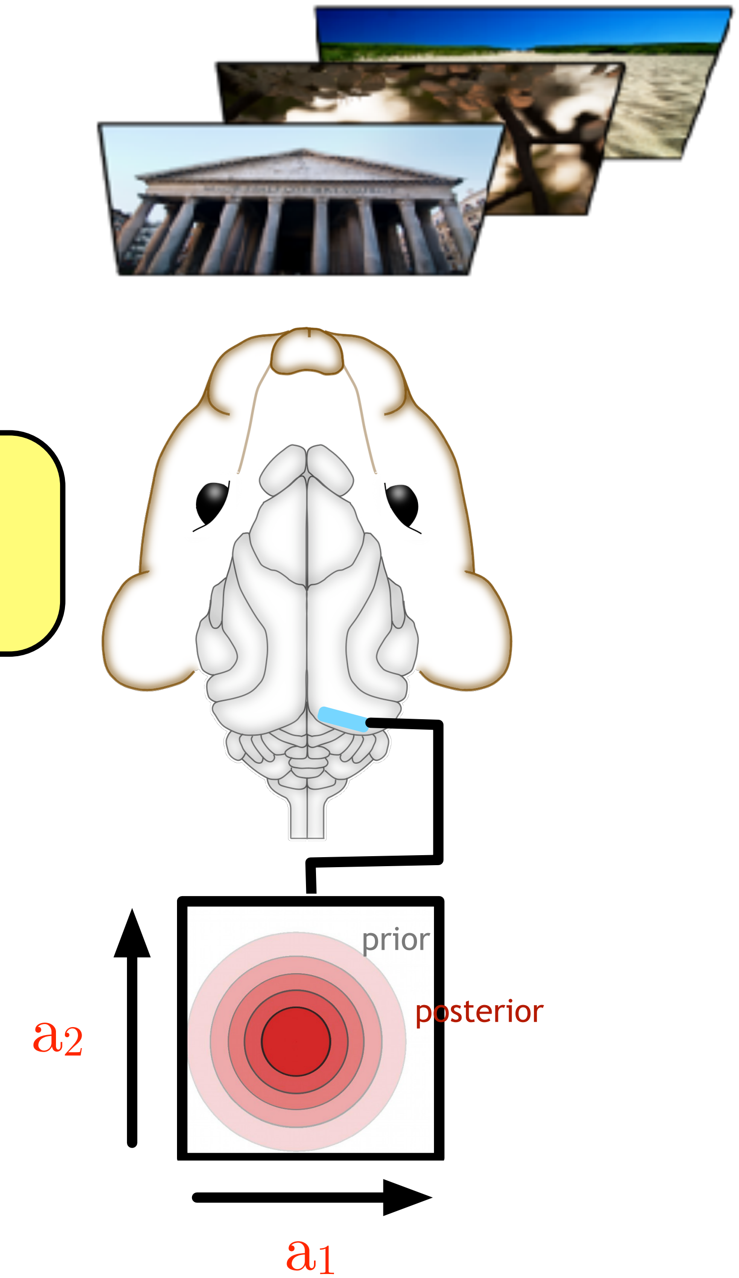
Full response statistics

prior expectations



average inferences



expectations | *inference* | stimulus statistics

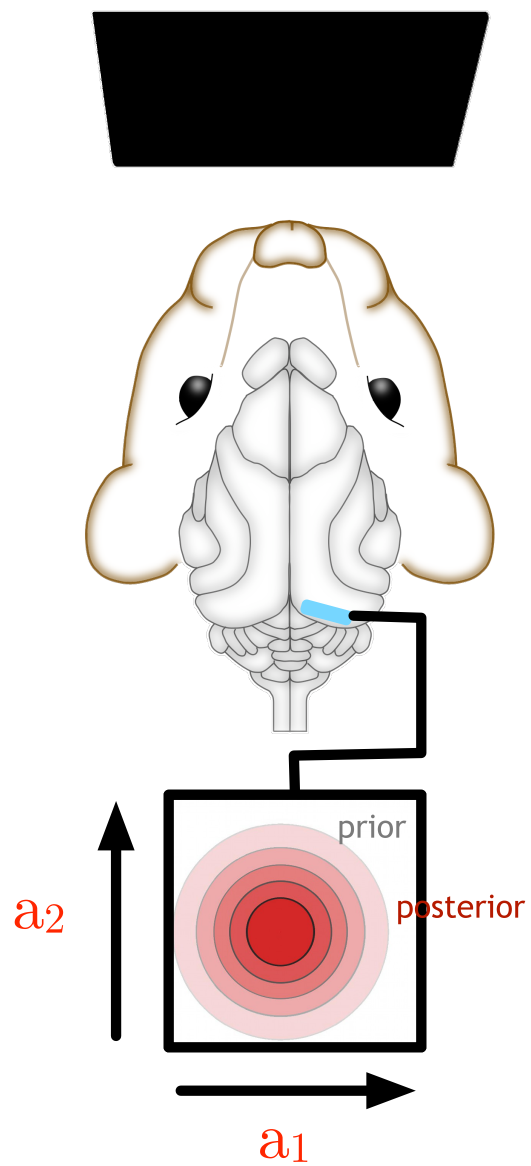
$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

spontaneous activity $\stackrel{?}{=}$ average evoked activity

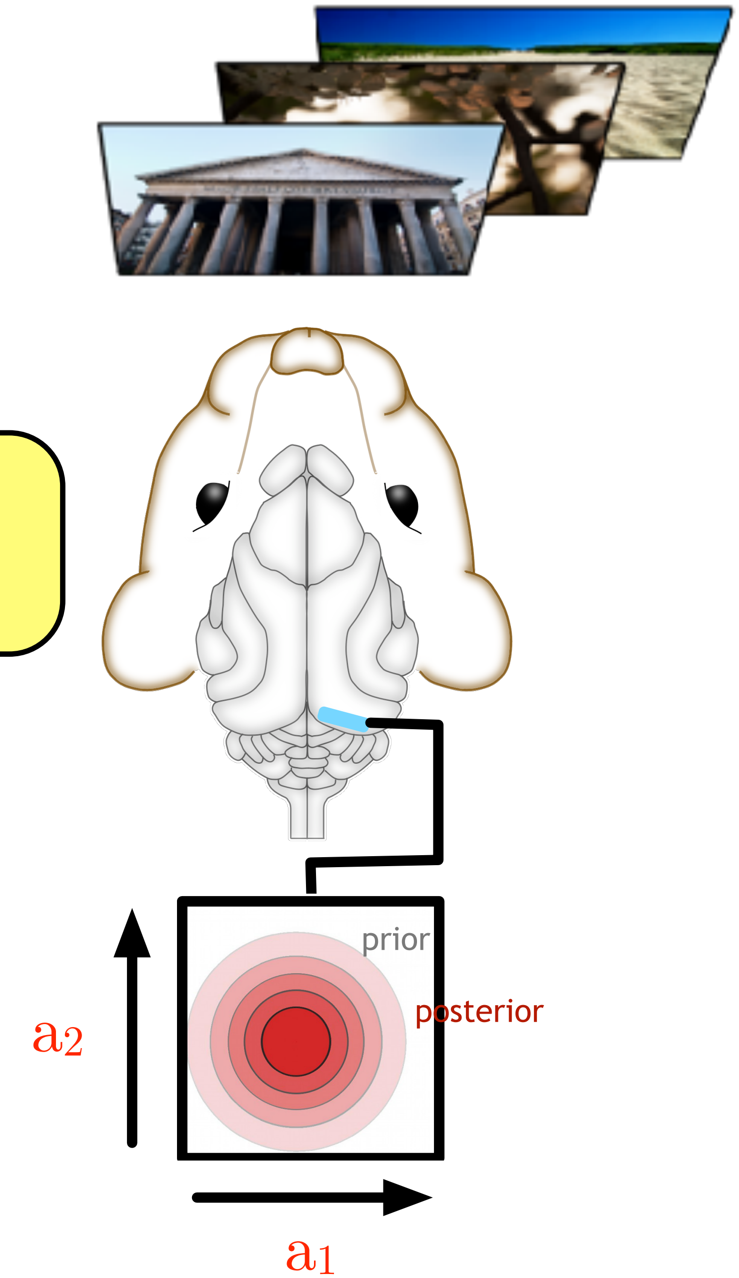
$P(\mathbf{a})$ $P(\mathbf{a}\,|\,\mathbf{x})$

Full response statistics

prior expectations



average inferences



expectations — *inference* — stimulus statistics

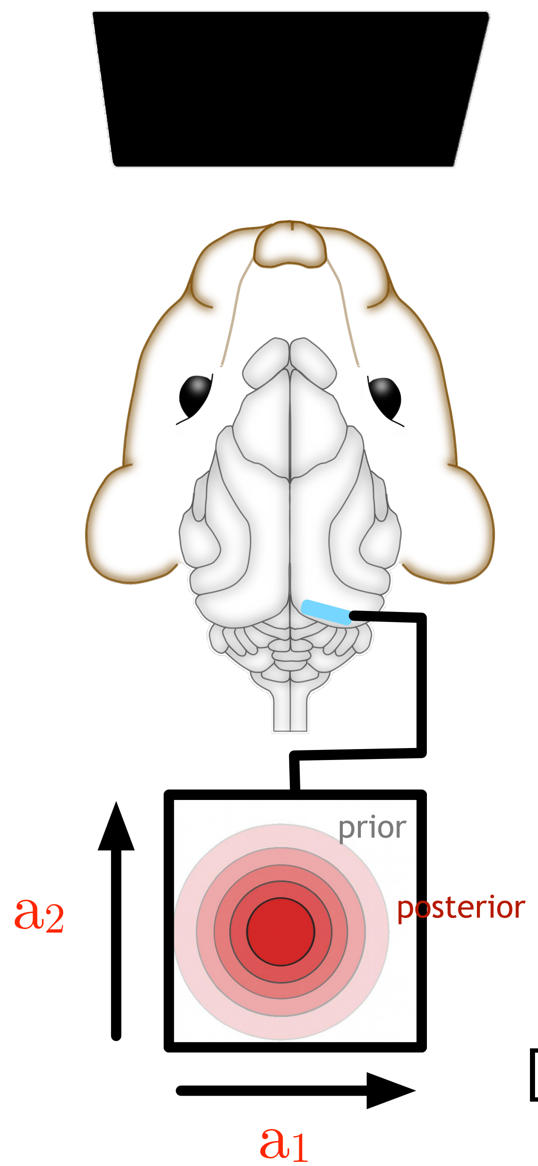
$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

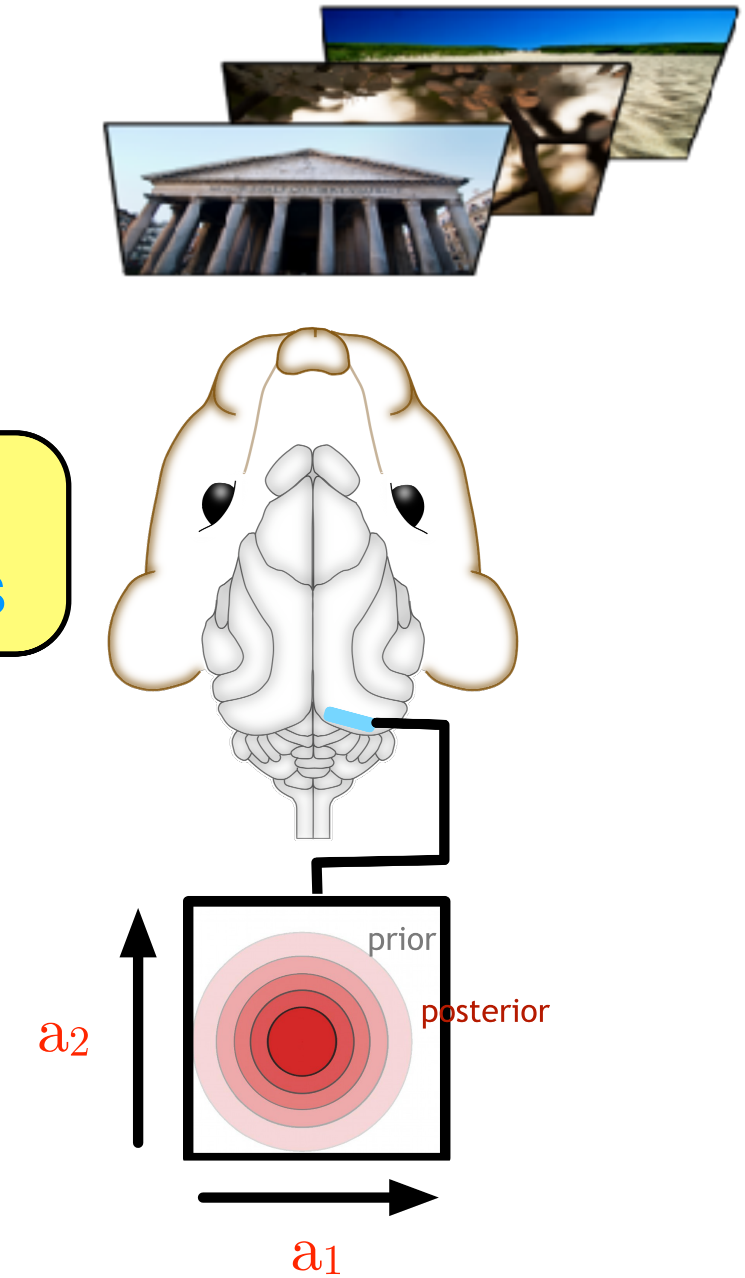
$$\langle P(\mathbf{a}\,|\,\mathbf{x})\rangle_{P(\mathbf{x})}$$

spontaneous activity $P(\mathbf{a})$ $\stackrel{?}{=}$ average evoked activity $P(\mathbf{a}\,|\,\mathbf{x})$

Full response statistics

prior expectations *average inferences*





stimulus statistics

expectations

inference

$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

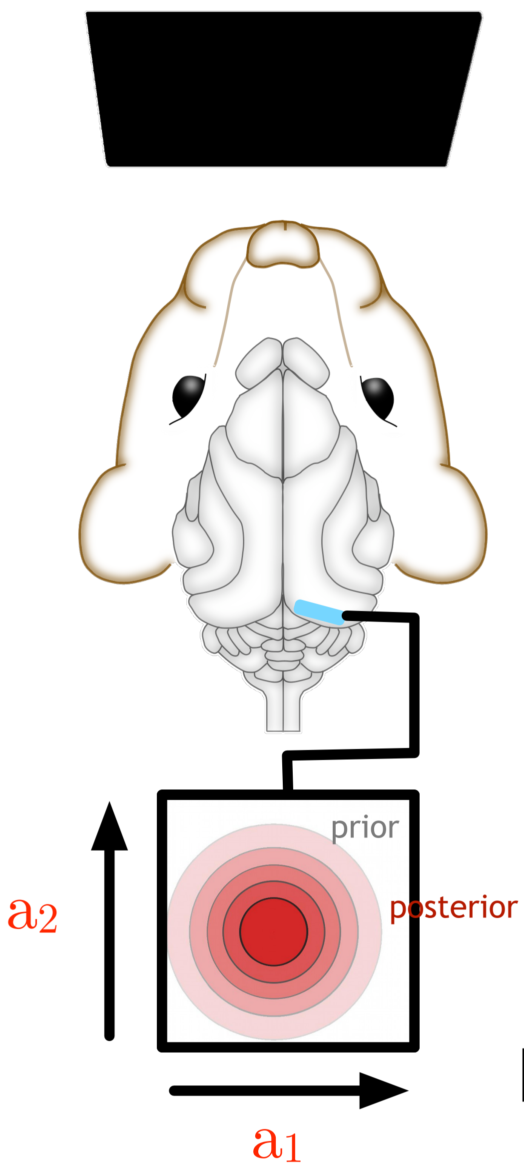
Dissimilarity: $\mathrm{KL}[P(\mathbf{a})\,||\langle P(\mathbf{a}\,|\,\mathbf{x})\rangle_{P(\mathbf{x})}]$

spontaneous activity $\stackrel{?}{=}$ average evoked activity

$P(\mathbf{a})$ $P(\mathbf{a}\,|\,\mathbf{x})$

Full response statistics

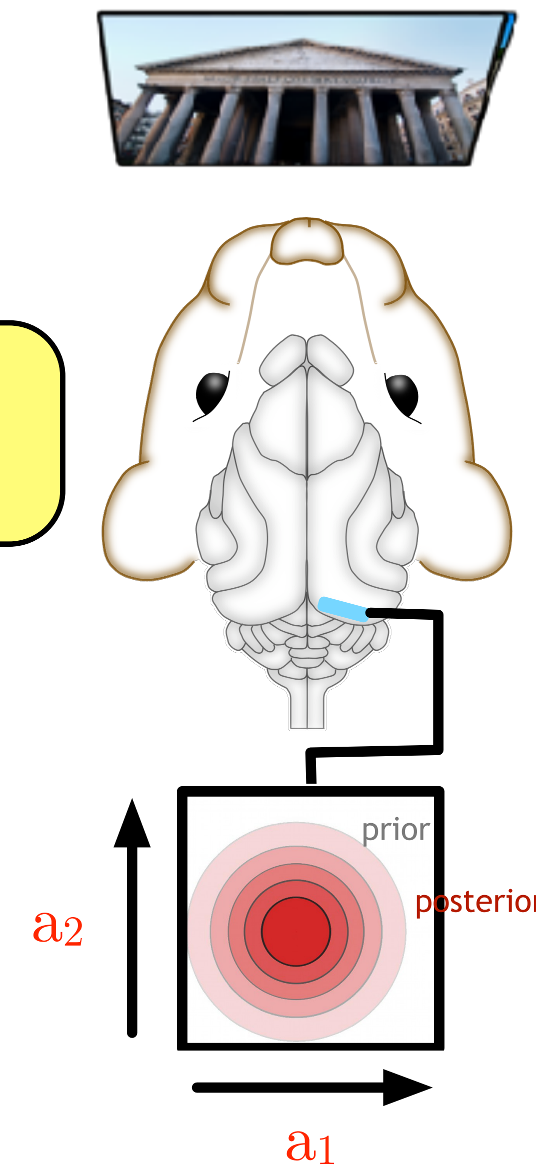
prior expectations *average inferences*



expectations *inference* stimulus statistics

$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

Dissimilarity: $\mathrm{KL}[P(\mathbf{a})\;||\langle P(\mathbf{a}\,|\,\mathbf{x})\rangle_{P(\mathbf{x})}]$



spontaneous activity $\stackrel{?}{=}$ average evoked activity

$P(\mathbf{a})$ $P(\mathbf{a}\,|\,\mathbf{x})$

Full response statistics

$$P(\mathbf{a}) = \int dx\, P(\mathbf{a}\,|\,\mathbf{x})\, P(\mathbf{x})$$

spontaneous activity $\stackrel{?}{=}$ average evoked activity

$P(\mathbf{a})$ $\qquad$ $P(\mathbf{a}\,|\,\mathbf{x})$

Full response statistics

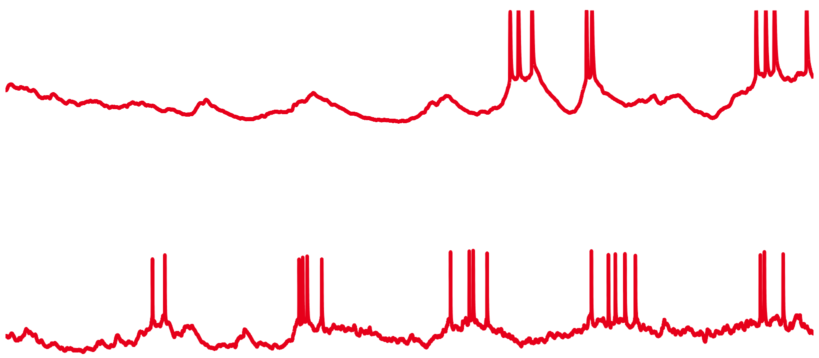
★ the model has been adapted to the appropriate model of the world

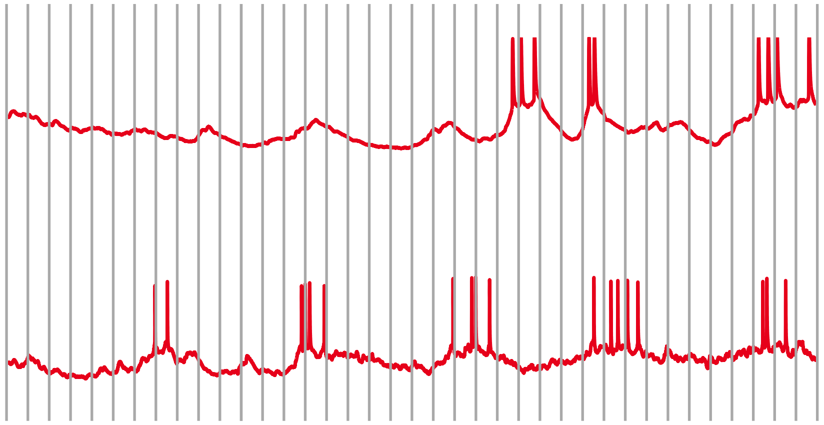
★ the stimulus statistics tested is appropriate

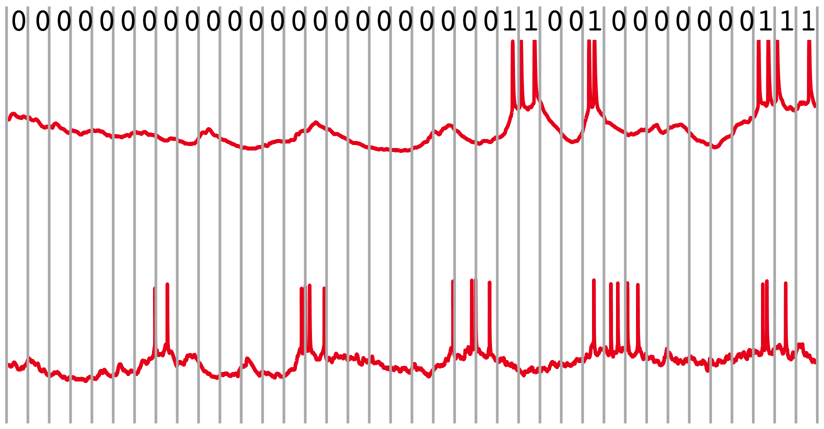
$$P(\mathbf{a}) = \int dx \, P(\mathbf{a} \,|\, \mathbf{x}) \, P(\mathbf{x})$$

