

# Effects of higher-order statistics on activity in V1



Mihály Bánya, Gergő Orbán

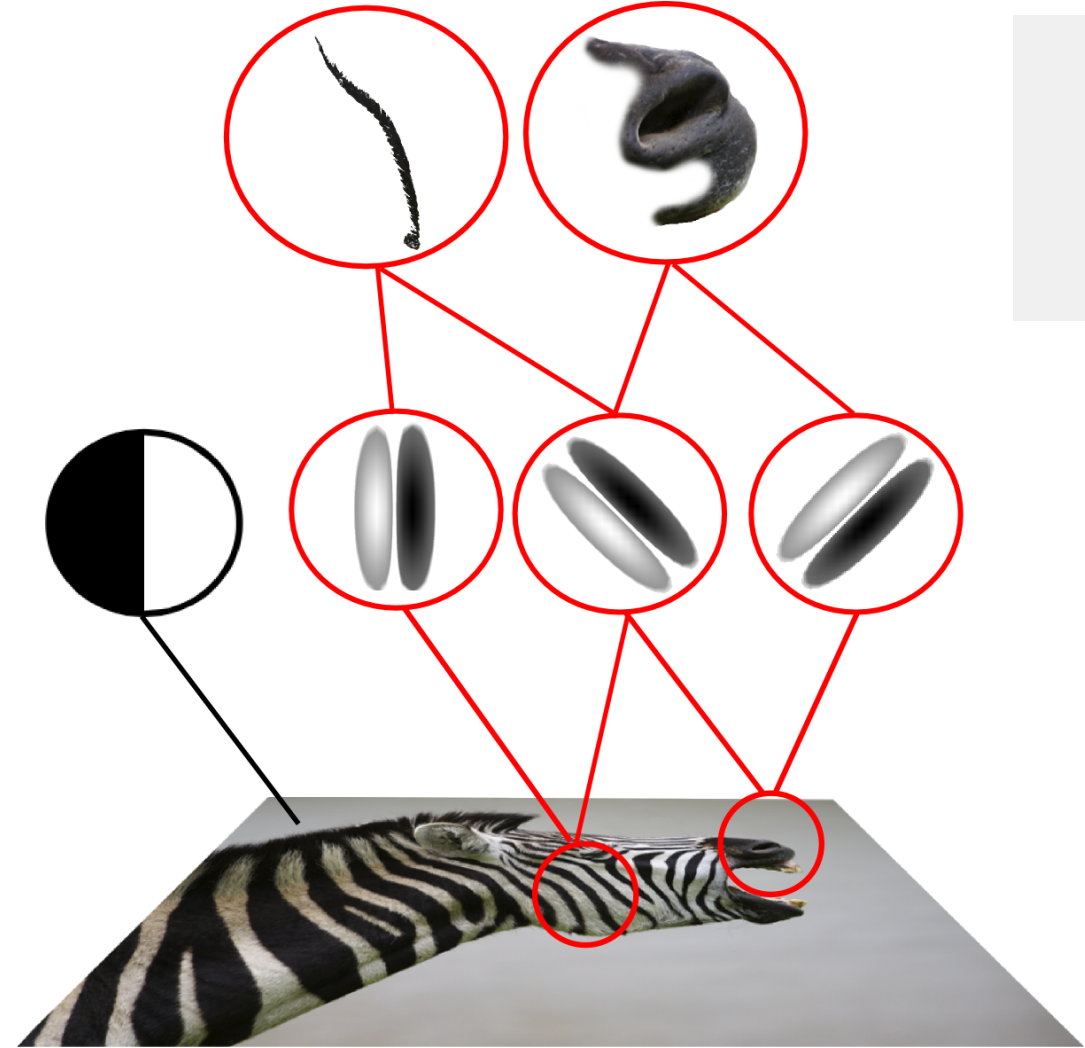
Computational Systems Neuroscience Lab  
Wigner Research Centre for Physics, Budapest



## Introduction

- The visual system is representing a hierarchical **generative model** of the environment.
- V1 simple cell responses are organised by **latent variables** representing higher level statistics of sensory input.
- The latent structure determining the covariance structure of V1 simple cells corresponds to **Gestalt principles**.
- Full **Bayesian inference** is assumed in the model, posteriors are represented by stochastic **samples**.

## The model



$$p(v | g) = \mathcal{N}(v; 0, \sum_{j=1}^K g_j C_j)$$

$$p(x | v, z) = \mathcal{N}(x; zAv, \sigma_x I)$$

- Gestalts are learned from data as covariance components  $C_{1..K}$
- Coefficient variables of covariance components,  $g$ , are generated from Gamma priors
- The global contrast variable,  $z$ , is also generated from a Gamma prior
- Linear filter set  $A$  transforms V1-level variables,  $v$  to pixels,  $x$ , adding independent observation noise

## Sampling model posteriors

- Gibbs sampling
- Conditional  $v$  activations can be sampled directly from a Gaussian conditional

$$p(v | x, g, z) = \mathcal{N}\left(v; \frac{z}{\sigma_x} C_{v|x,g,z} A^T x, C_{v|x,g,z}\right), \quad C_{v|x,g,z} = \left(\frac{z^2}{\sigma_x} A^T A + \left(\sum_{j=1}^K g_j C_j\right)^{-1}\right)^{-1}$$

- Conditional  $g$  and  $z$  activations can be sampled by MCMC schemes

$$\log p(g | x, v, z) \sim -\frac{1}{2} \left[ \log \left( \det \left( \sum_{k=1}^K g_k C_k \right) \right) + v^T \left( \sum_{k=1}^K g_k C_k \right)^{-1} v \right] + \log p(g)$$

$$\log p(z | x, v, g) \sim -\frac{1}{2} \left[ D_x \log(\sigma_x) + \frac{1}{\sigma_x} (x - zAv)^T (x - zAv) \right] + \log p(z)$$

## Learning the parameters

- Iterative stochastic generalised expectation maximisation
- Collecting  $L$  samples with Gibbs sampling as E-step
- Reparametrise with Cholesky components to ensure validity of covariance matrices

$$C_v = \sum_{k=1}^K g_k U_k^T U_k$$

- Gradient of the complete-data log-likelihood over  $N$  observations

$$\frac{\partial \mathcal{L}}{\partial [U_k]_{i,j}} = \sum_{l=1}^{NL} \text{Tr} \left[ \frac{\partial \log p(x^l, v^l, g^l | U_{1..K})}{\partial C_v^l} \frac{\partial C_v^l}{\partial [U_k]_{i,j}} \right]$$