spontaneous activity $\stackrel{?}{=}$ average evoked activity

$P(\mathbf{a})$ $P(\mathbf{a} \,|\, \mathbf{x})$



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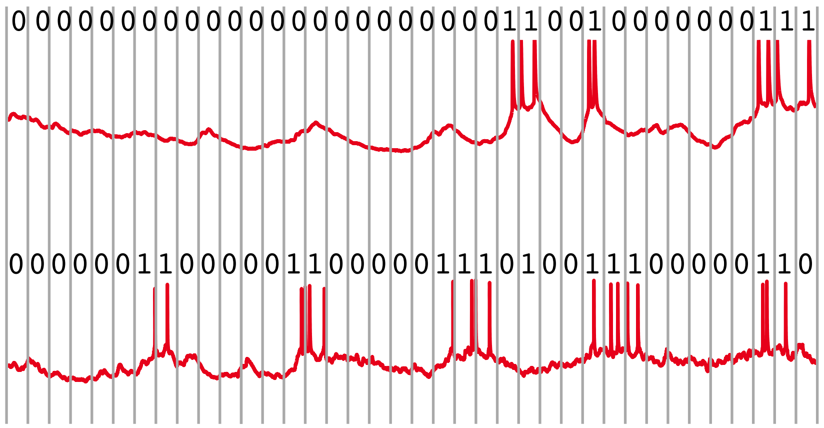
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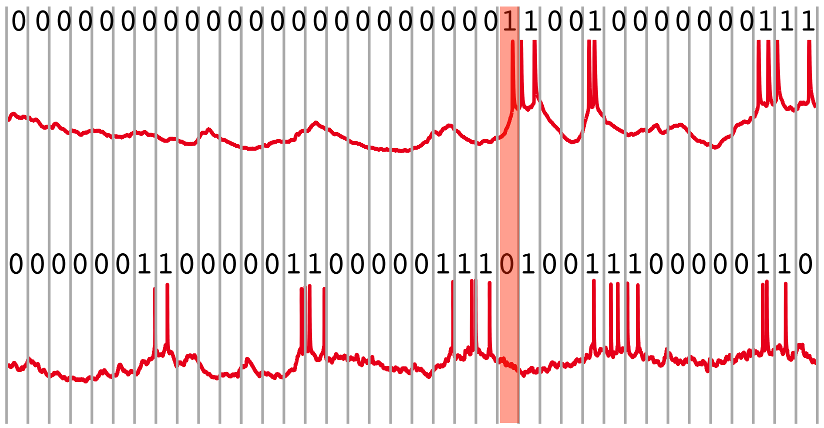
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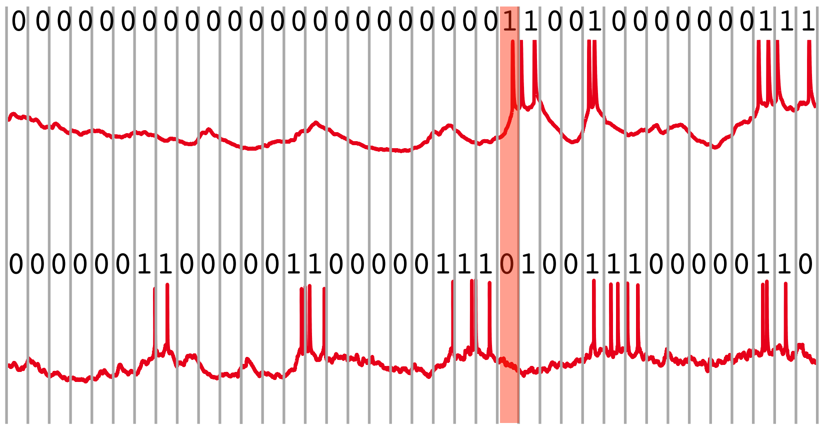
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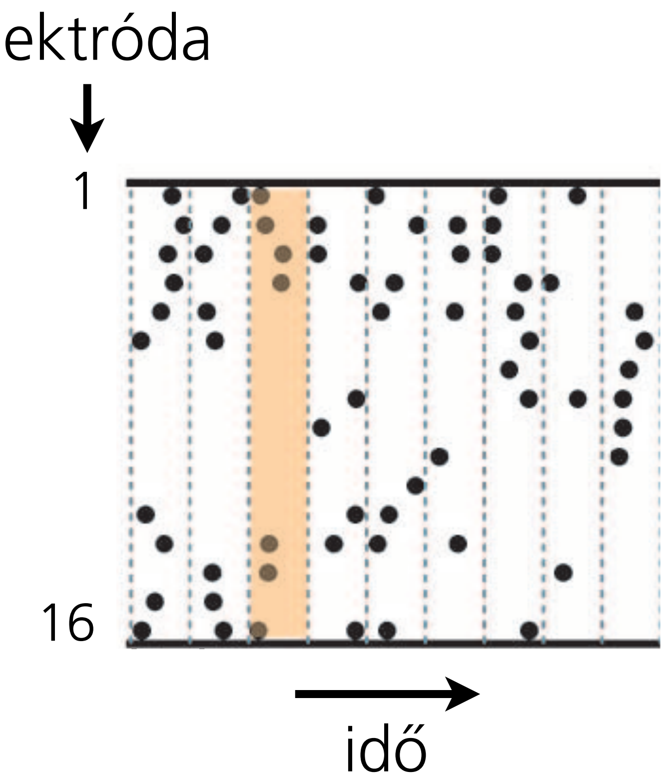
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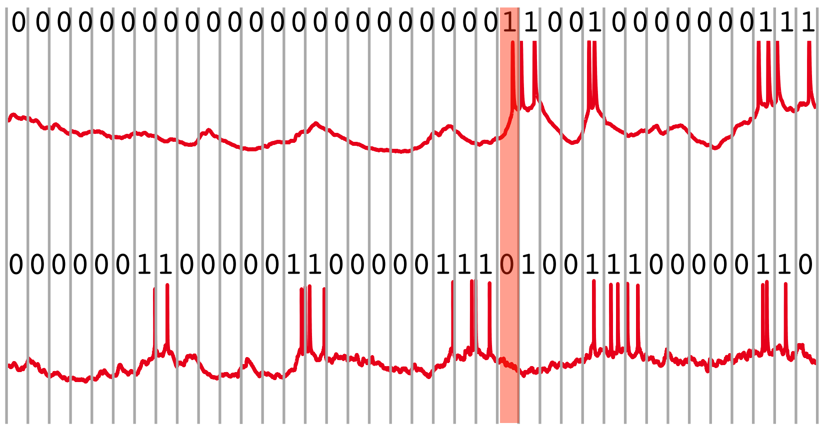
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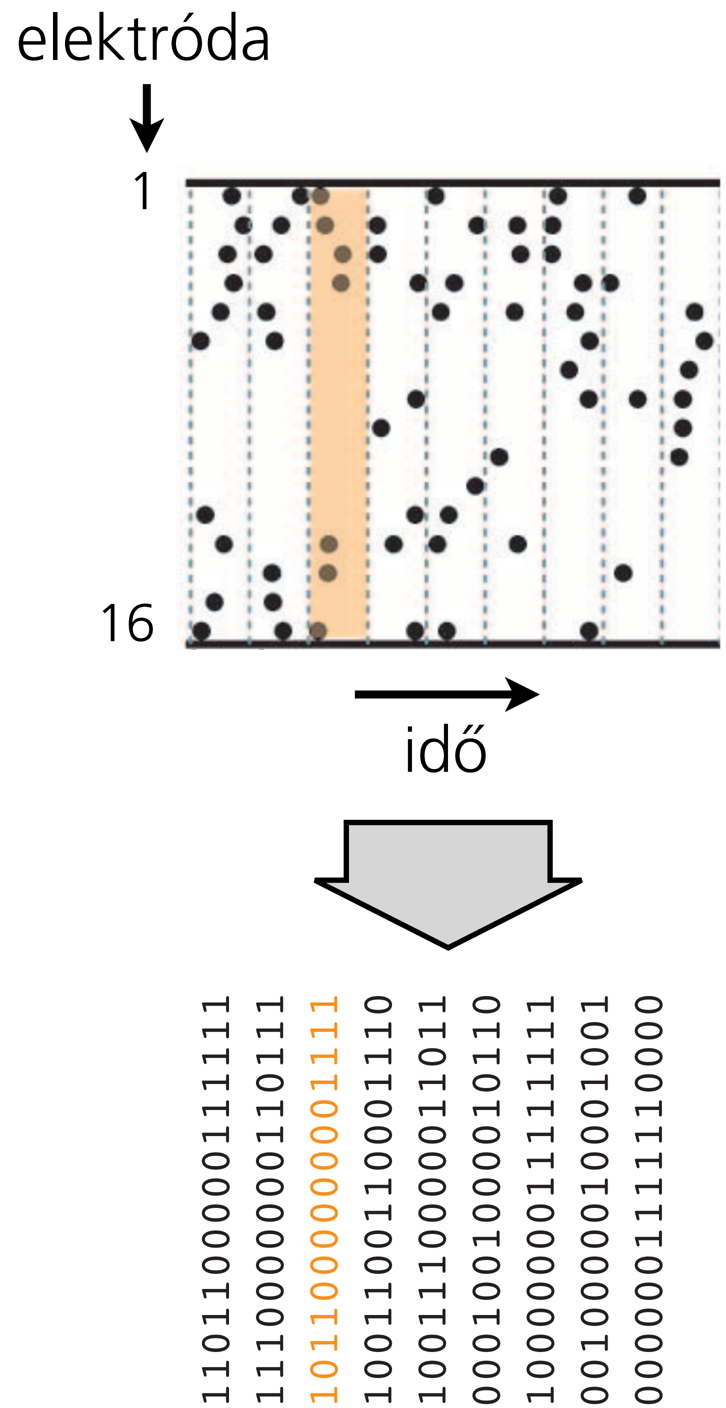
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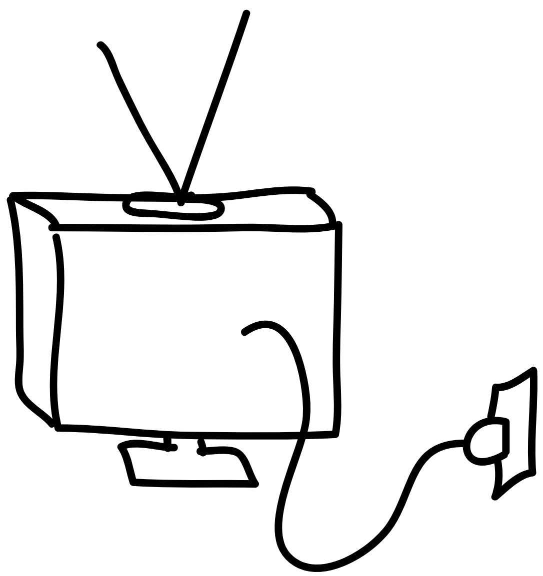

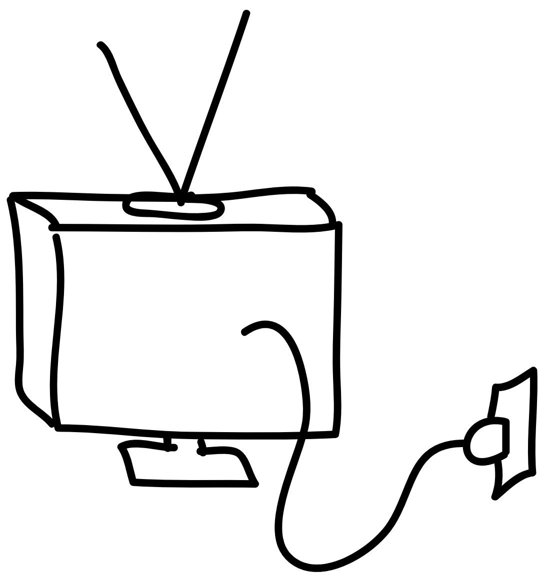

elektróda

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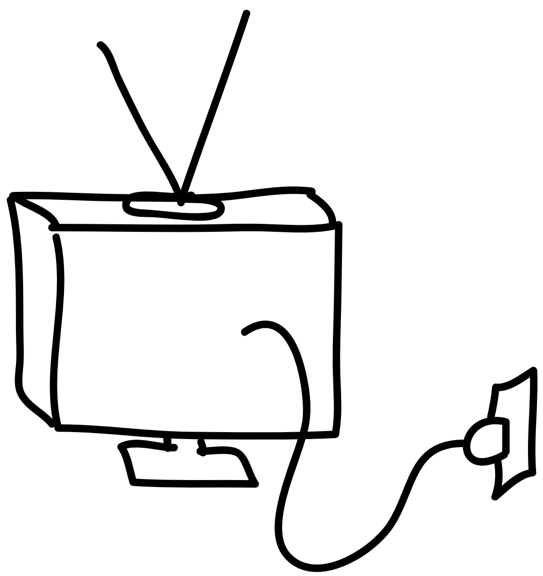

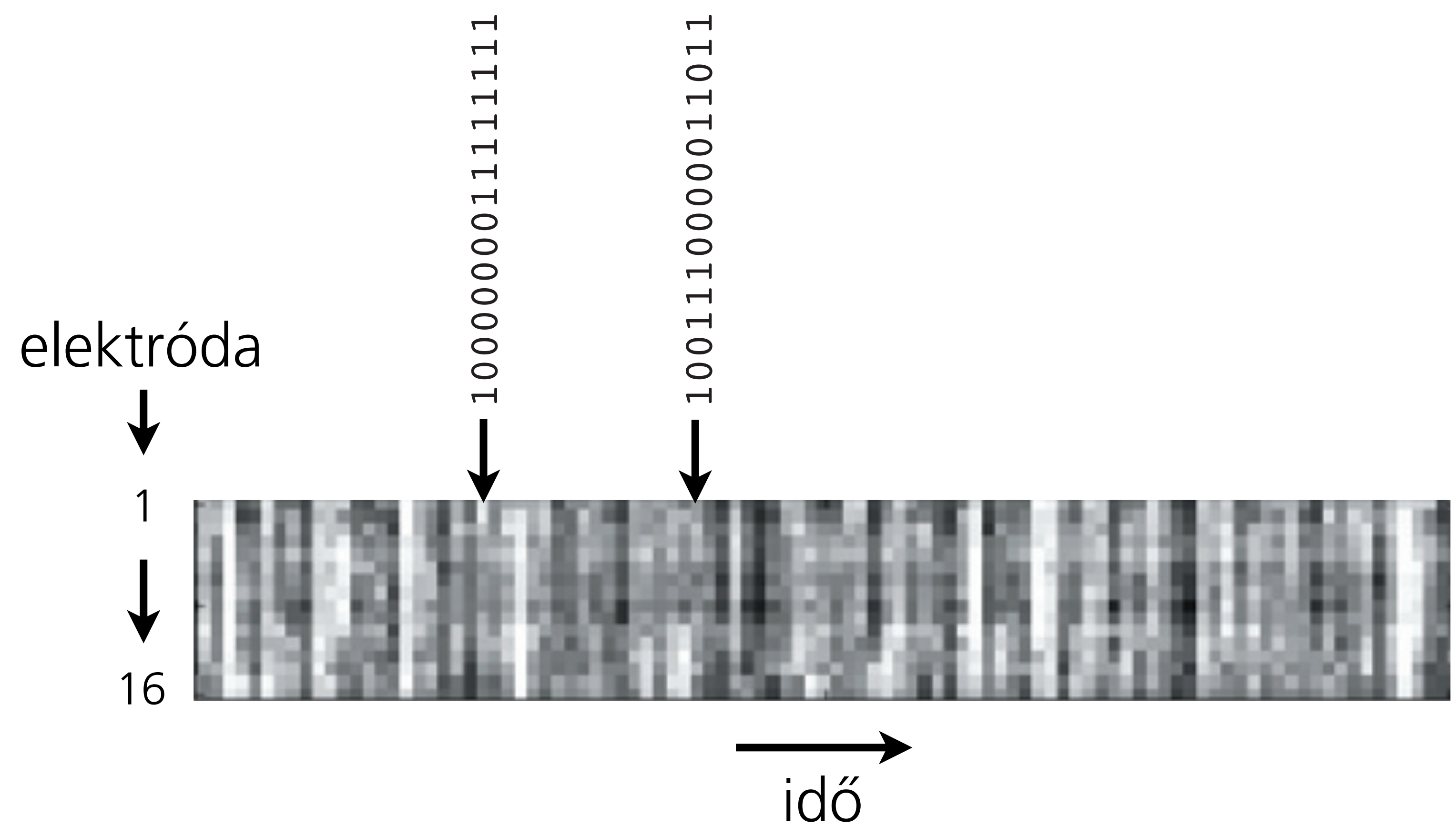
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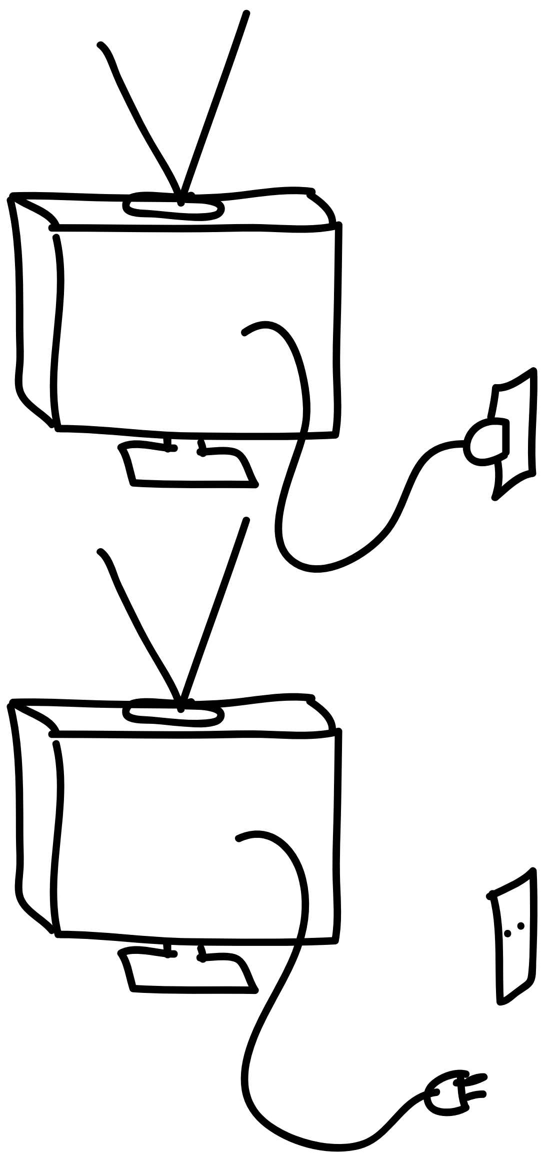

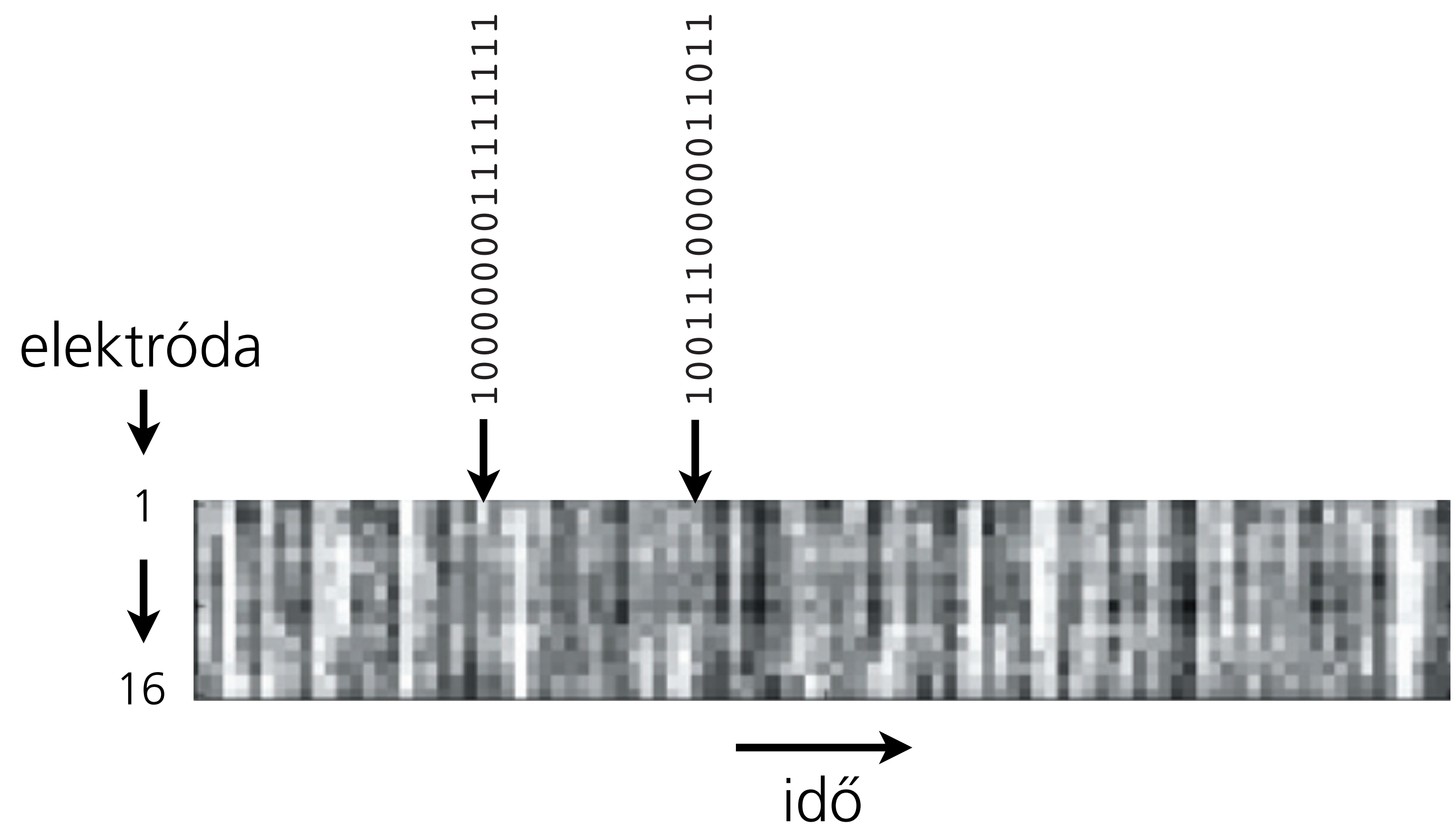
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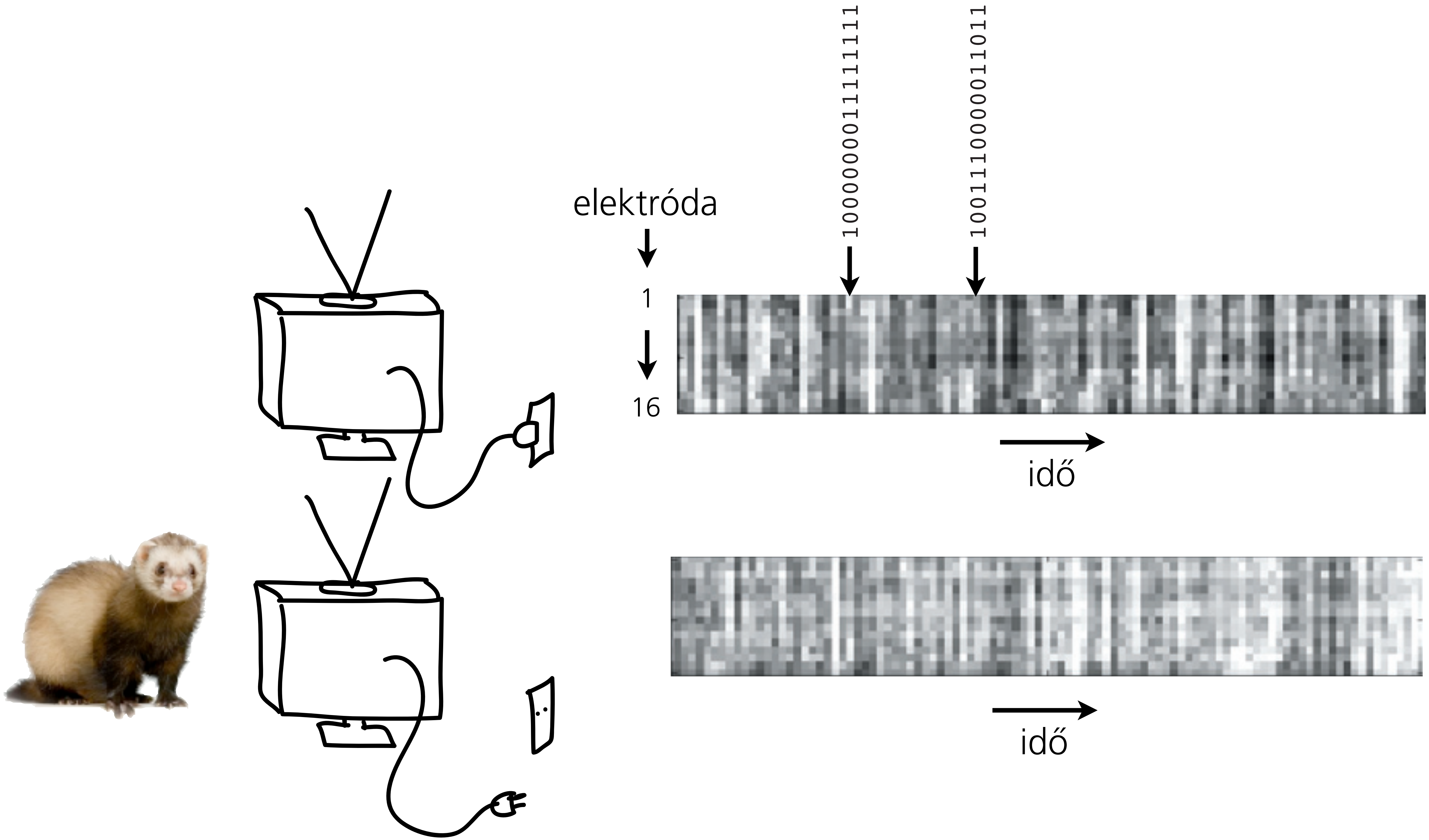

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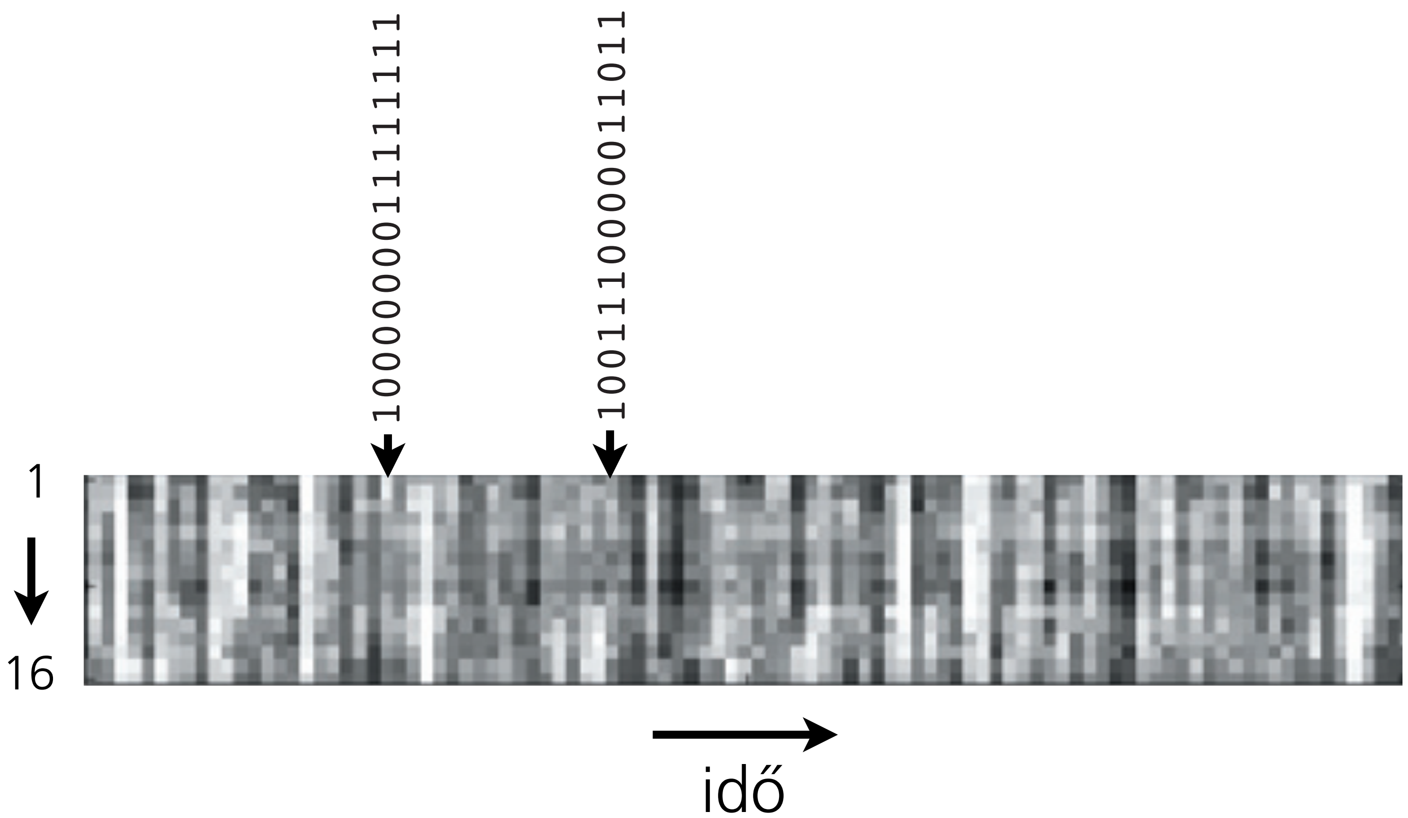
Hatékonyság?



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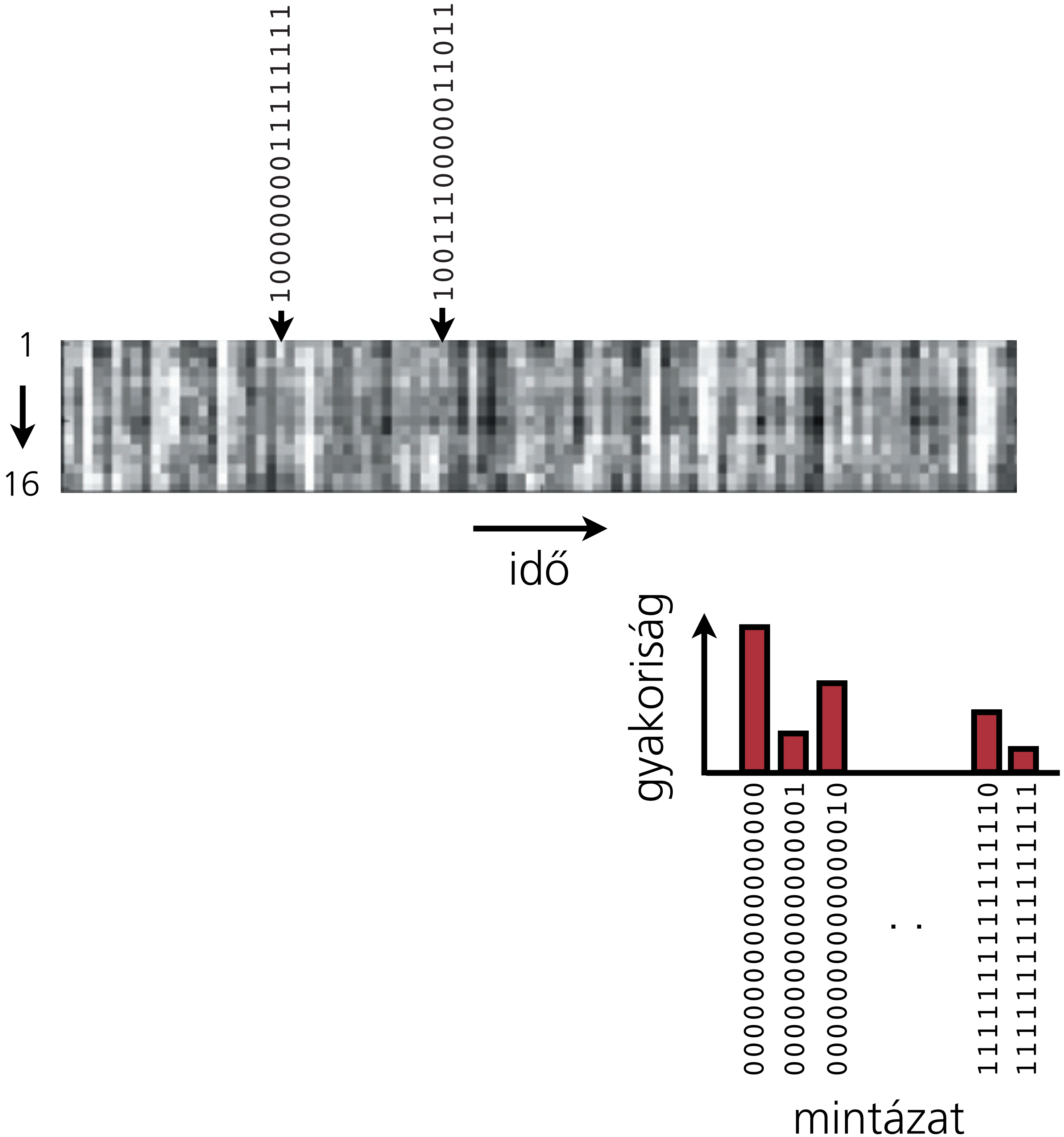

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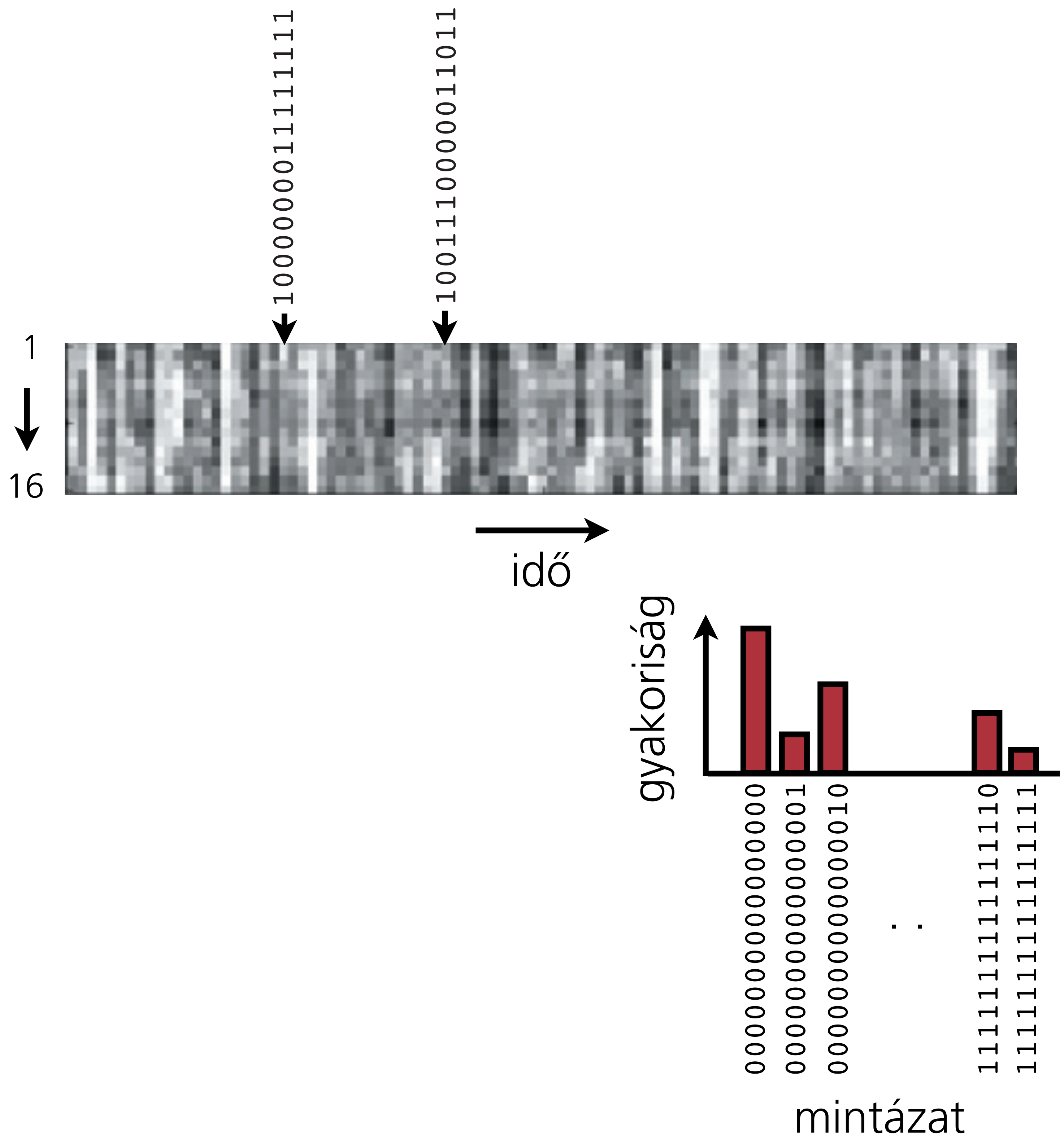

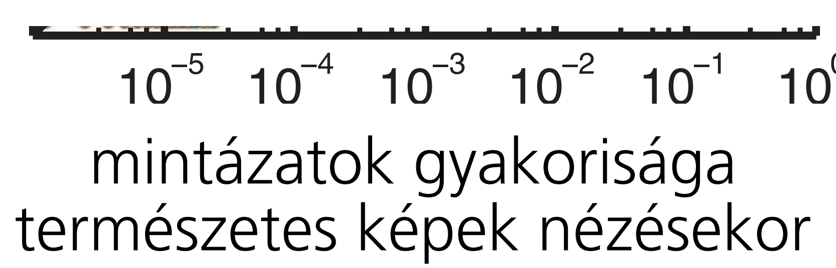

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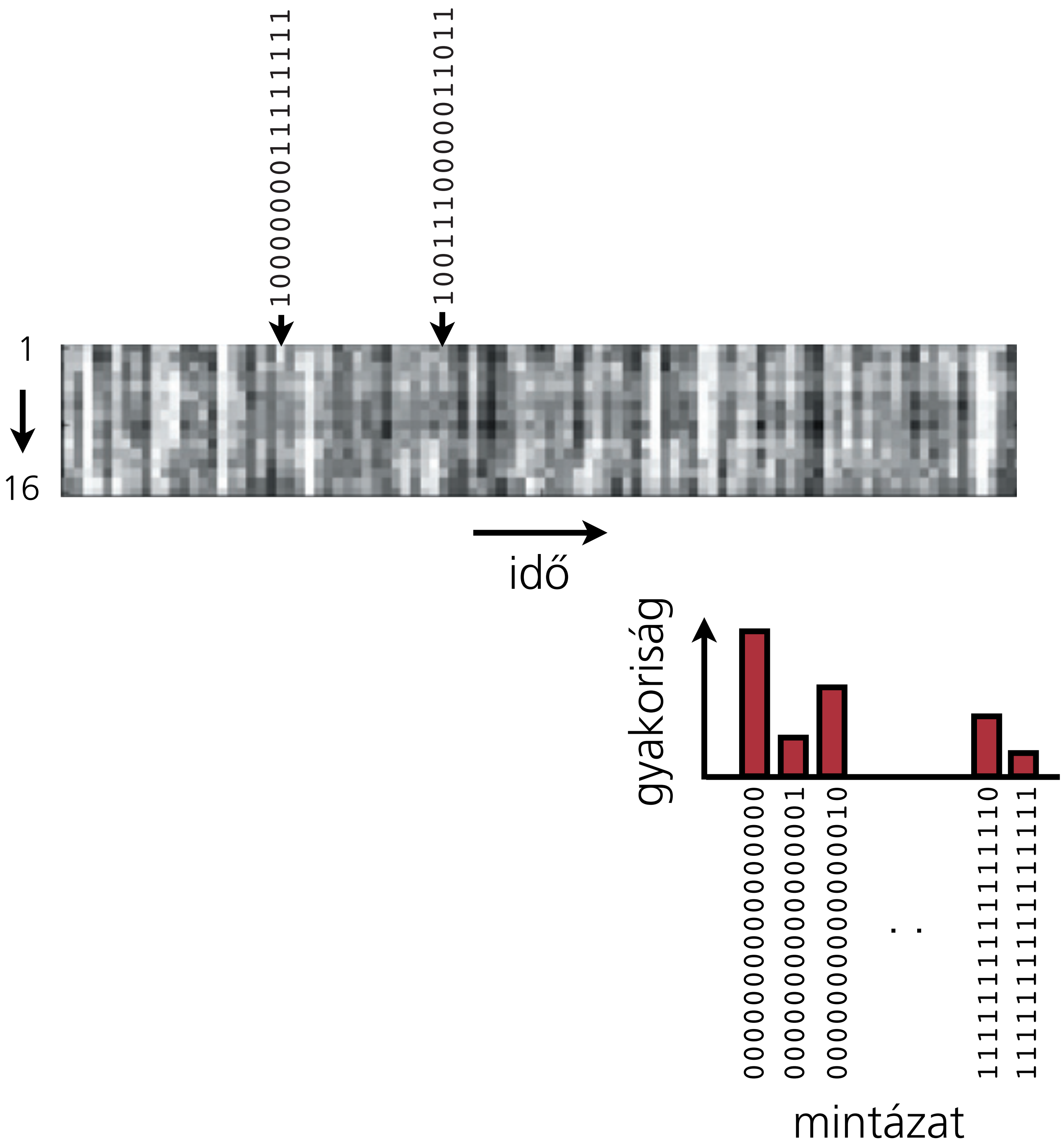

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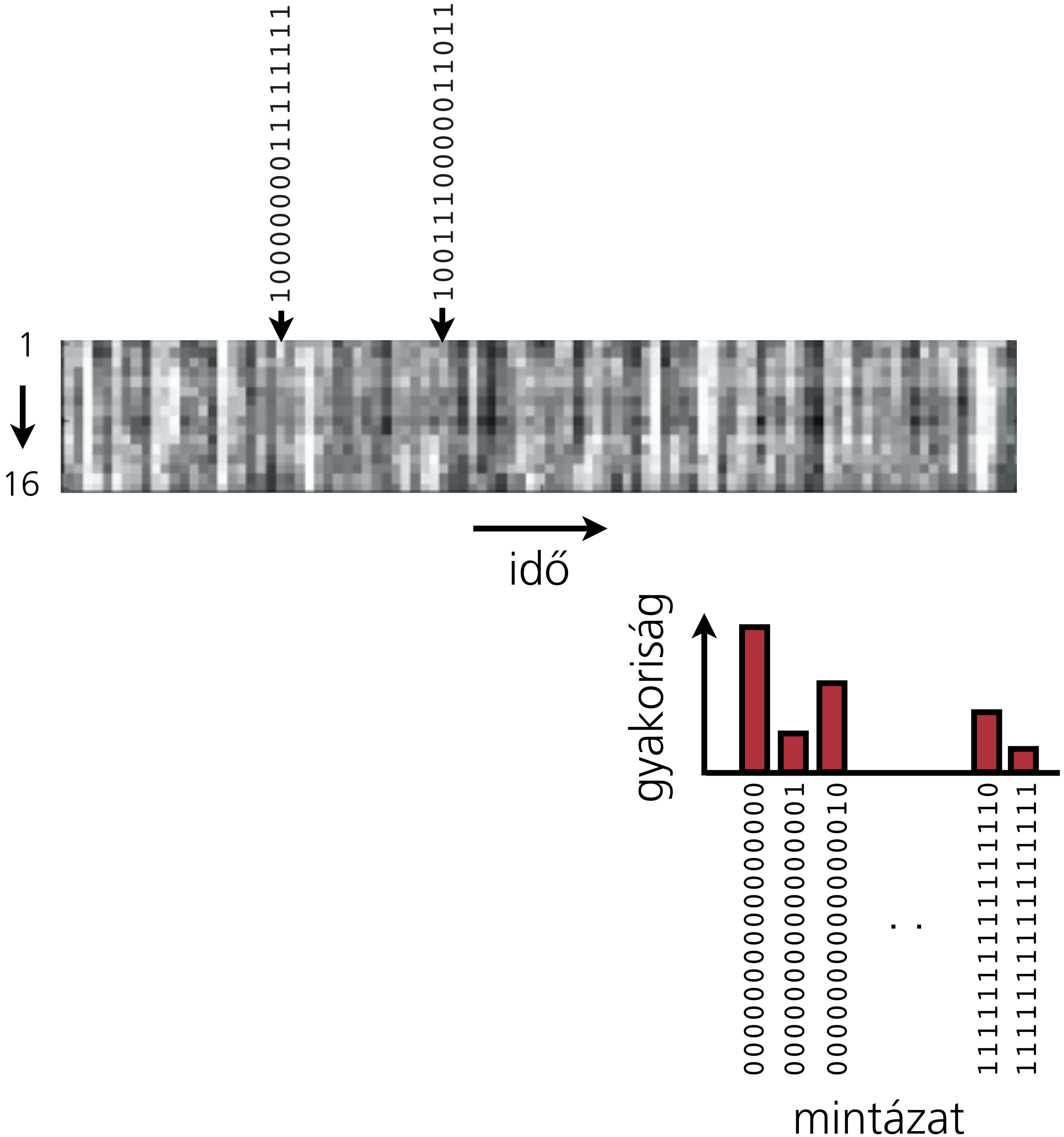

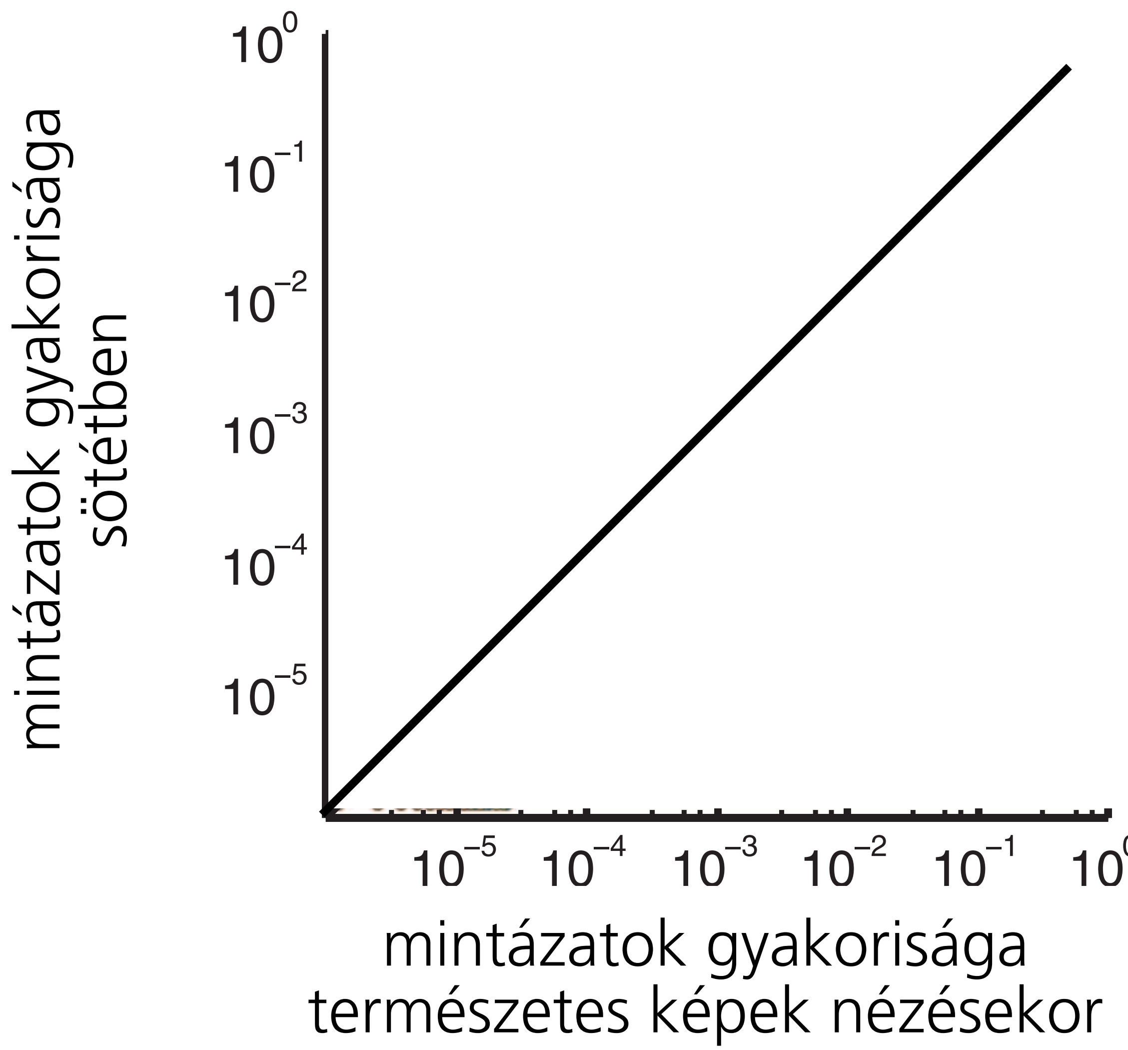

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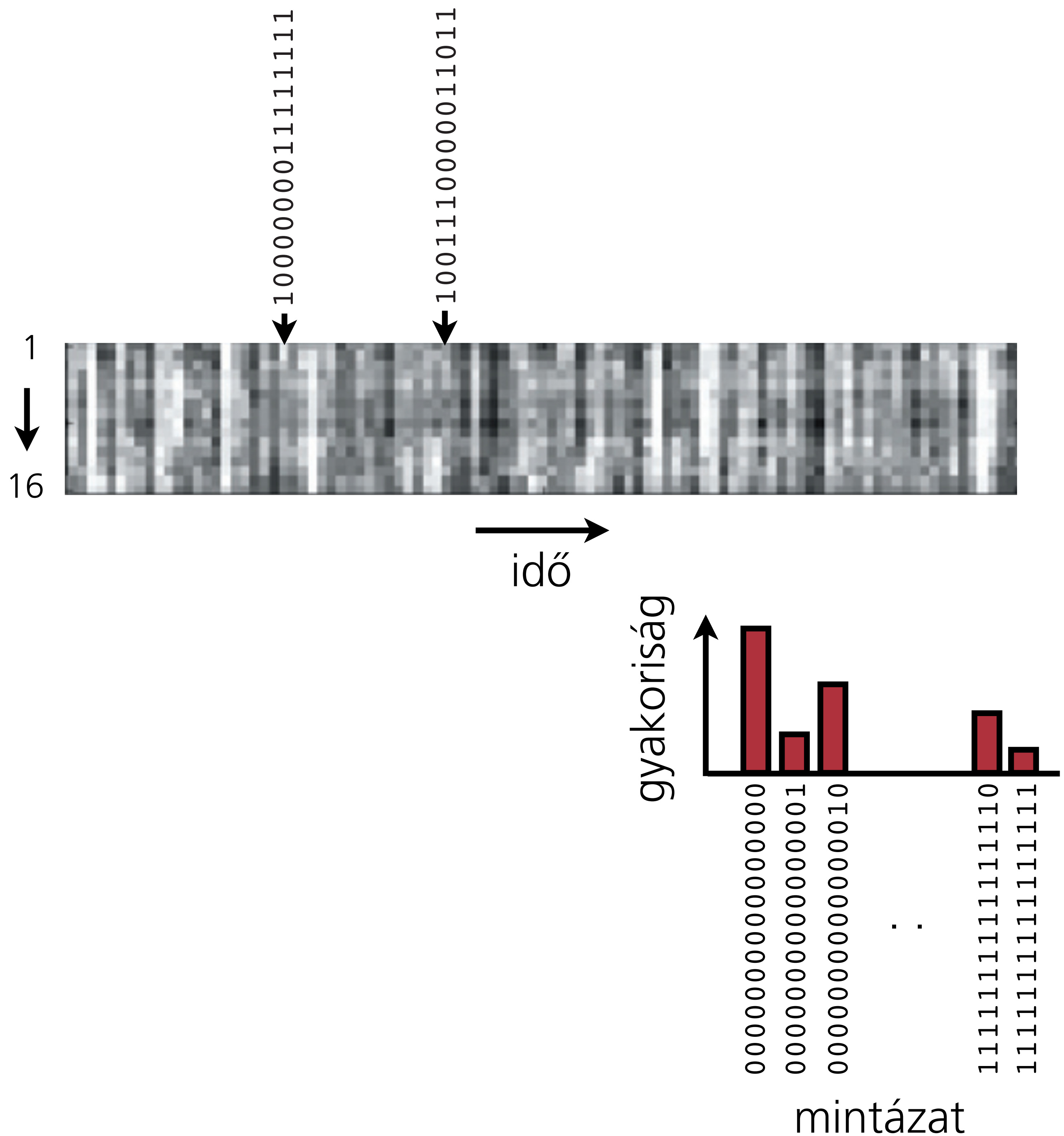
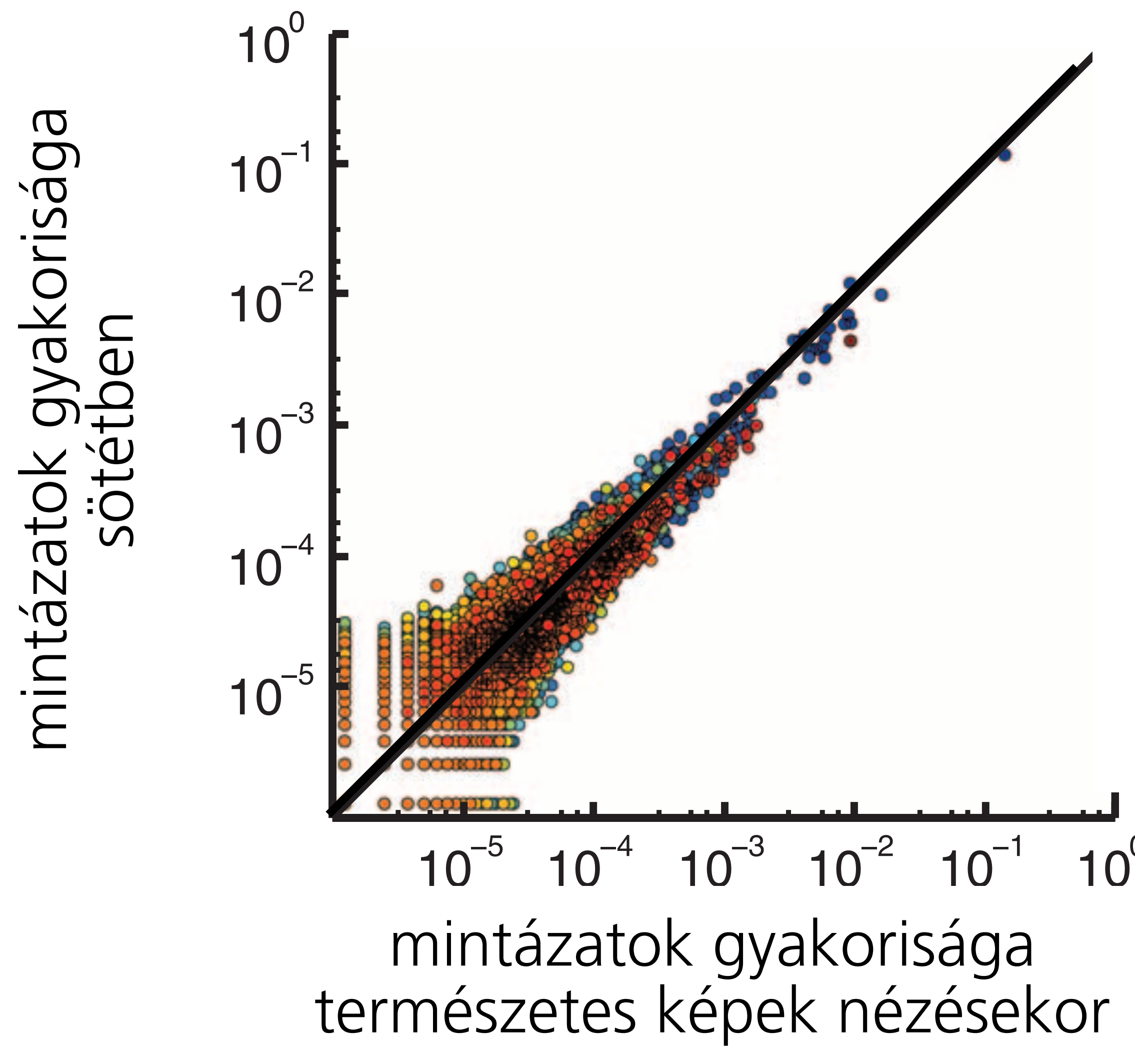
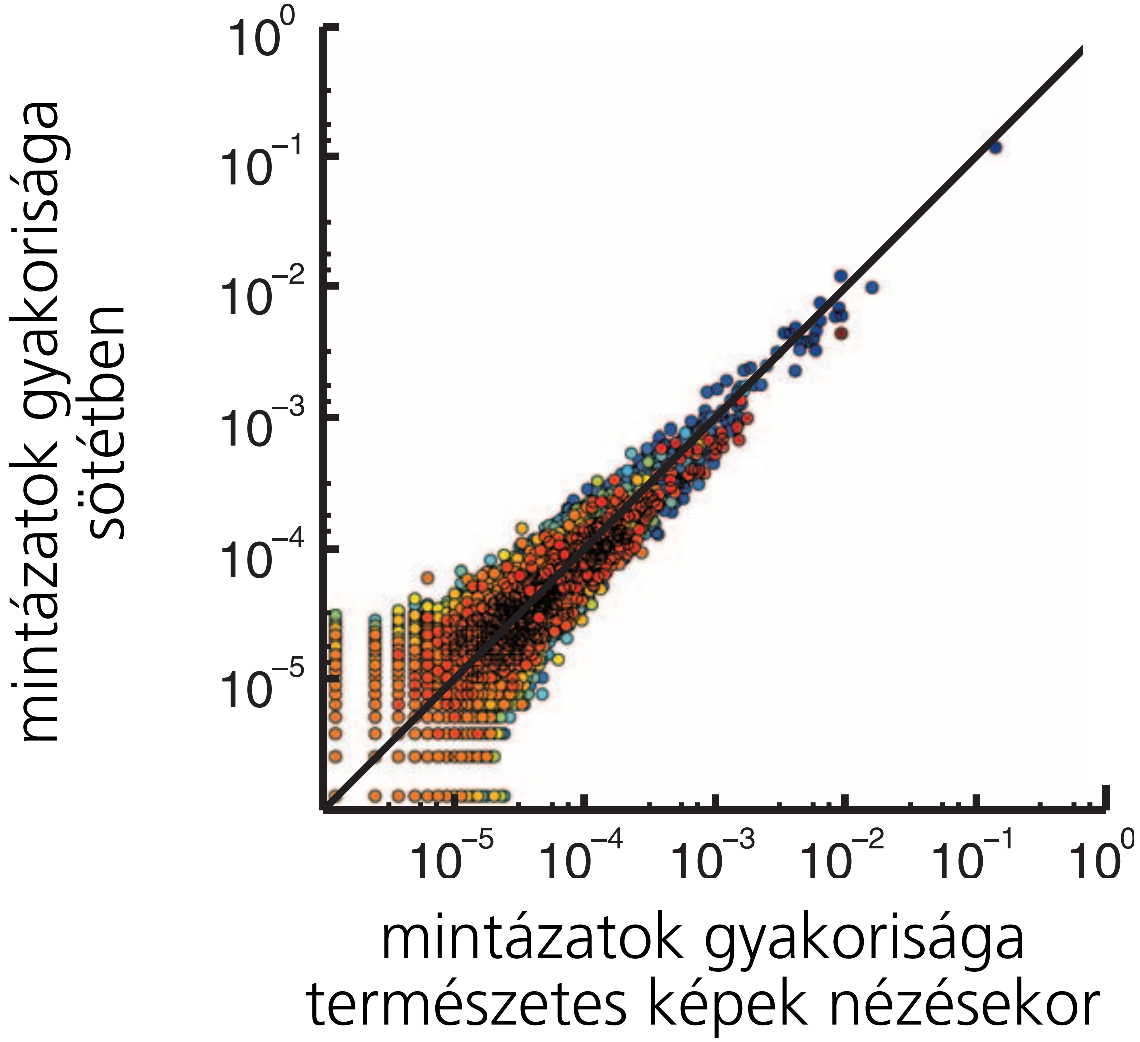
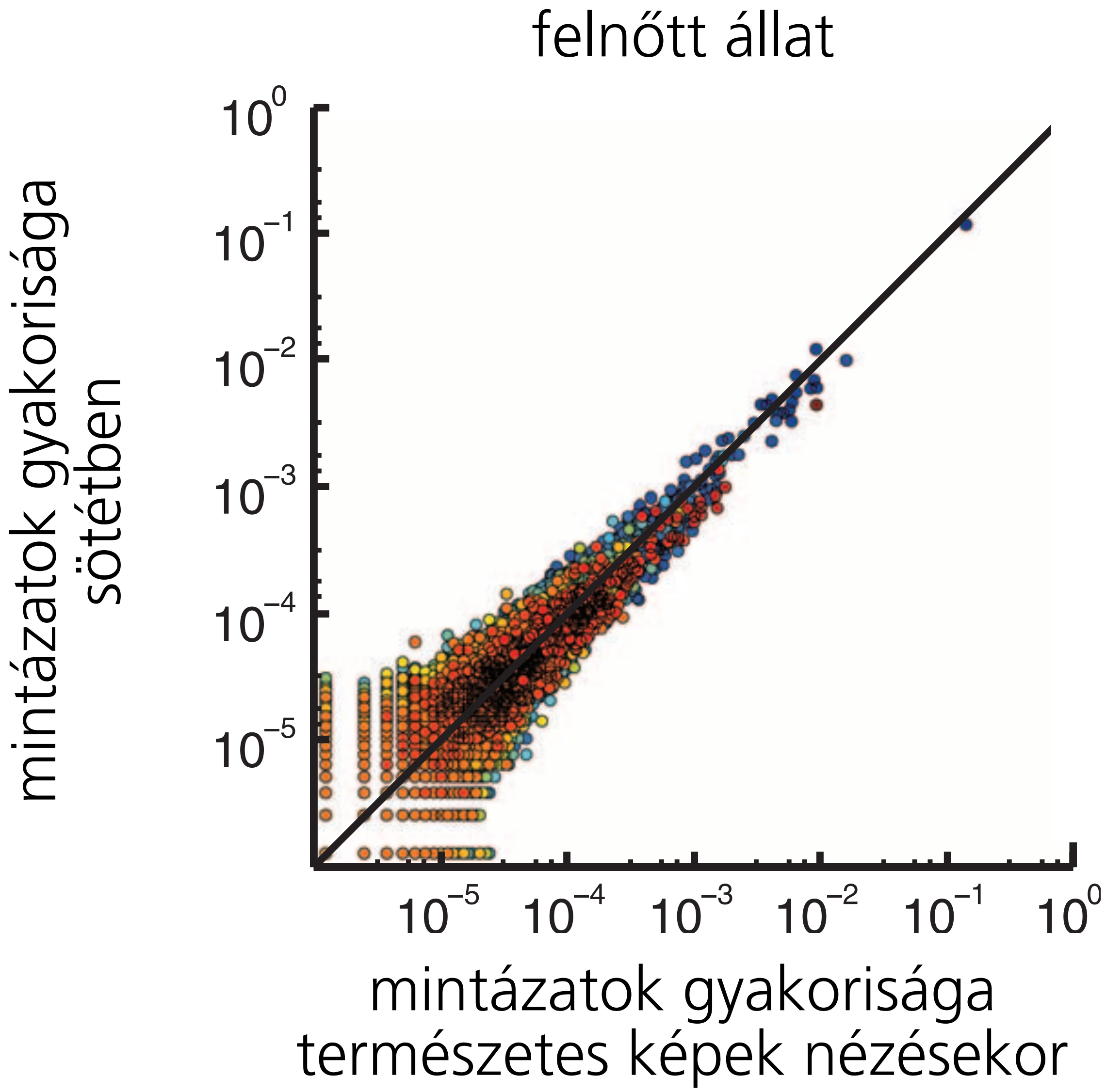




- Ha
- az idegrendszer ismeri a világ szerkezetét,
- akkor
- az elvárásai nem különböznek attól,
- amit általában érzékel



mintázatok gyakorisága
sötétben
10^0
10^{-1}
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-5} 10^{-4} 10^{-3} 10^{-2} 10^{-1} 10^0
mintázatok gyakorisága
természetes képek nézésekor



felnőtt állat
10^{0}
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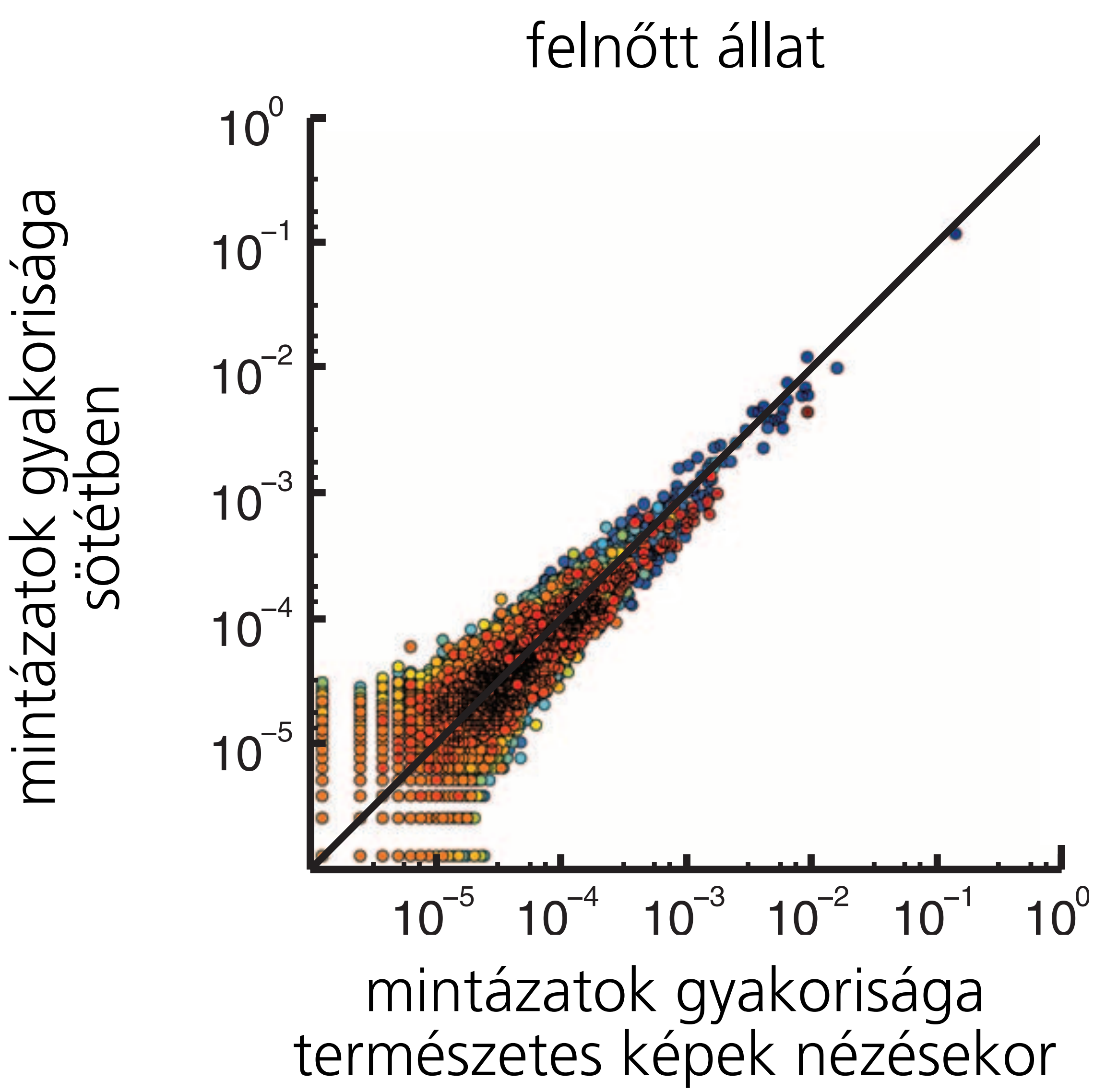
10^{-4}
10^{-5}
mintázatok gyakorisága sötétben
10^{-5} 10^{-4} 10^{-3} 10^{-2} 10^{-1} 10^{0}
mintázatok gyakorisága természetes képek nézésekor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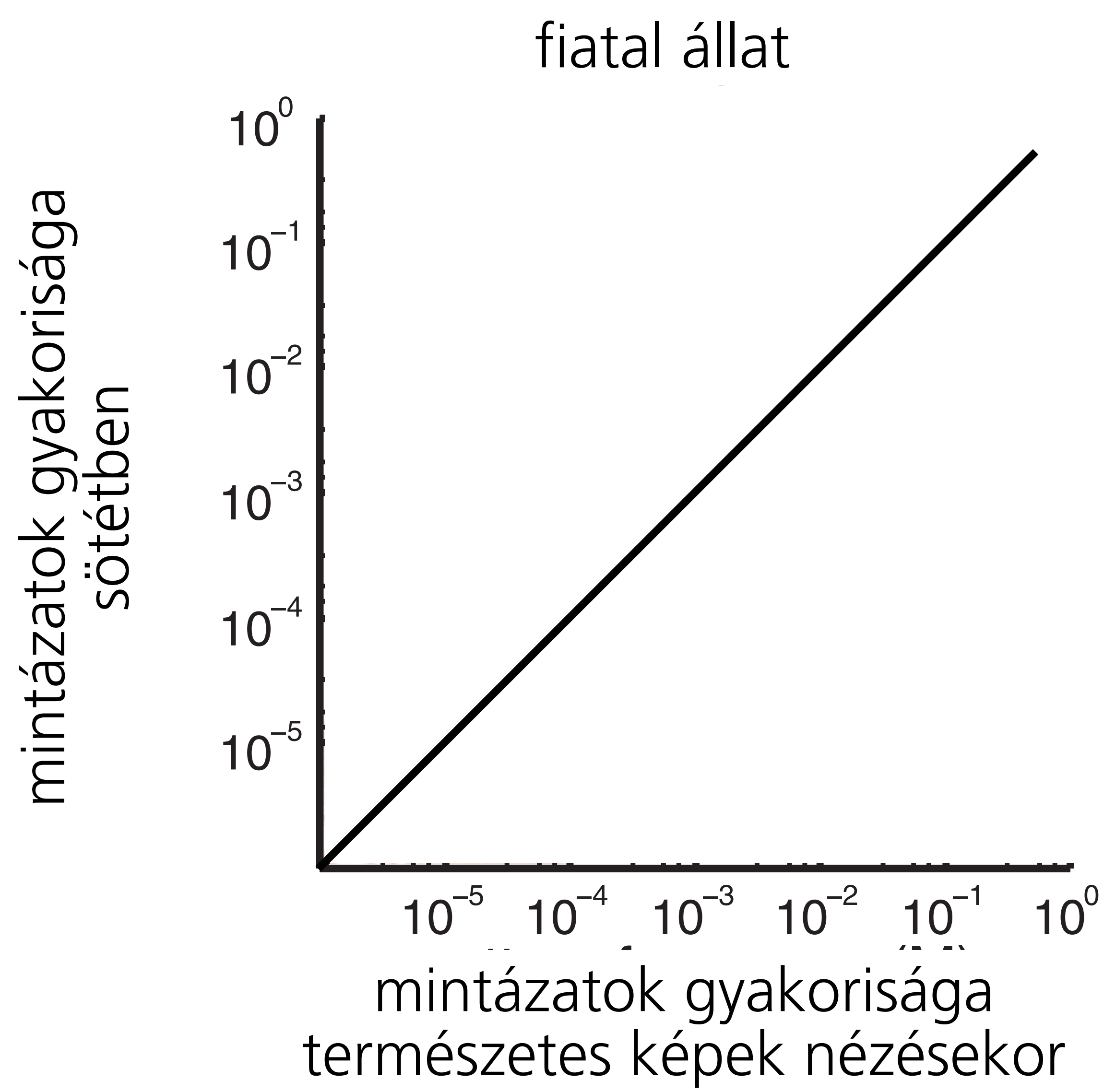
fiatal állat
mintázatok gyakorisága sötétben
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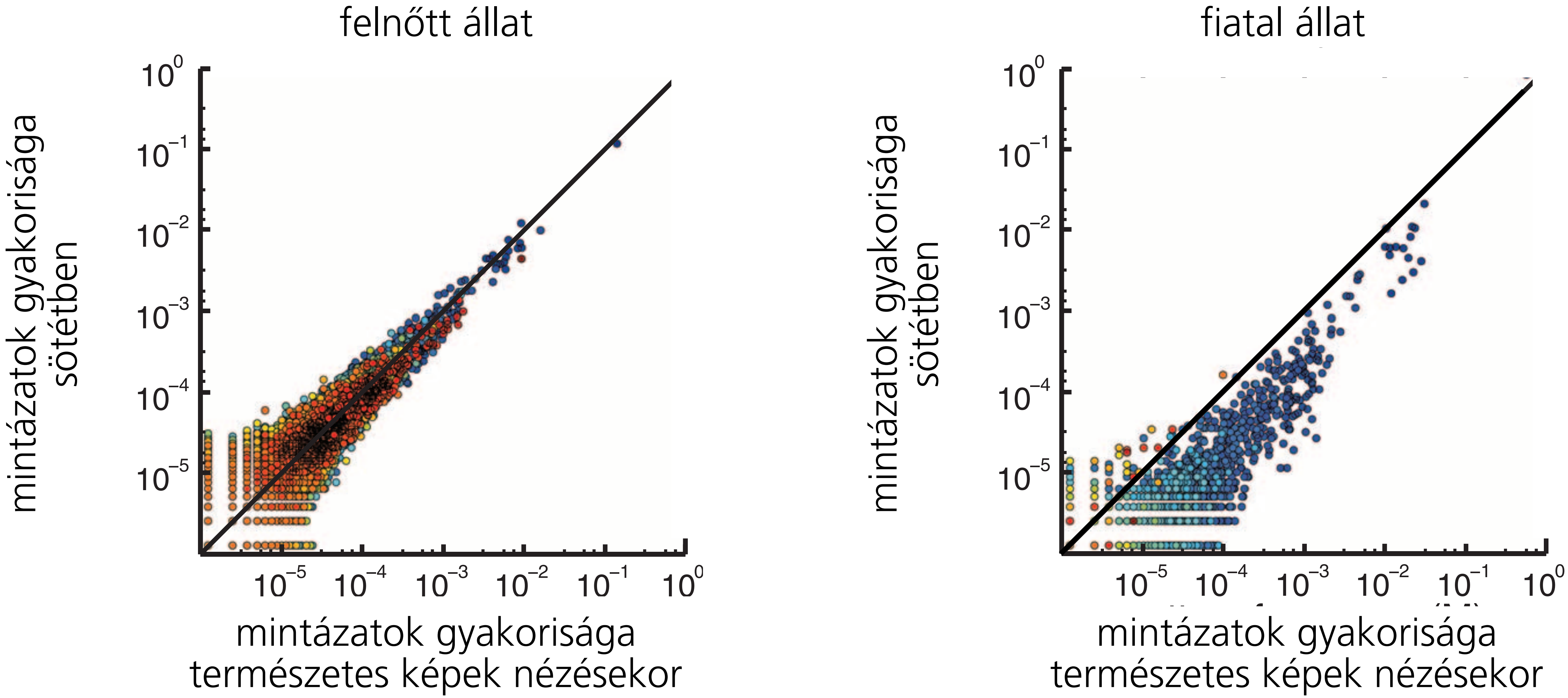
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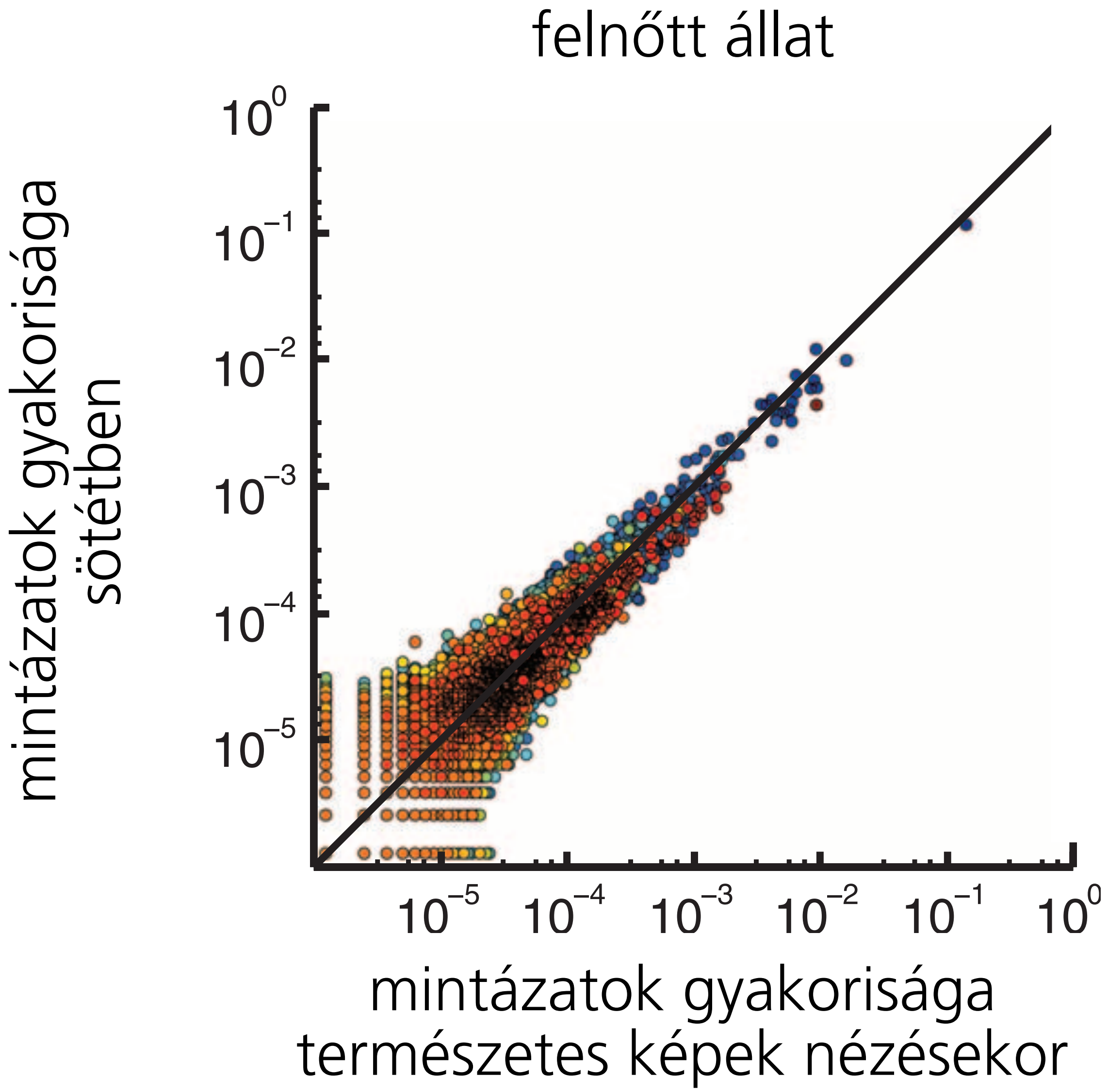
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mintázatok gyakorisága
sötétben
10^{-5} 10^{-4} 10^{-3} 10^{-2} 10^{-1} 10^0
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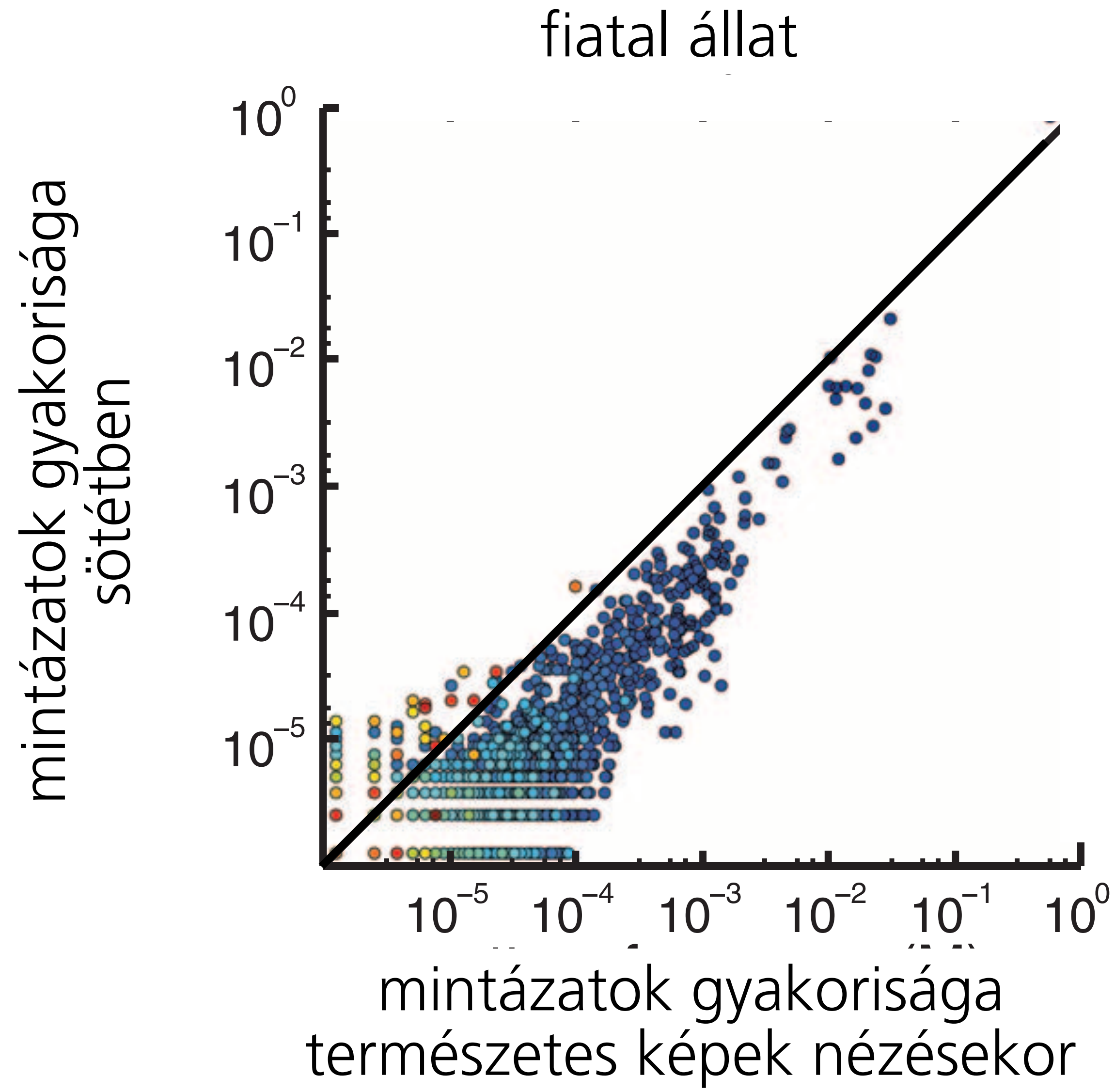
természetes képek nézésekor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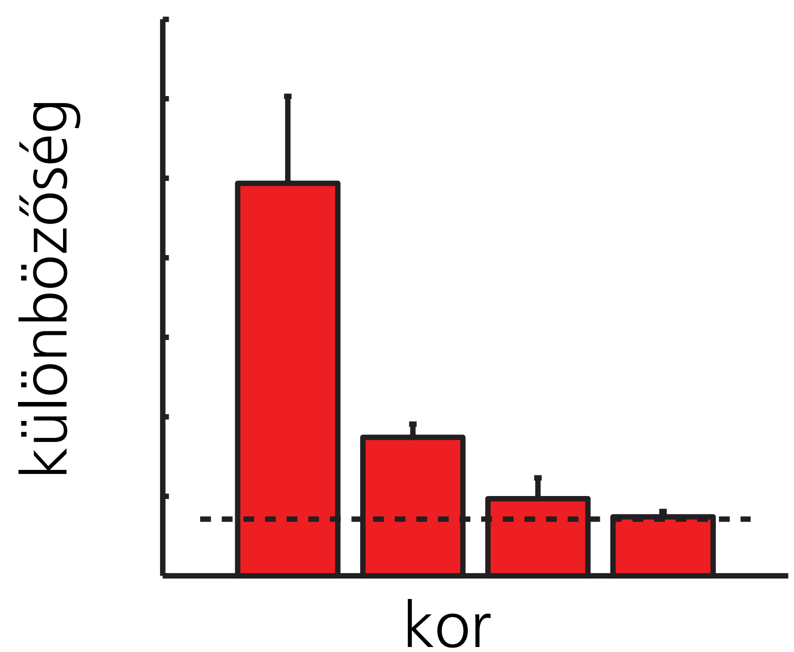
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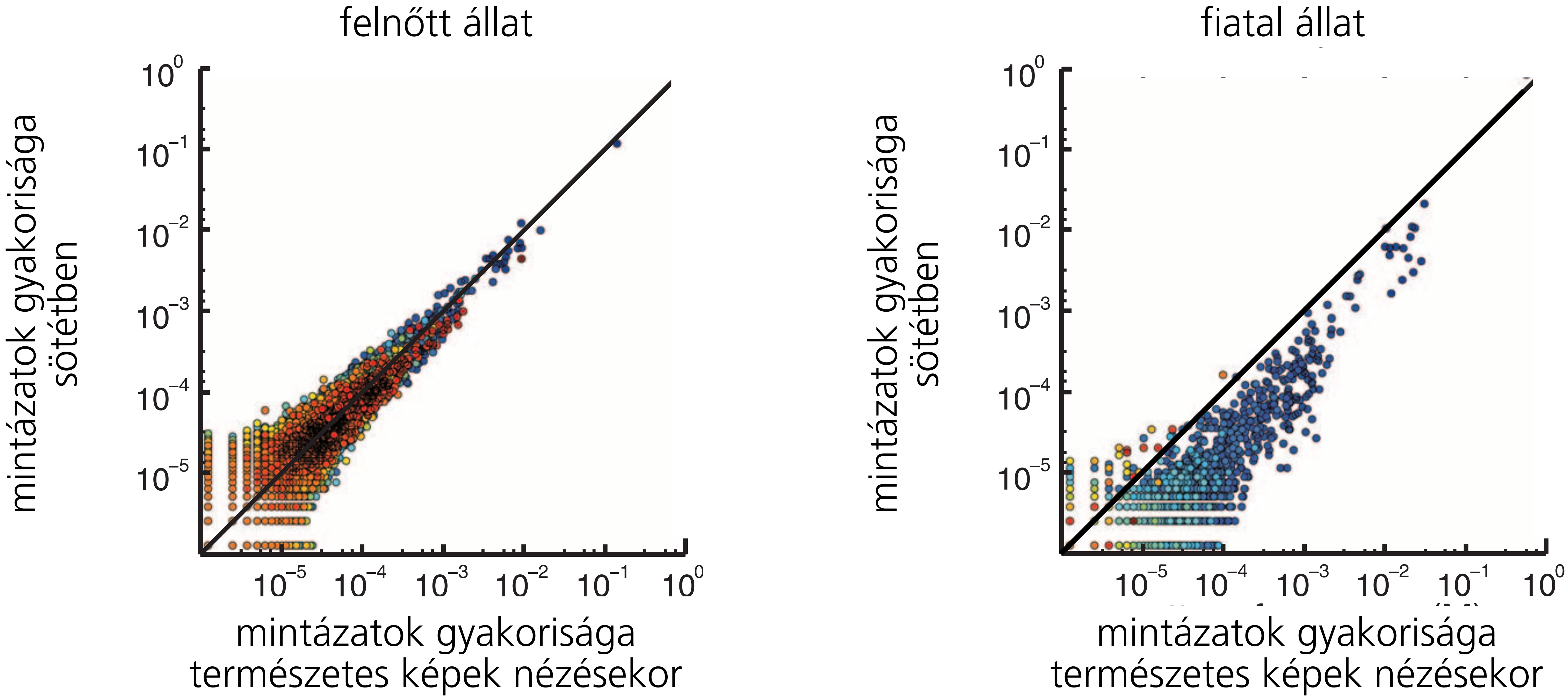
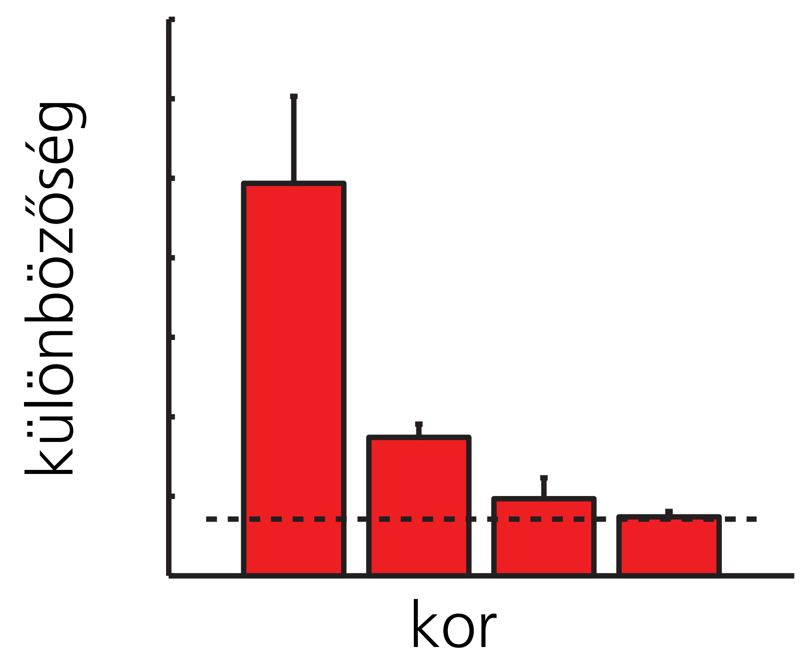
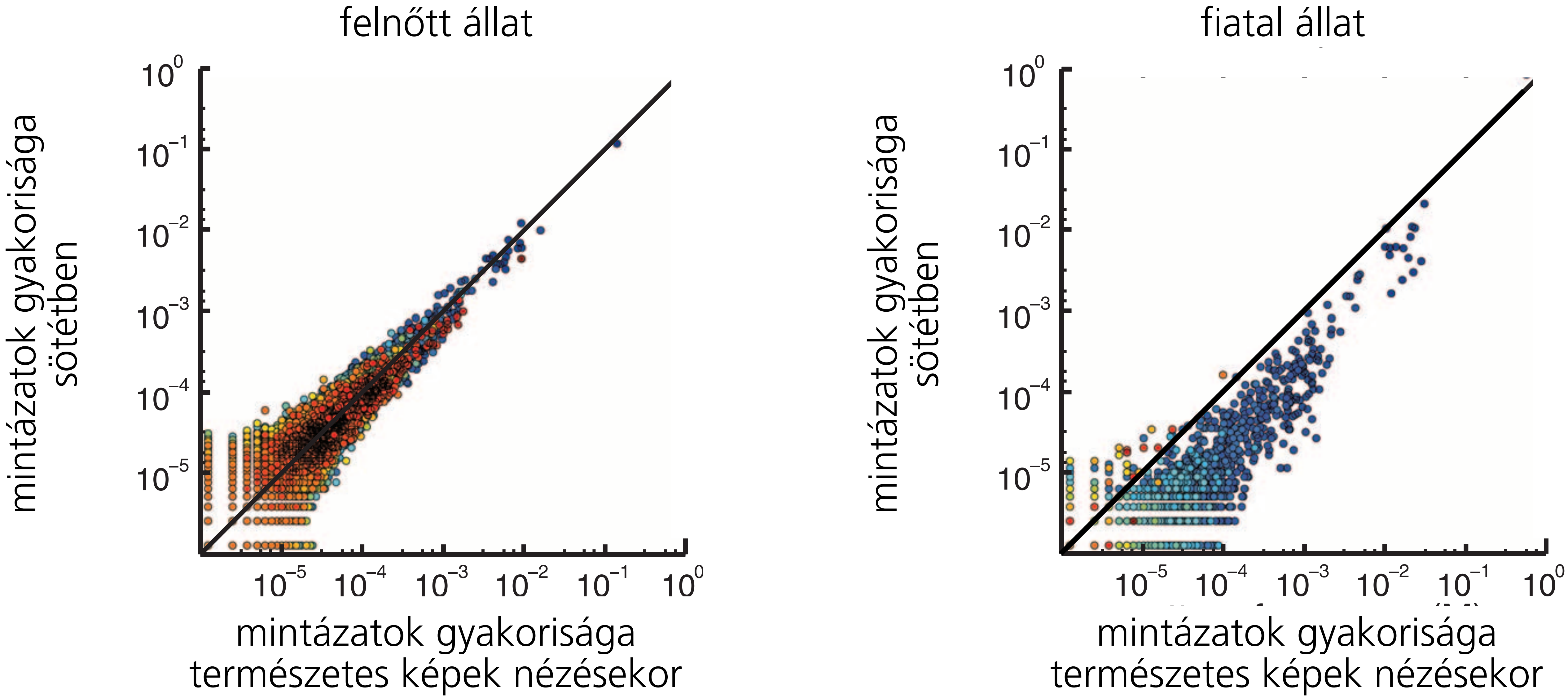




természetes képek
zaj
periodikusan sávozott képek


felnőtt állat
fiatal állat
mintázatok gyakorisága sötétben
mintázatok gyakorisága természetes képek nézésekor
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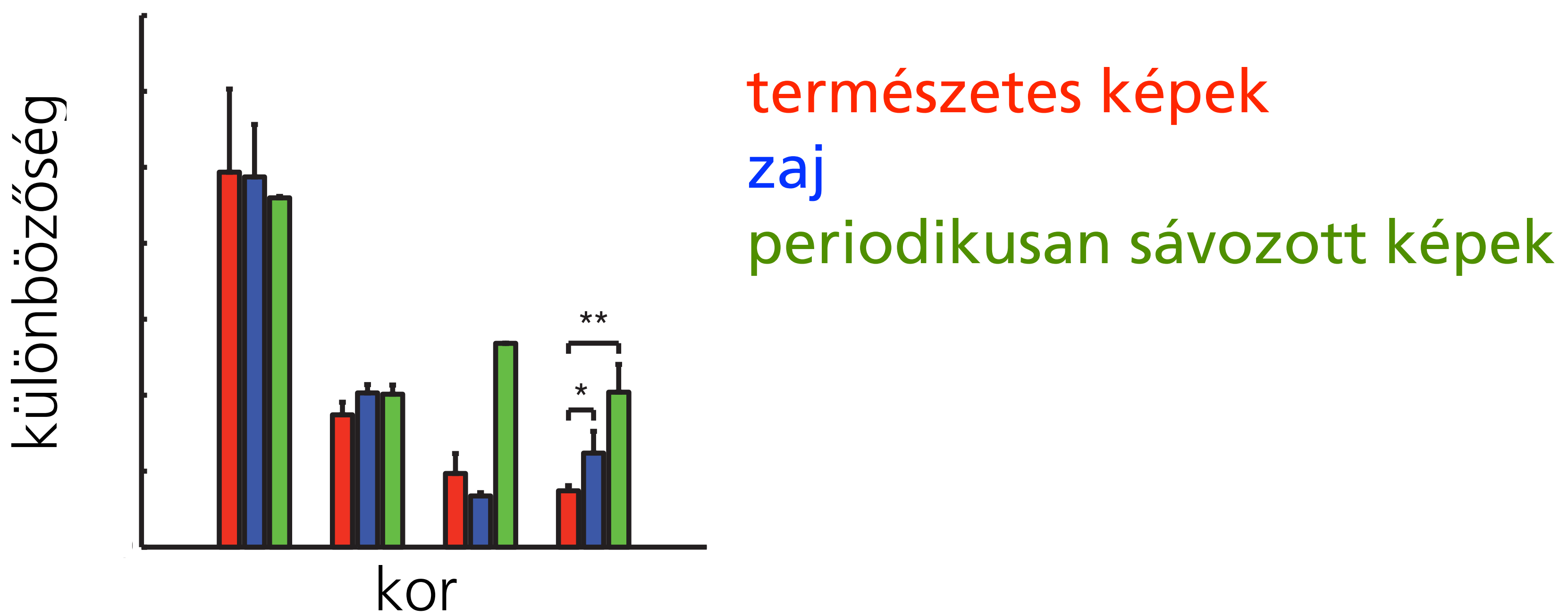
10^{-1}
10^{-2}
10^{-3}
10^{-4}
10^{-5}


különbözőség
kor
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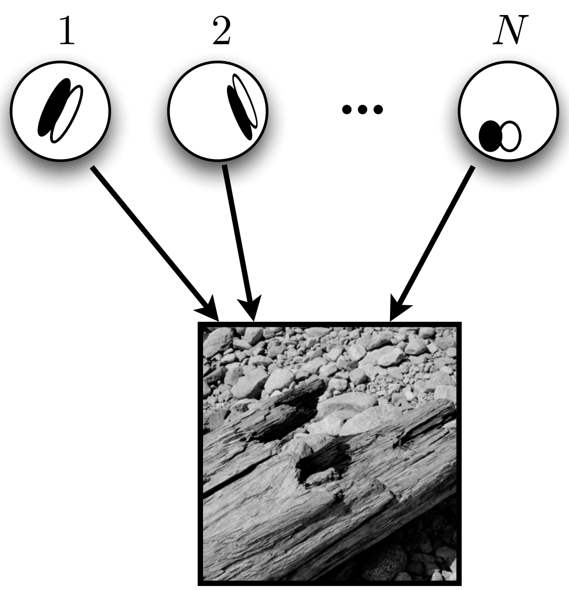
**
természetes képek
zaj
periodikusan sávozott képek

Bayesian inference

image

Bayesian inference

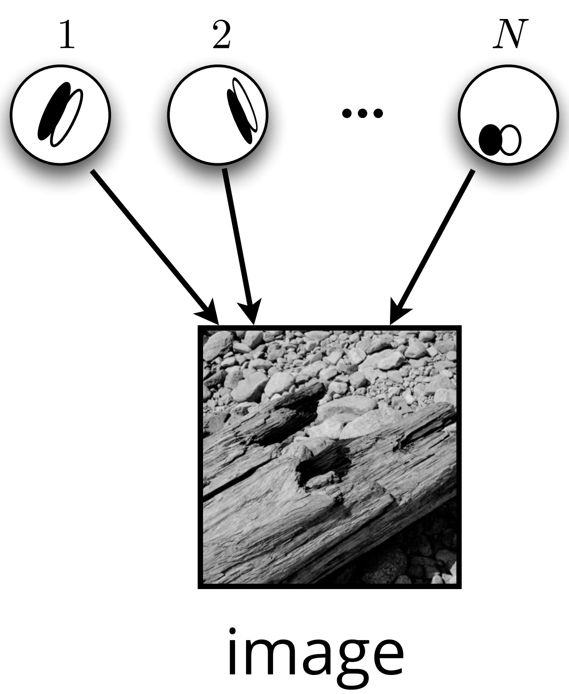
linear features



image

Bayesian inference

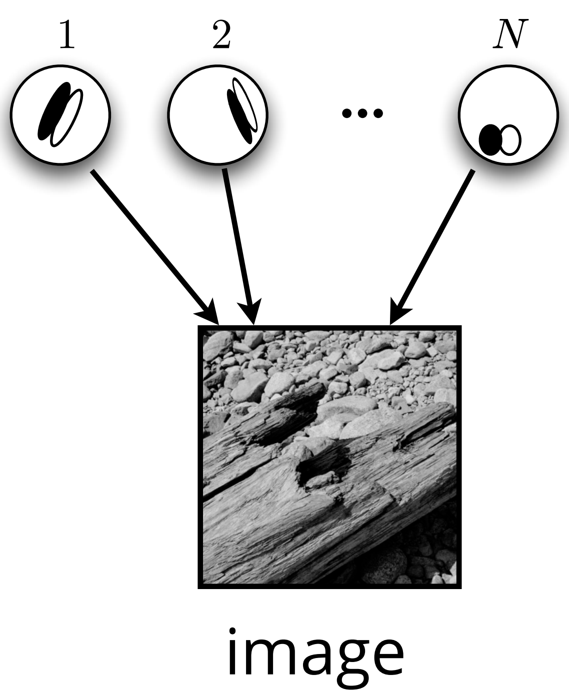
linear features



$$\color{red}{\text{image}} = \color{red}{a_1}\,\text{feature}_1 + \color{red}{a_2}\,\text{feature}_2 + \ldots + \color{red}{a_N}\,\text{feature}_N + \color{magenta}{\text{noise}}$$

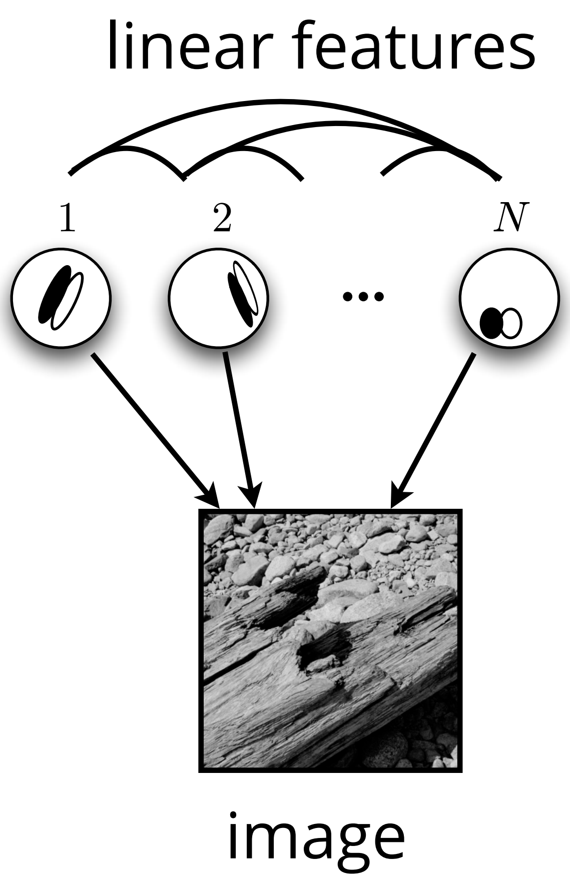
Bayesian inference

linear features



neural activities
[a_1, a_2, …, a_N]

$$\text{image} = \quad a_1\,\text{feature}_1 + a_2\,\text{feature}_2 + \ldots + a_N\,\text{feature}_N \quad + \text{noise}$$

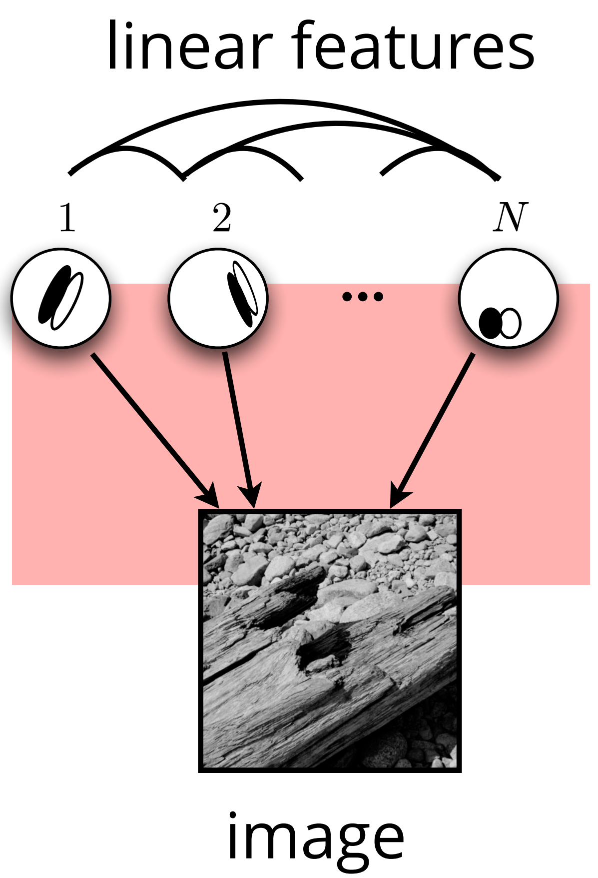


neural activities

$[\ a_1,\ a_2,\ \ldots,\ a_N\ ]$

$$\text{image} = \quad a_1\,\text{feature}_1 + a_2\,\text{feature}_2 + \ldots + a_N\,\text{feature}_N \quad + \text{noise}$$

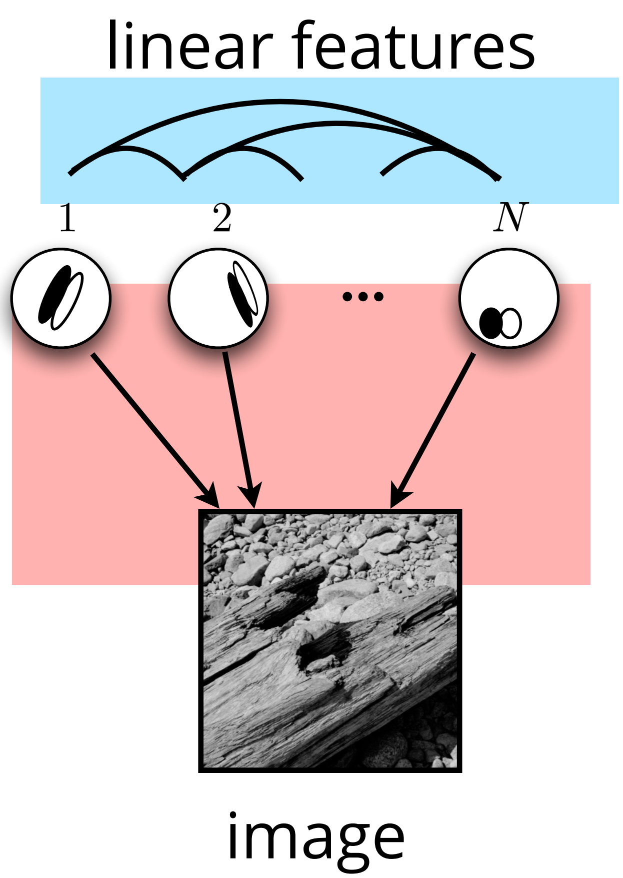
Bayesian inference



neural activities
[a_1, a_2, ..., a_N]
evidence

$$\text{image} = a_1\,\text{feature}_1 + a_2\,\text{feature}_2 + \ldots + a_N\,\text{feature}_N + \text{noise}$$

Bayesian inference



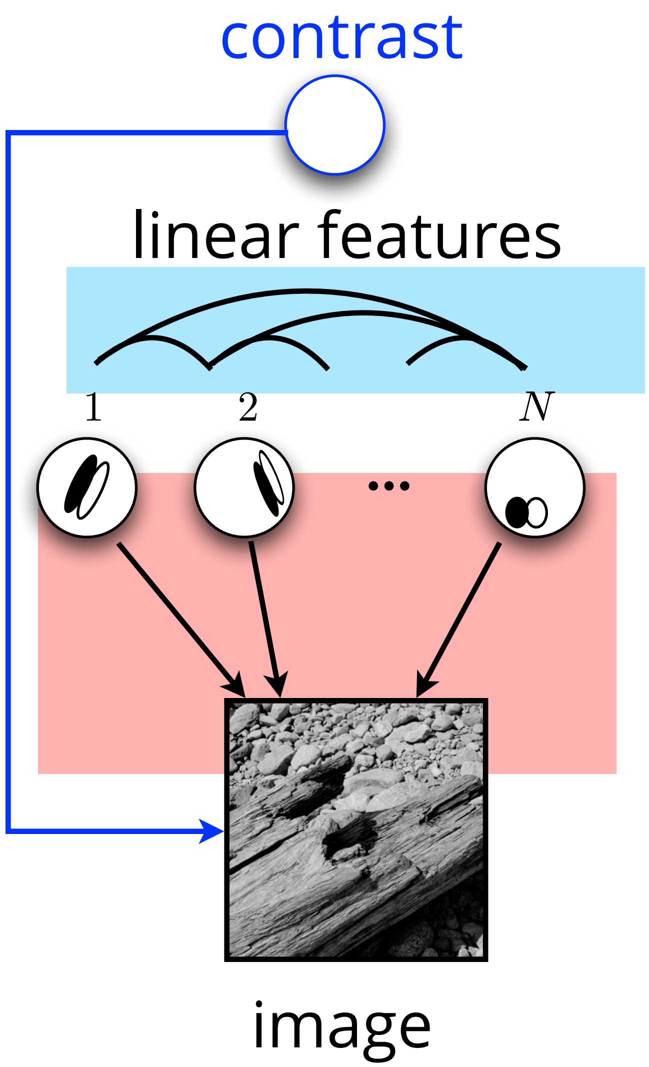
expectation

neural activities

[a_1, a_2, …, a_N]

evidence

$$\text{image} = a_1\,\text{feature}_1 + a_2\,\text{feature}_2 + \ldots + a_N\,\text{feature}_N + \text{noise}$$



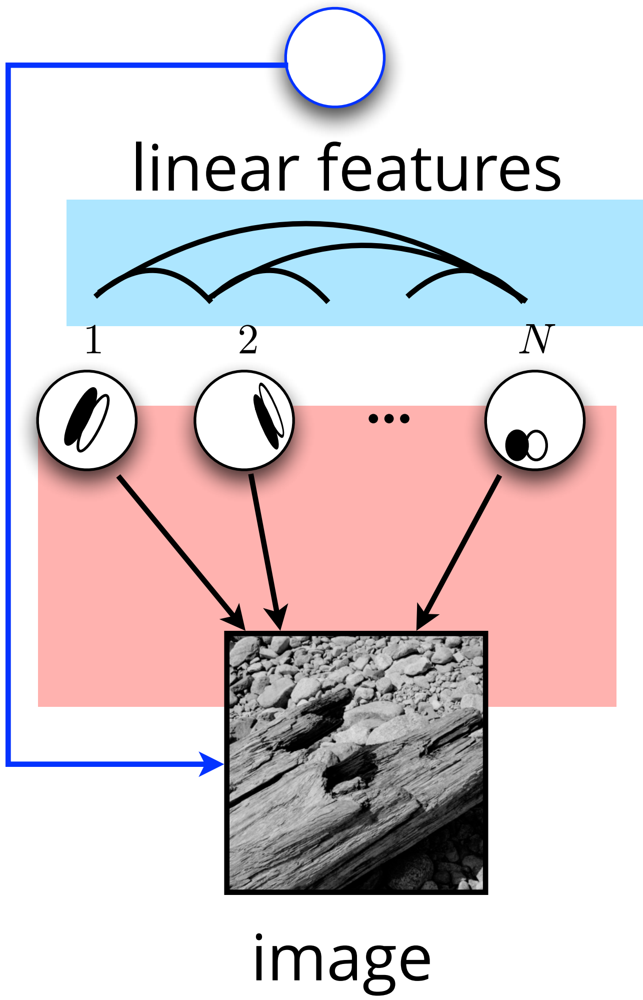
expectation

neural activities

[a_1, a_2, ..., a_N]

evidence

$$\text{image} = \text{contrast} \times \left(a_1 \, \text{feature}_1 + a_2 \, \text{feature}_2 + \ldots + a_N \, \text{feature}_N \right) + \text{noise}$$



expectation

neural activities

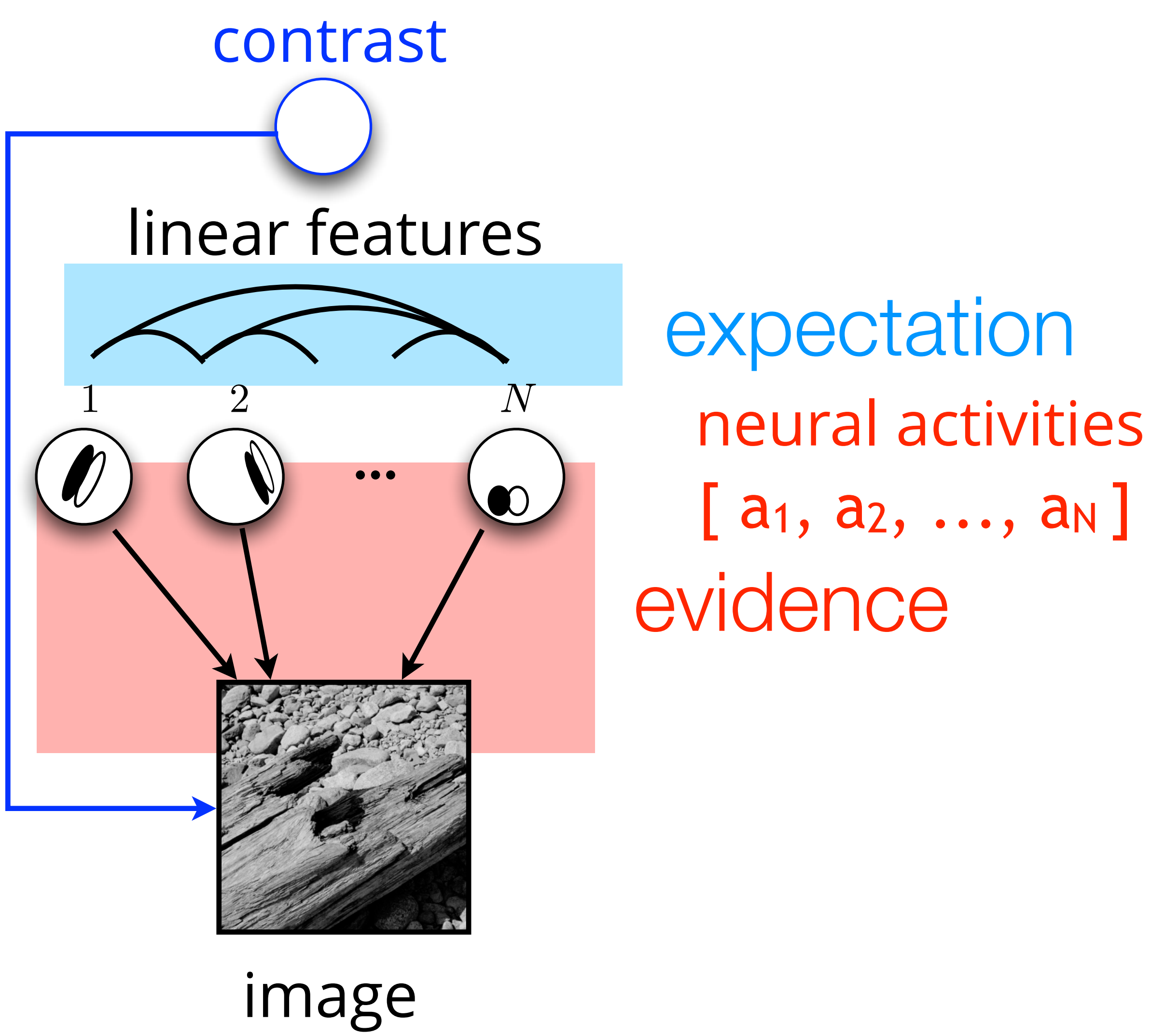
[a_1, a_2, ..., a_N]

evidence

$$\text{image} = \text{contrast} \times \left(a_1\, \text{feature}_1 + a_2\, \text{feature}_2 + \ldots + a_N\, \text{feature}_N\right) + \text{noise}$$

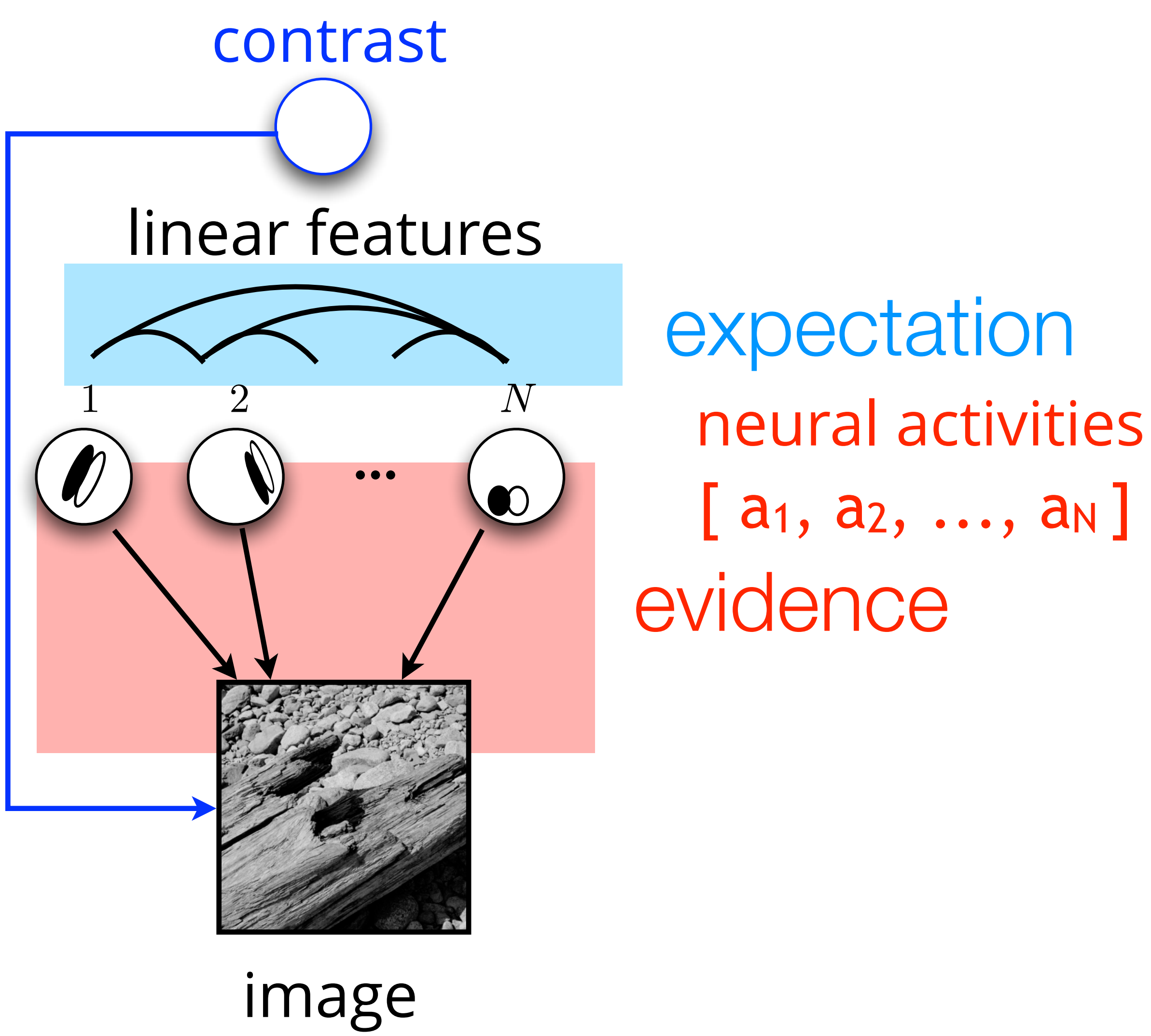
$$\underbrace{P(\text{image}|a_1, a_2, \ldots, a_N, c)}_{\text{sensory evidence}}$$

Bayesian inference



$$\text{image} = \text{contrast} \times \left(a_1\,\text{feature}_1 + a_2\,\text{feature}_2 + \ldots + a_N\,\text{feature}_N\right) + \text{noise}$$

$$\underbrace{P(a_1, a_2, \ldots, a_N \mid \text{image}, c)}_{\text{posterior}} \propto \underbrace{P(a_1, a_2, \ldots, a_N \mid c)}_{\text{prior}} \times \underbrace{P(\text{image} \mid a_1, a_2, \ldots, a_N, c)}_{\text{sensory evidence}}$$



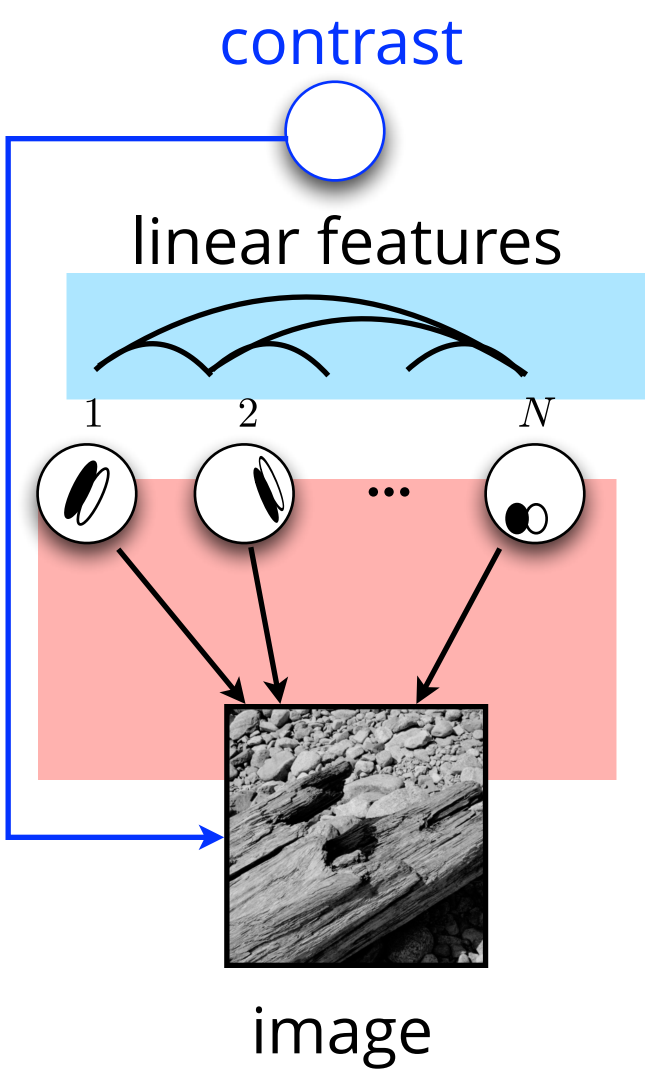
Demonstrated efficiency in:

- ★ pattern-completion
- ★ compression
- ★ denoising

$$\text{image} = \text{contrast} \times \left(a_1\,\text{feature}_1 + a_2\,\text{feature}_2 + \ldots + a_N\,\text{feature}_N \right) + \text{noise}$$

$$\underbrace{\mathrm{P}(a_1, a_2, \ldots, a_N \mid \text{image}, c)}_{\text{posterior}} \propto \underbrace{\mathrm{P}(a_1, a_2, \ldots, a_N \mid c)}_{\text{prior}} \times \underbrace{\mathrm{P}(\text{image} \mid a_1, a_2, \ldots, a_N, c)}_{\text{sensory evidence}}$$

Bayesian inference



expectation

neural activities

[a_1, a_2, …, a_N]

evidence

Demonstrated efficiency in:

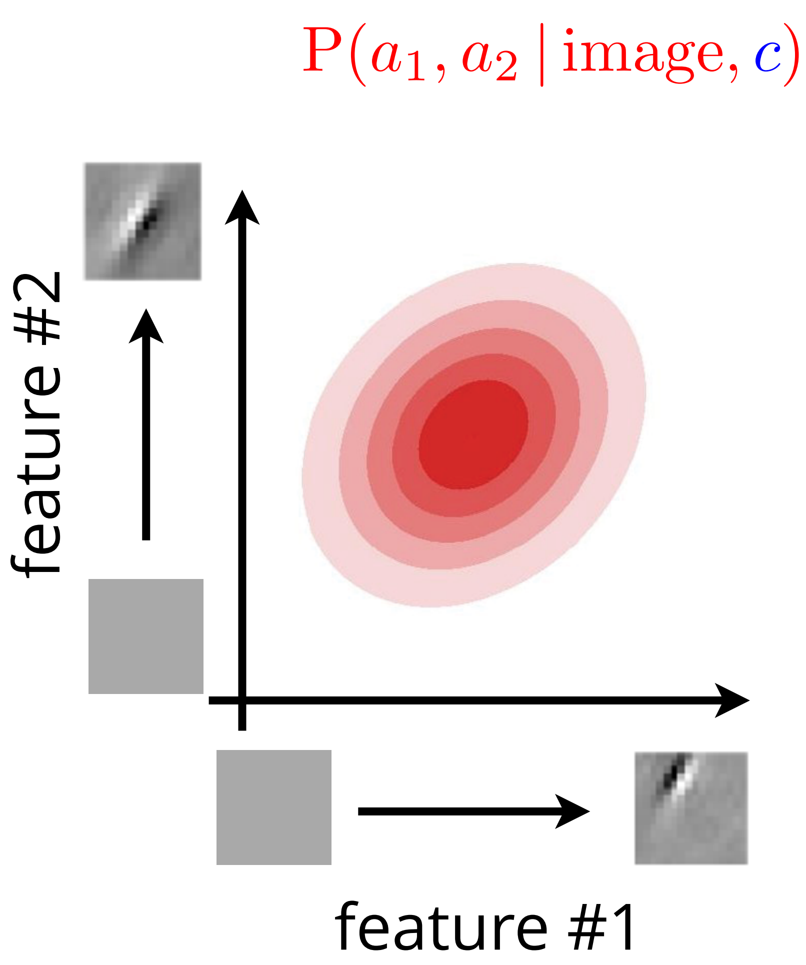
- ★ pattern-completion
- ★ compression
- ★ denoising

the parametric form of both
evidence and expectation is determined by
natural image statistics

mean responses

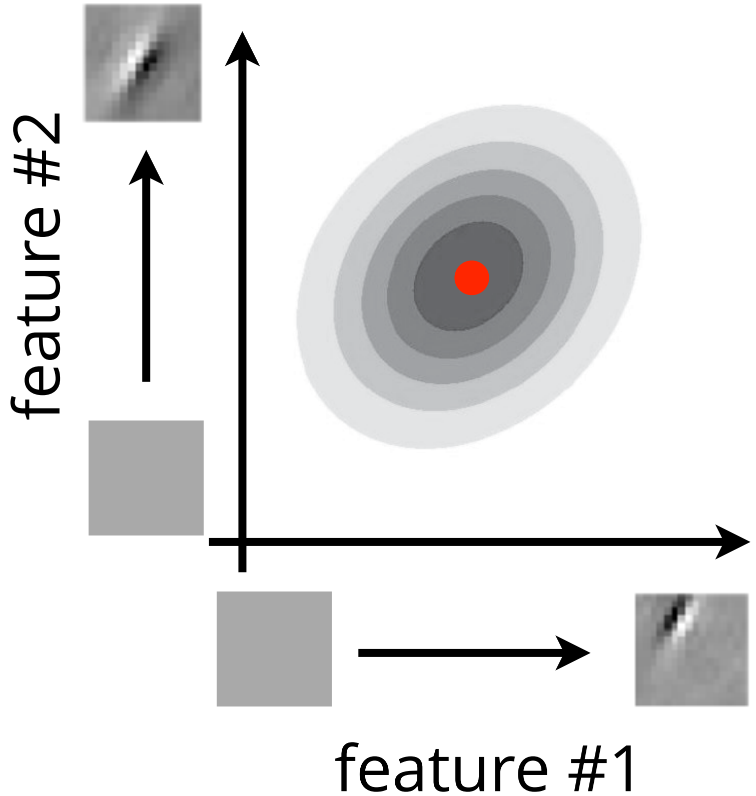
$$\mathrm{P}(a_1, a_2 \,|\, \mathrm{image}, c)$$

mean responses

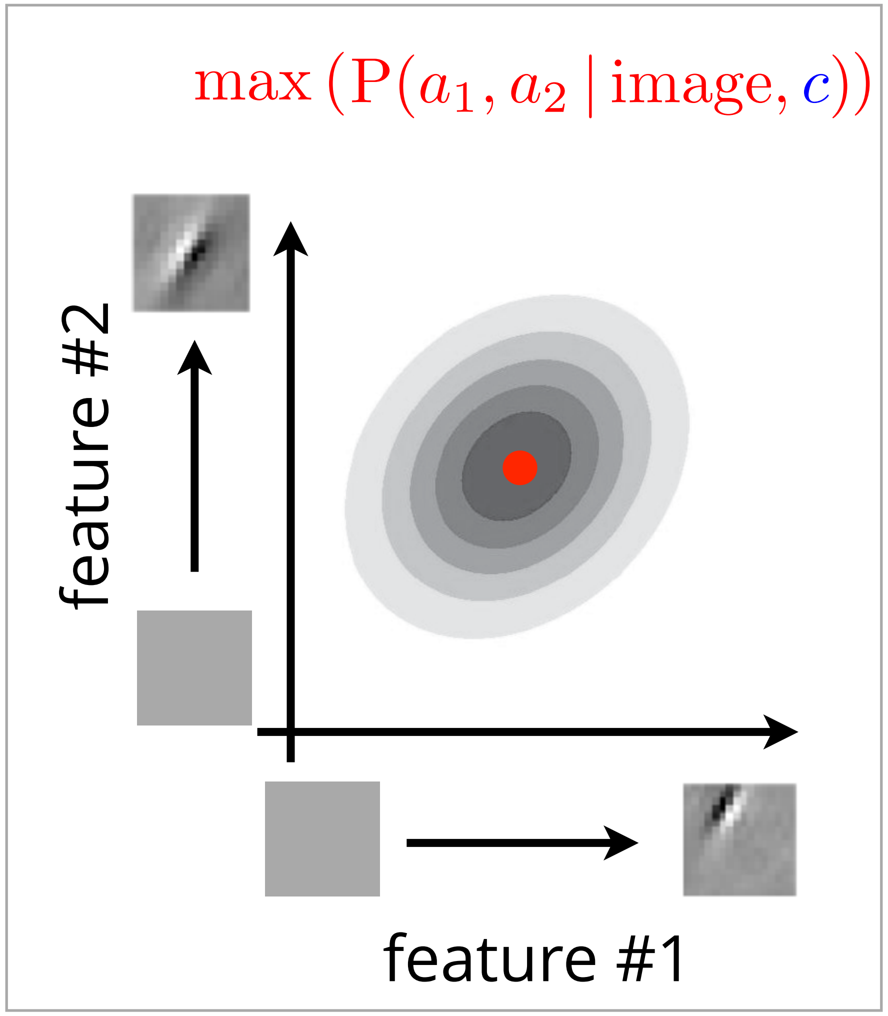


mean responses

$$\max\left(\mathrm{P}(a_1, a_2 \,|\, \mathrm{image}, c)\right)$$



mean responses



traditional theories
e.g. Olshausen & Field, Nature 1996, Schwartz & Simoncelli, Nat Neurosci 2001

mean response $\rightsquigarrow$ maximum a posteriori inference

roadmap

- image model
- consequence of the representation of prior
- stimulus-dependence of variability
- stimulus dependence of covariability of multiple neurons

inference and uncertainty

$$\underbrace{\mathrm{P}(a_1, a_2, \ldots, a_N \,|\, \mathrm{image}, c)}_{\text{posterior}} \propto \underbrace{\mathrm{P}(a_1, a_2, \ldots, a_N \,|\, c)}_{\text{prior}} \times \underbrace{\mathrm{P}(\mathrm{image}|a_1, a_2, \ldots, a_N, c)}_{\text{sensory evidence}}$$

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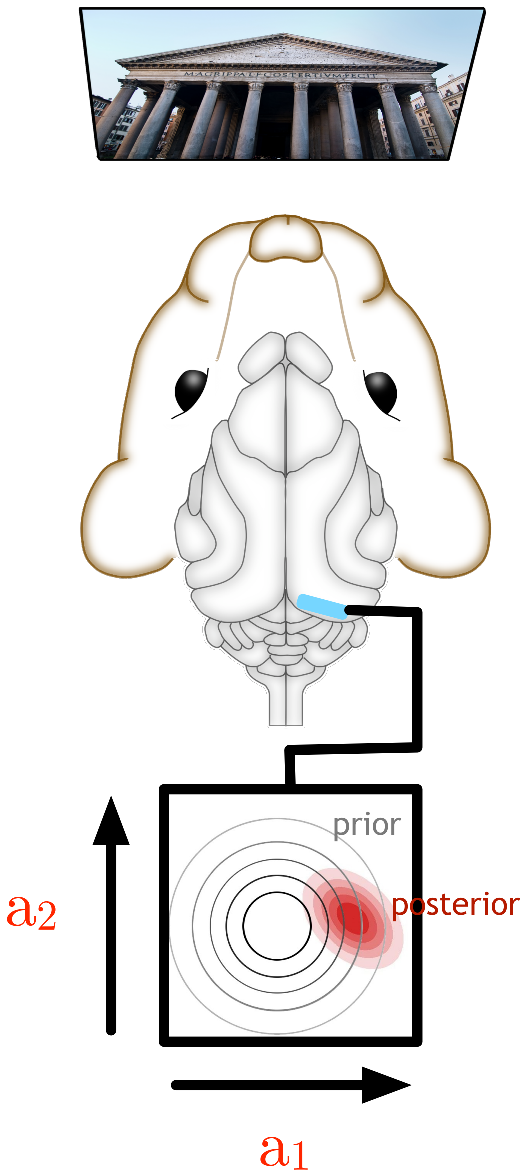

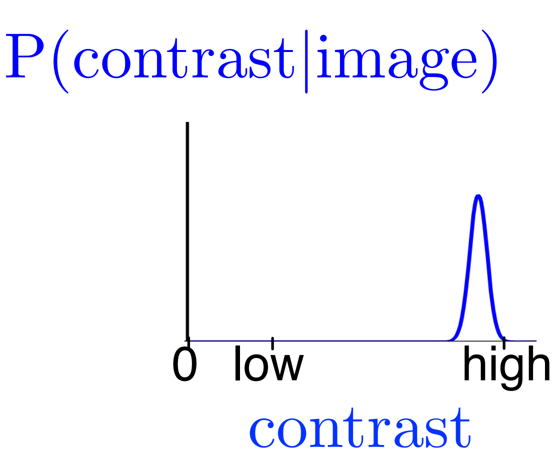

inference and uncertainty

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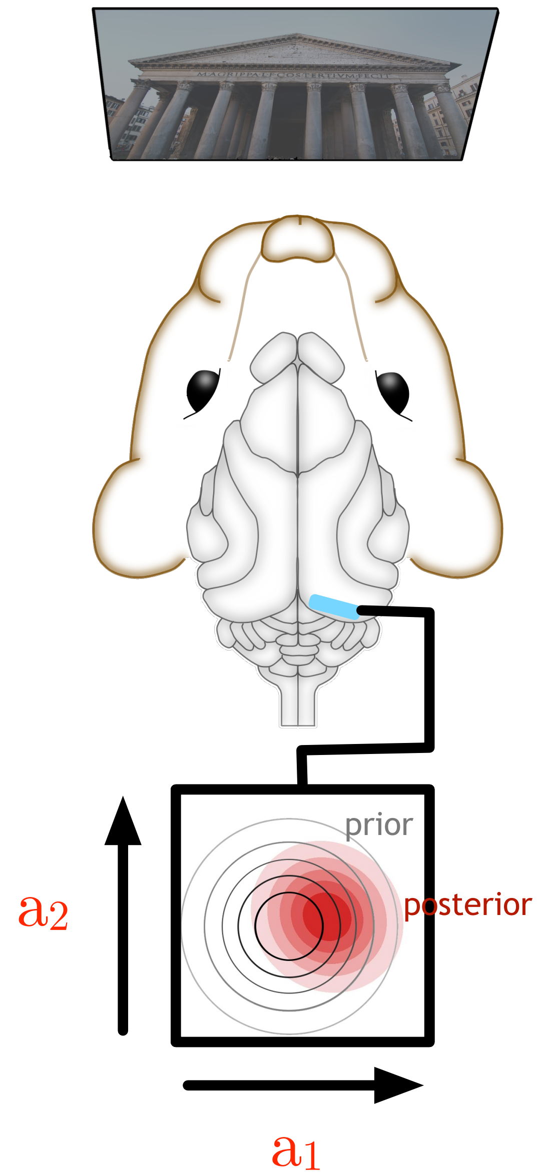

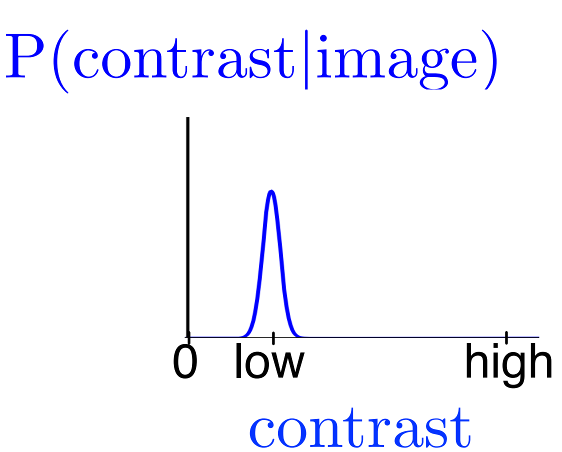

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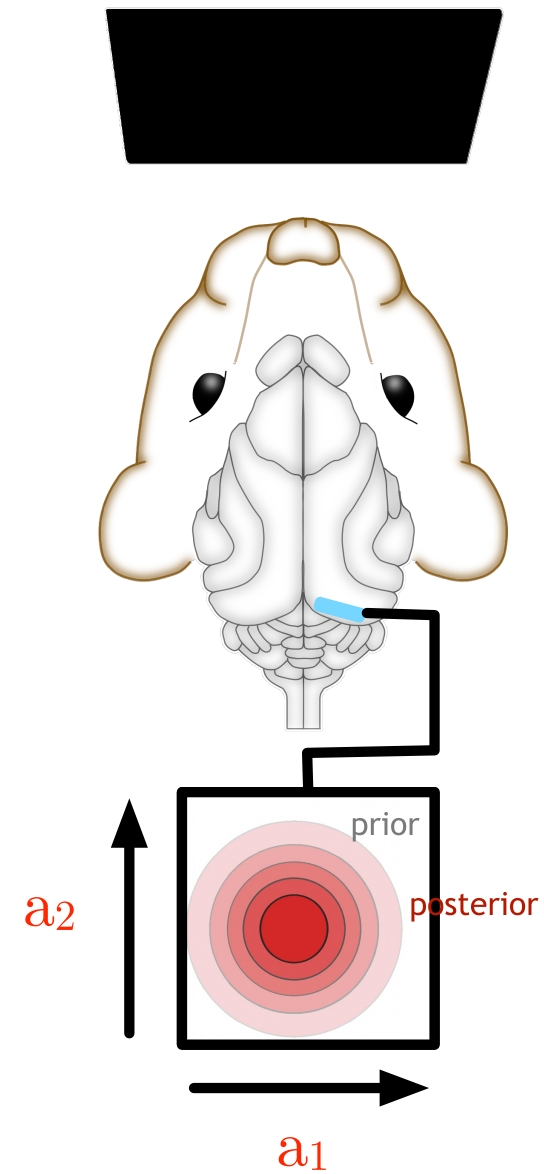
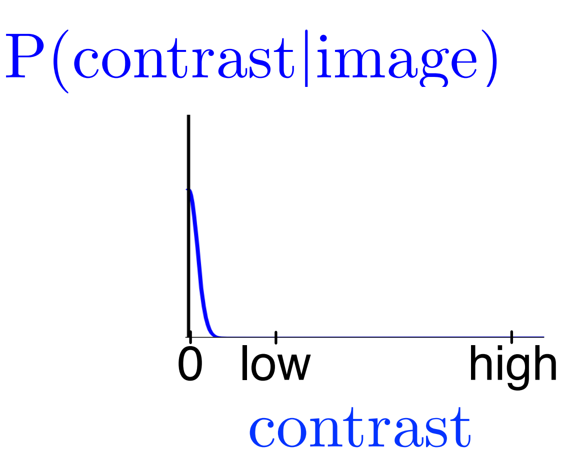
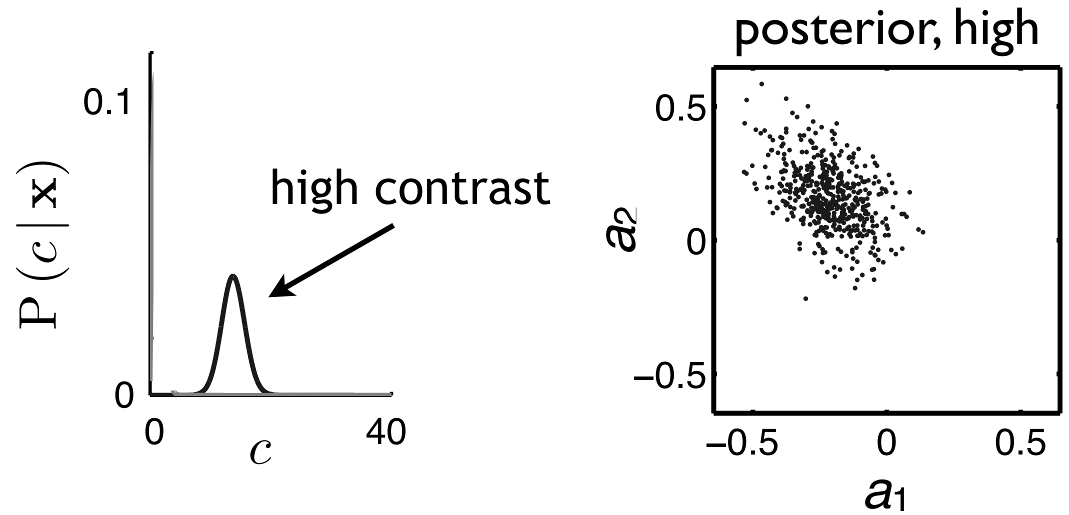




roadmap

- image model
- consequence of the representation of prior
- stimulus-dependence of variability
- stimulus dependence of covariability of multiple neurons

Stimulus onset quenches neural variability



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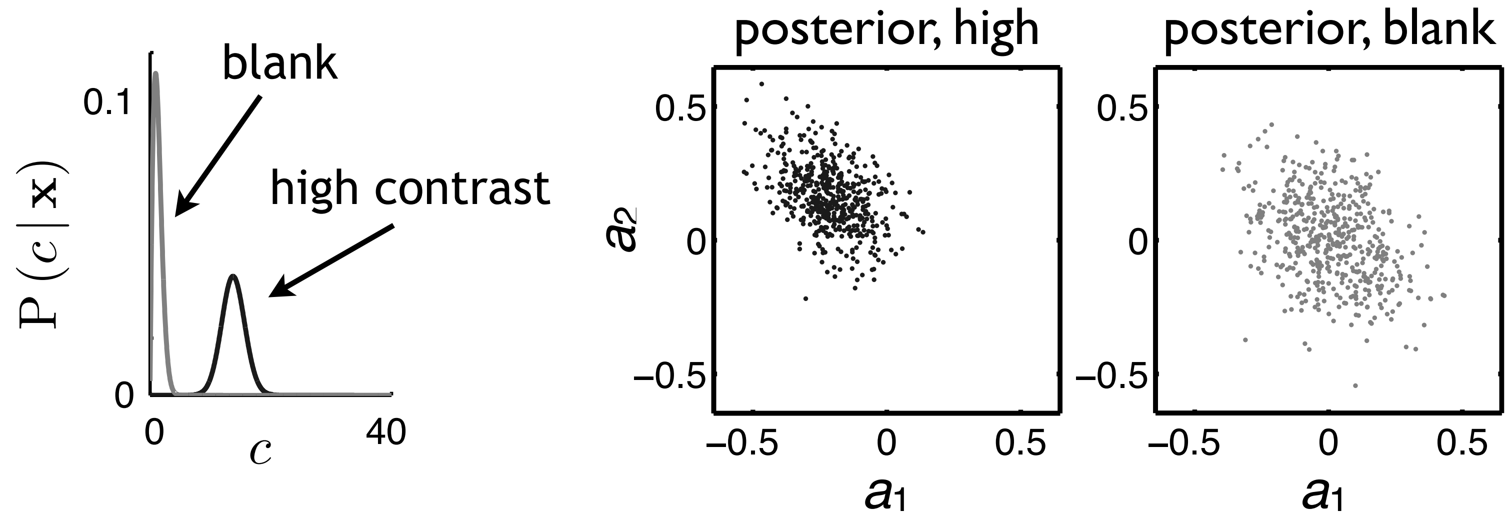

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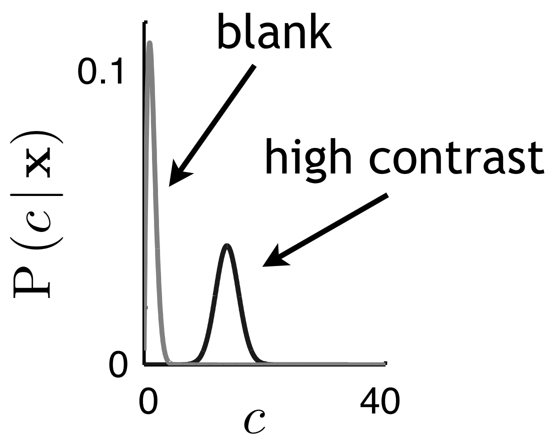

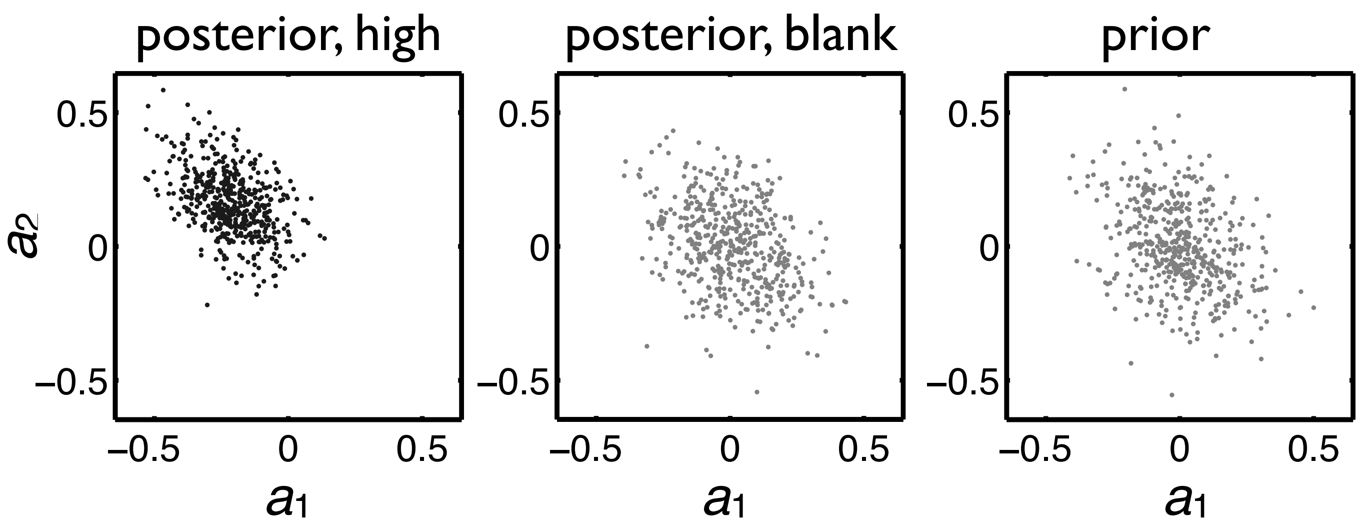

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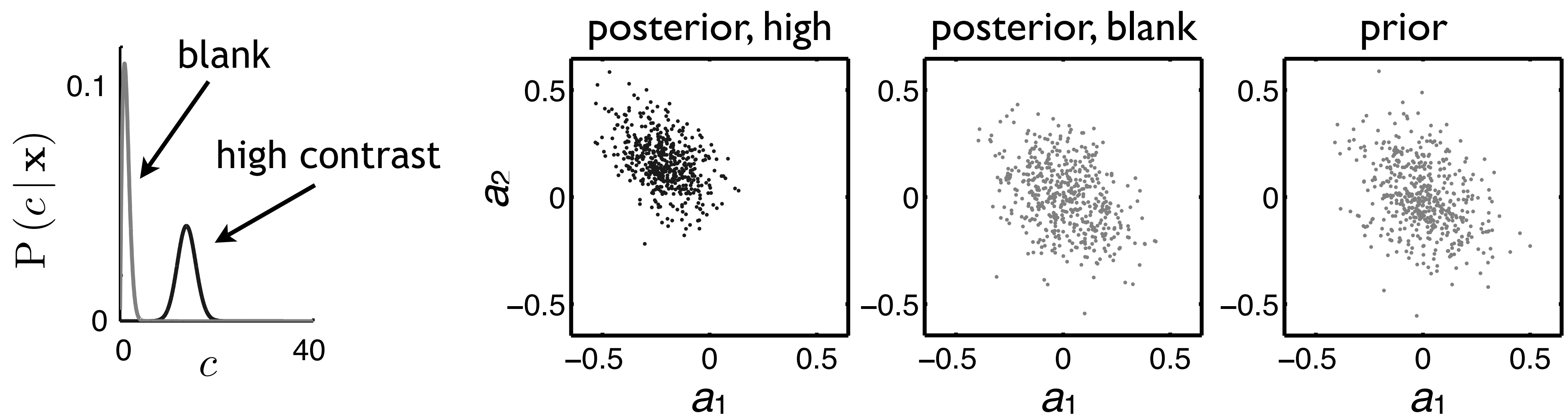
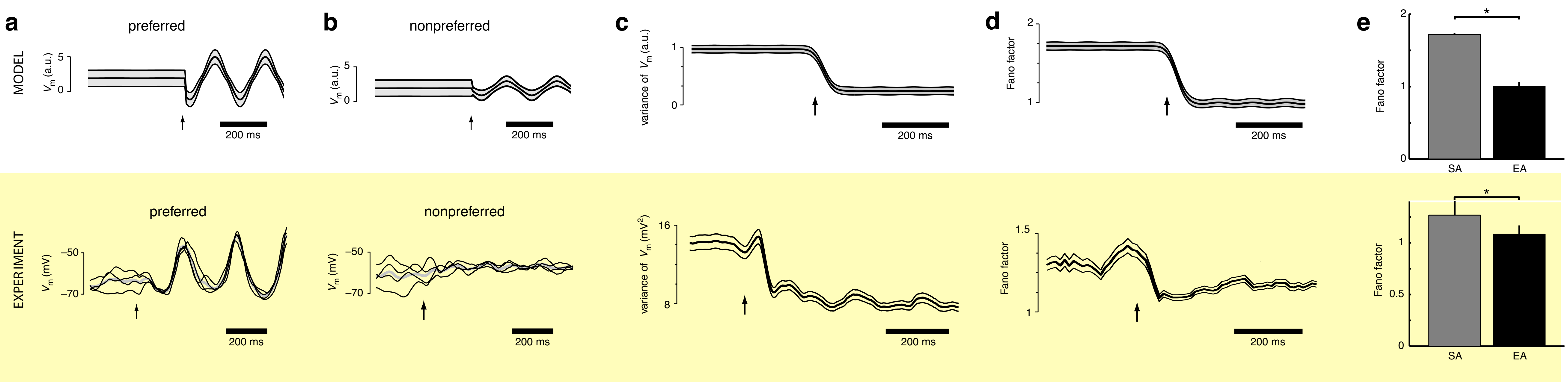
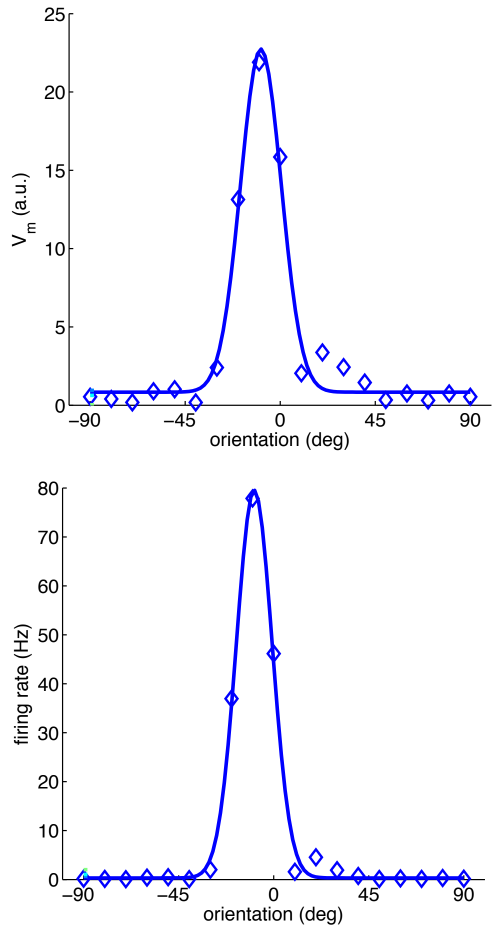


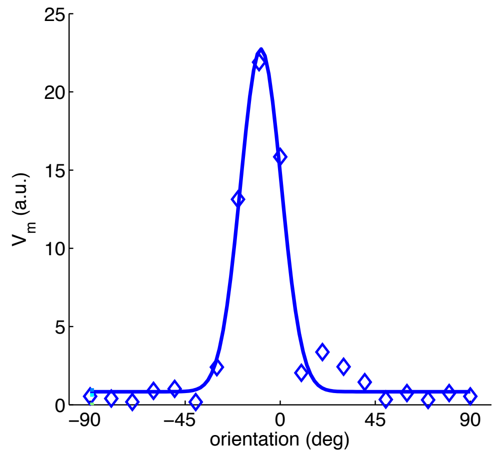


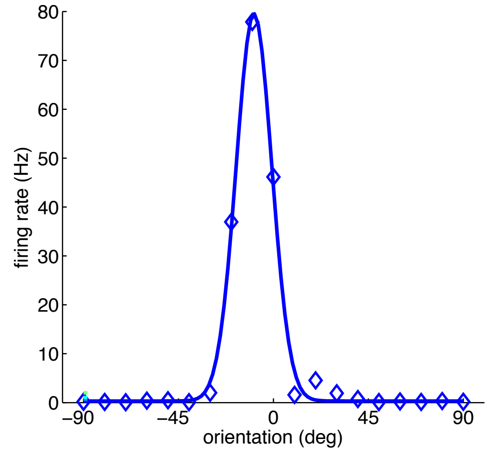
Orientation-dependence of response statistics

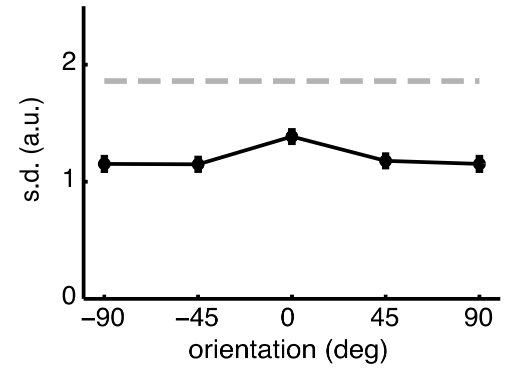


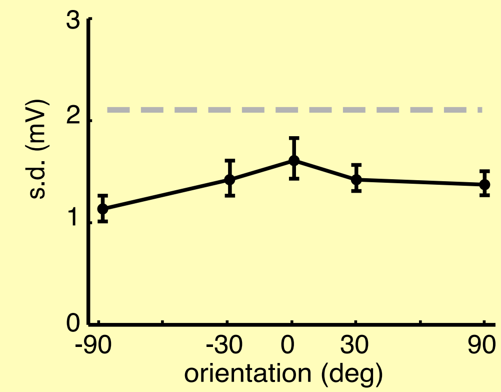
Orientation-dependence of response statistics

- orientation has a big impact on response mean
- however, no change in uncertainty is expected
- no significant change in variance is expected in membrane potential









Finn et al, Neuron 2007

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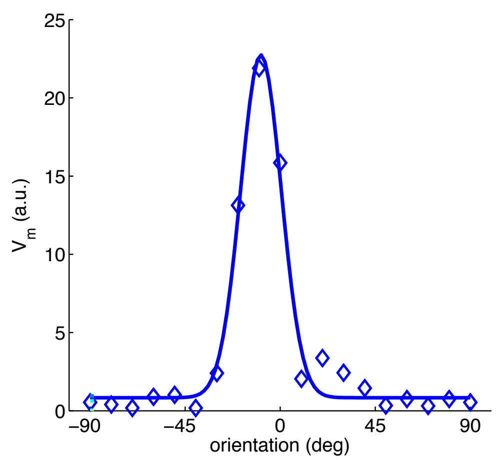
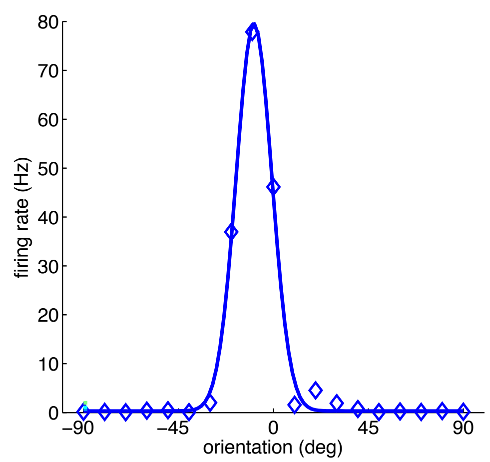
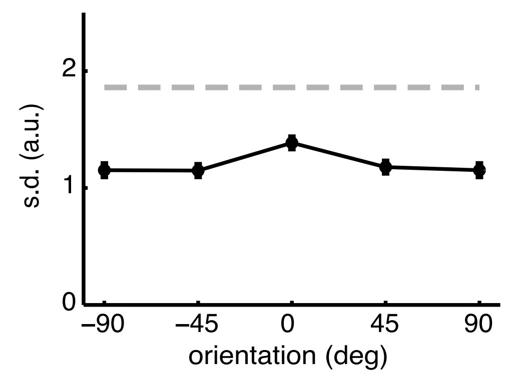
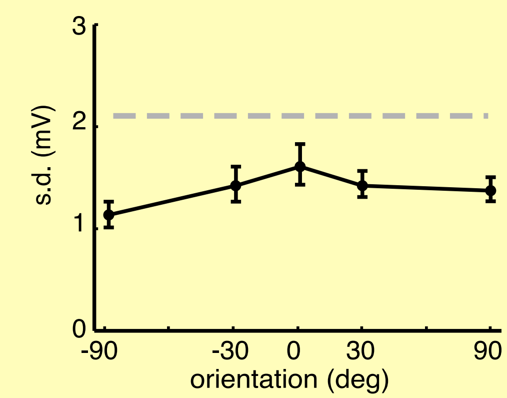


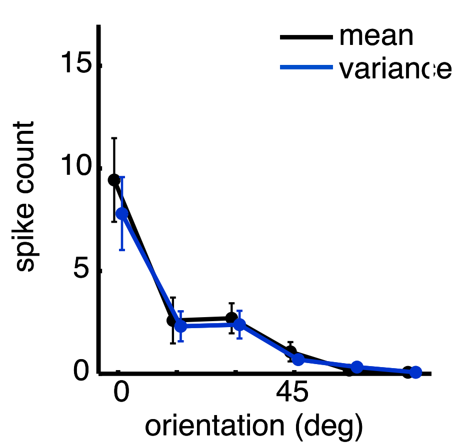


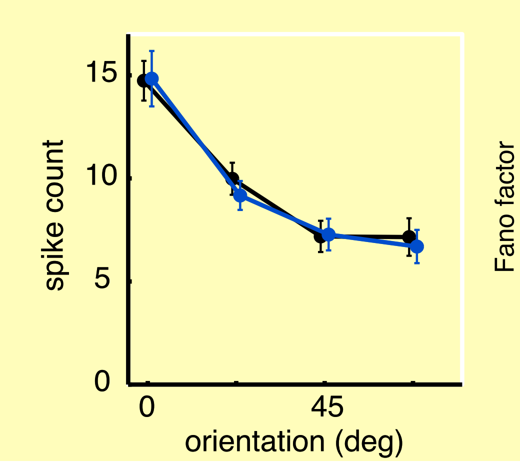


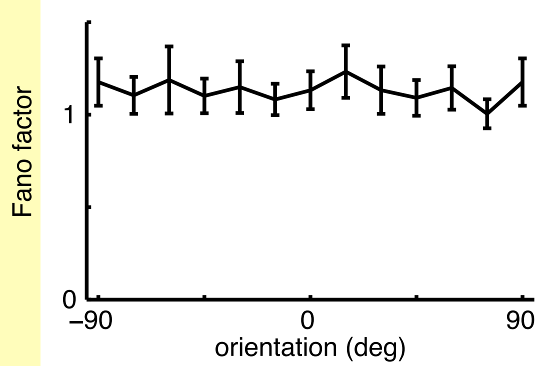


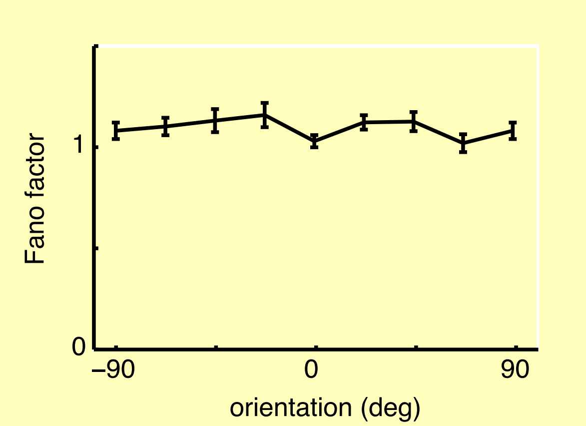
Finn et al, Neuron 2007

- spike count variance increases with firing rate
- Fano factor is still expected to be independent of orientation



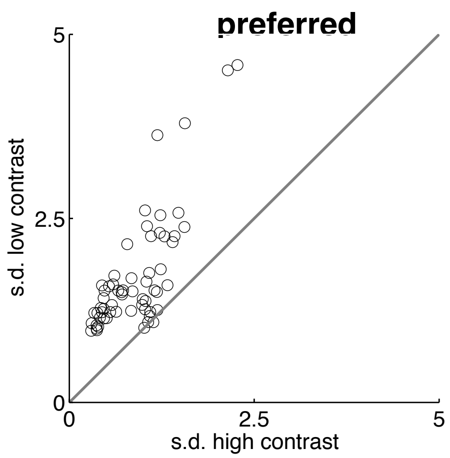


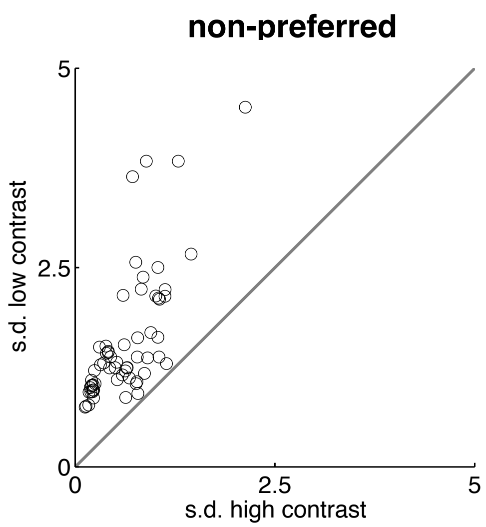


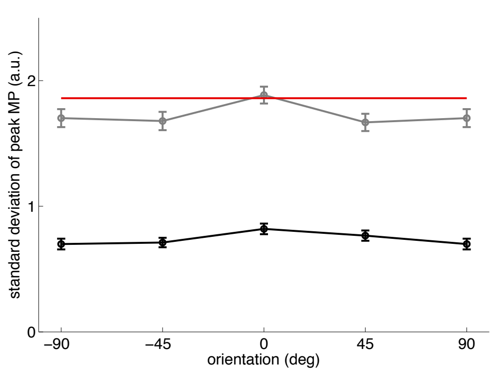


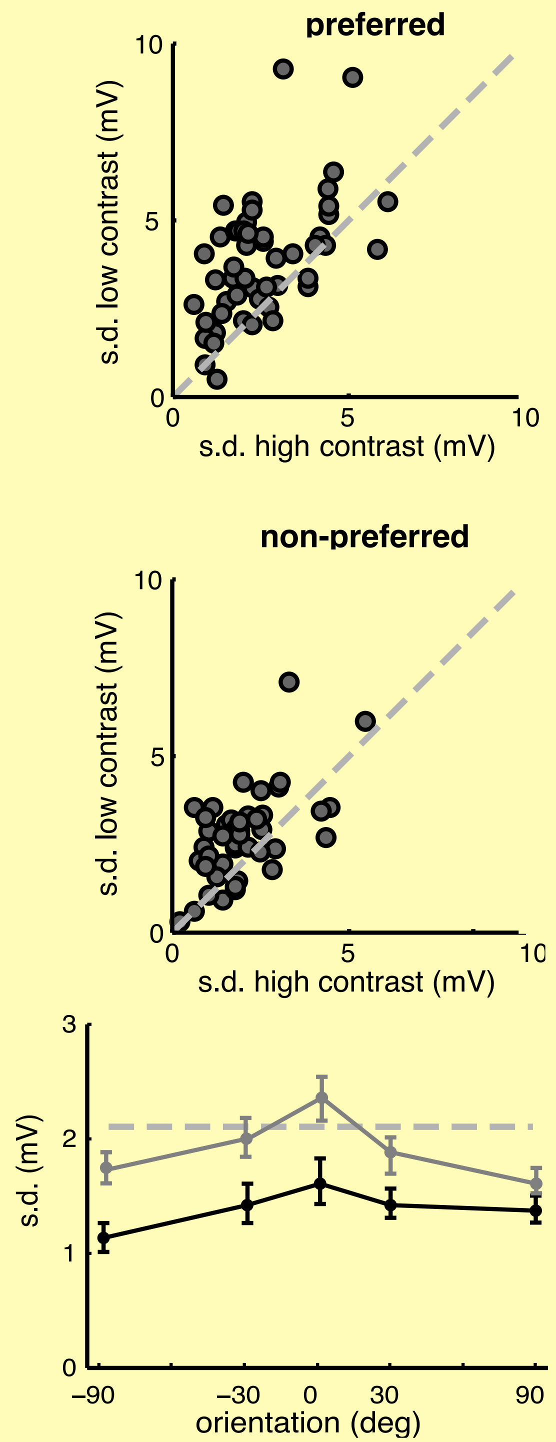
Contrast-dependence of response statistics

- contrast has fundamental effect on mean: *decreased* contrast results in *decreased* mean
- decreased *contrast* results in *increased* uncertainty

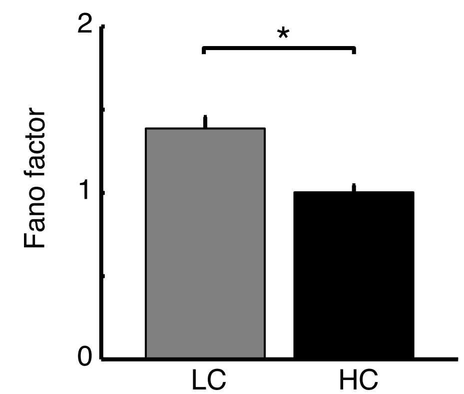


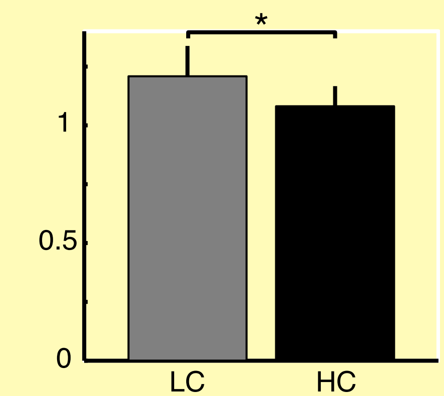






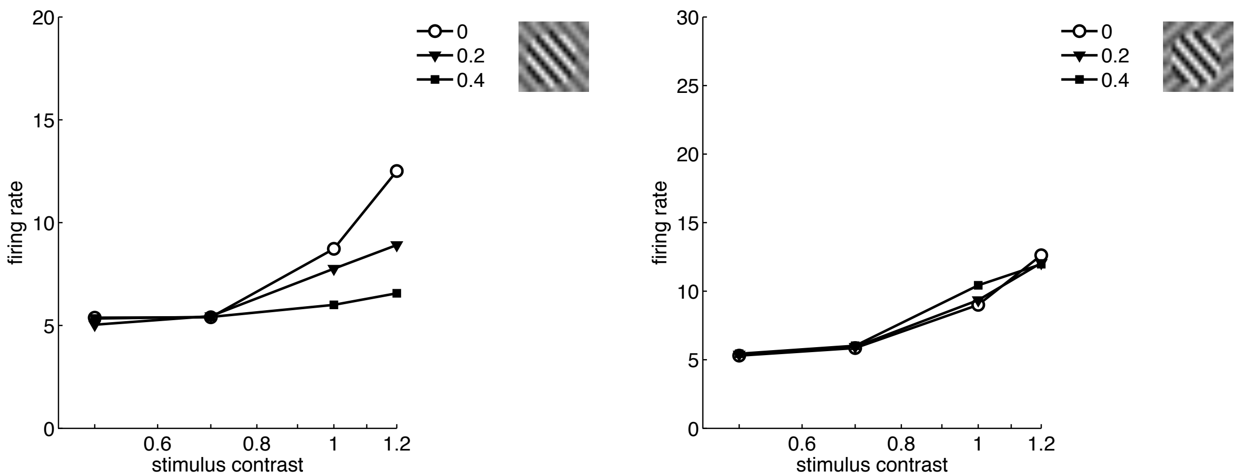
Finn et al, Neuron 2007

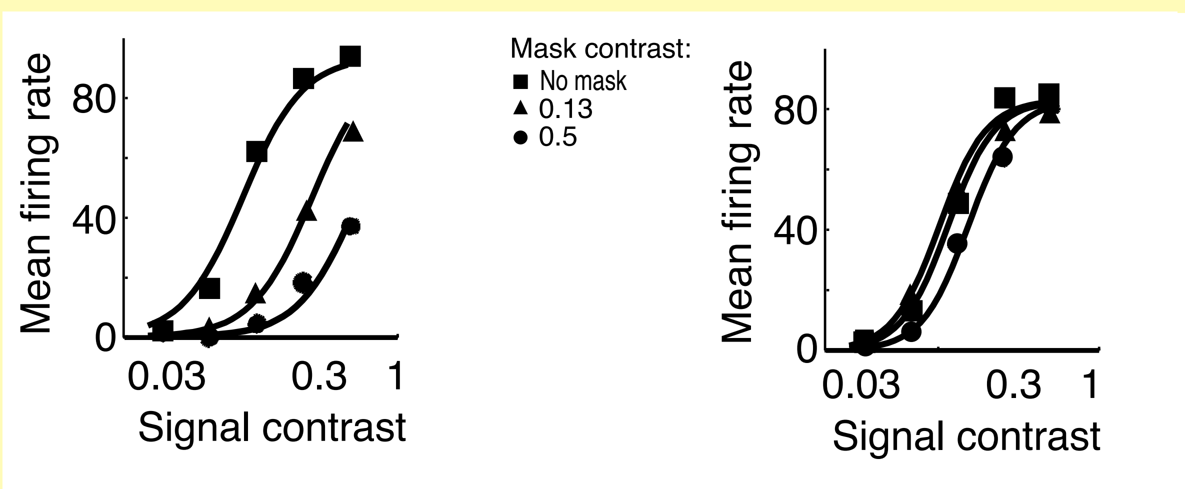




Non-classical RF dependence of response statistics

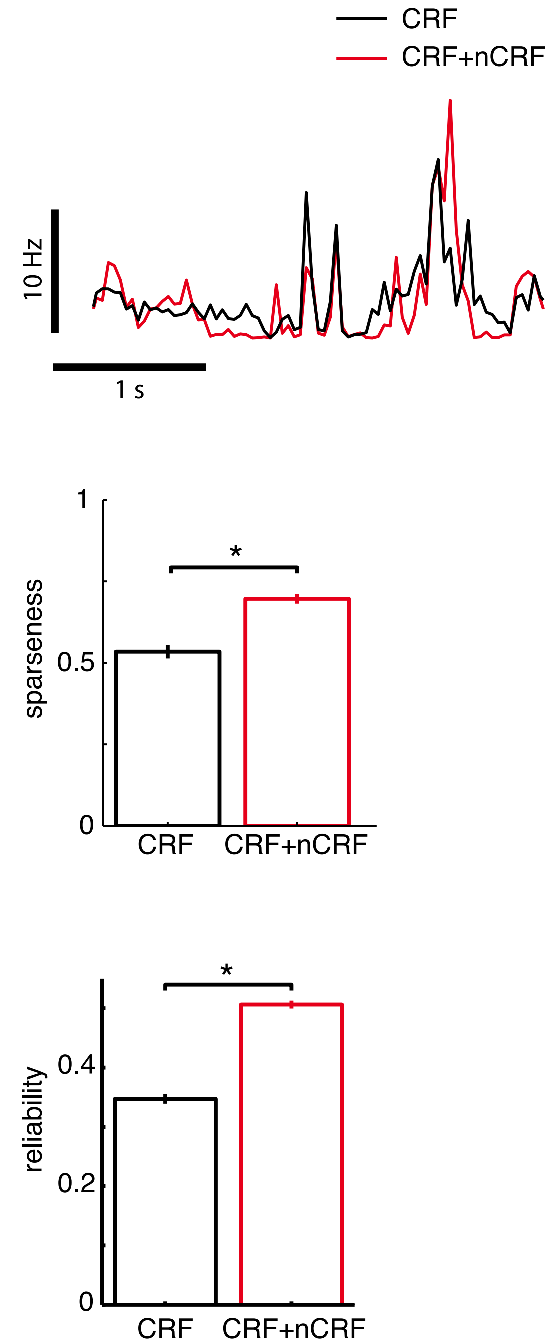
- non-linear interaction between with-receptive field and extra-receptive field stimulation

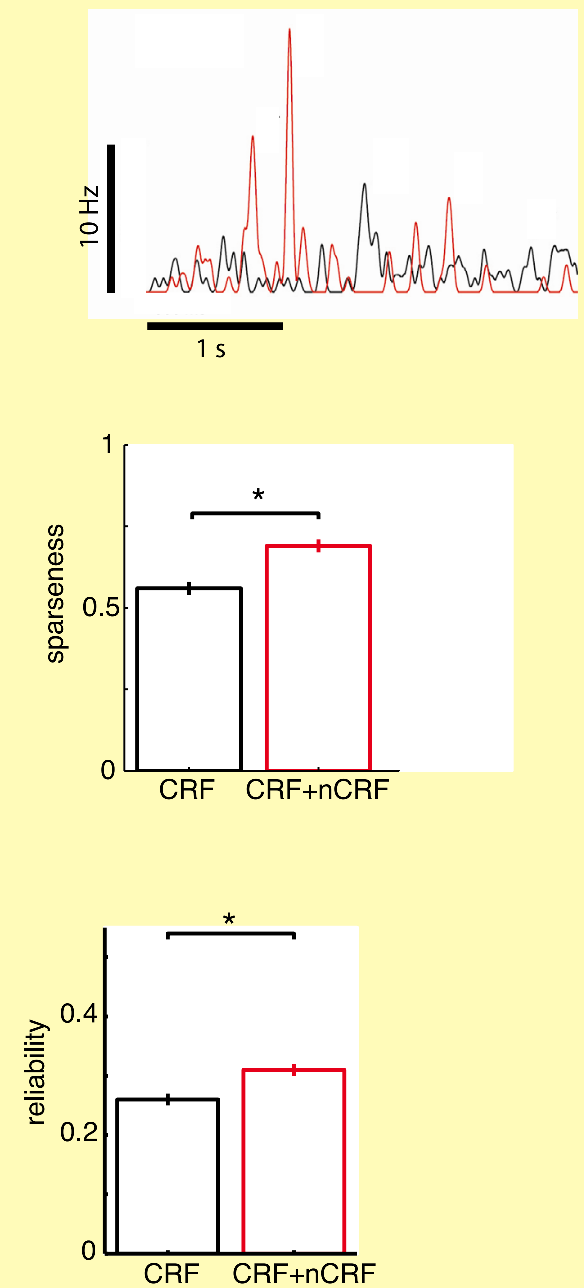




Cavanagh, 2000

- uncertainty is affected by extra information





Haider et al, Neuron 2010

roadmap

- image model
- consequence of the representation of prior
- stimulus-dependence of variability
- stimulus dependence of covariability of multiple neurons

Learning and correlations structure

$$P(\text{responses} \,|\, \text{stimulus}) \;\propto\; P(\text{stimulus} \,|\, \text{responses}) \;\times\; P(\text{responses})$$

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$$C^* \approx \frac{1}{T}\left(\sum_t \mathbf{\Sigma}(t) + \sum_t \mu(t)\,\mu^{\mathsf{T}}(t)\right)$$

Learning and correlations structure

$$P(\text{responses} \mid \text{stimulus}) \propto P(\text{stimulus} \mid \text{responses}) \times P(\text{responses})$$

prior correlation

posterior correlation

signal correlation

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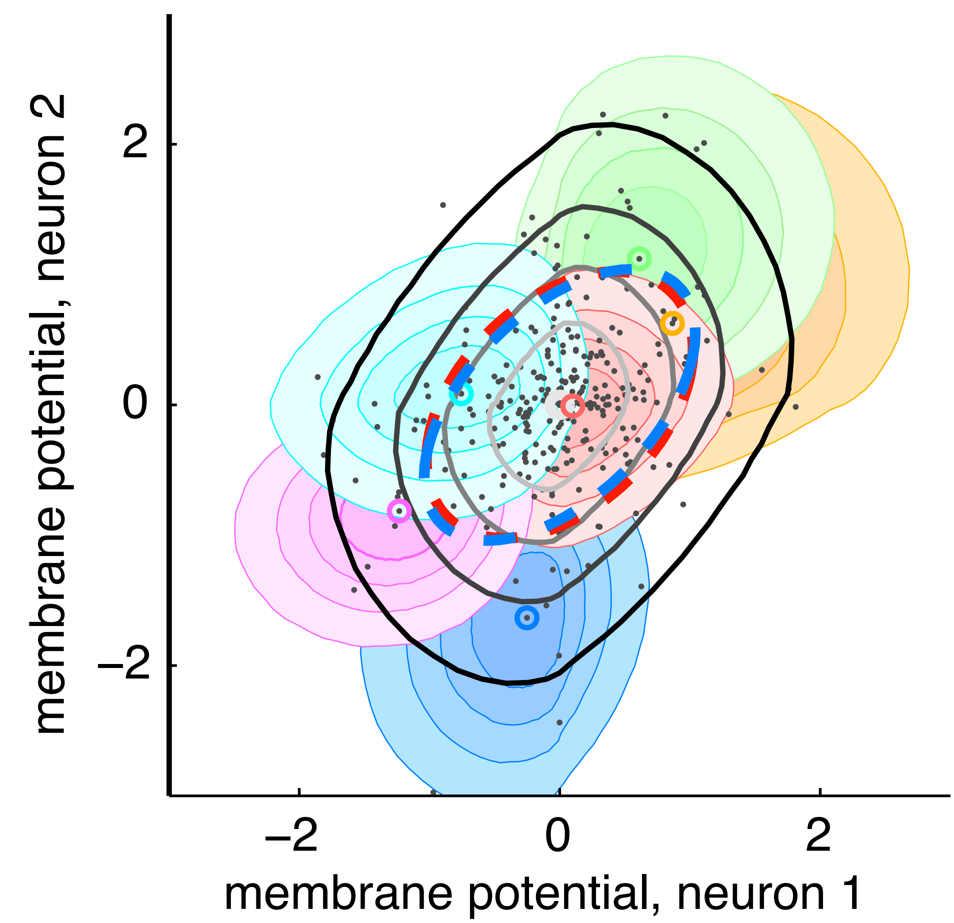

Relationship between various forms of correlations

signal vs. spontaneous correlation

signal vs. noise correlation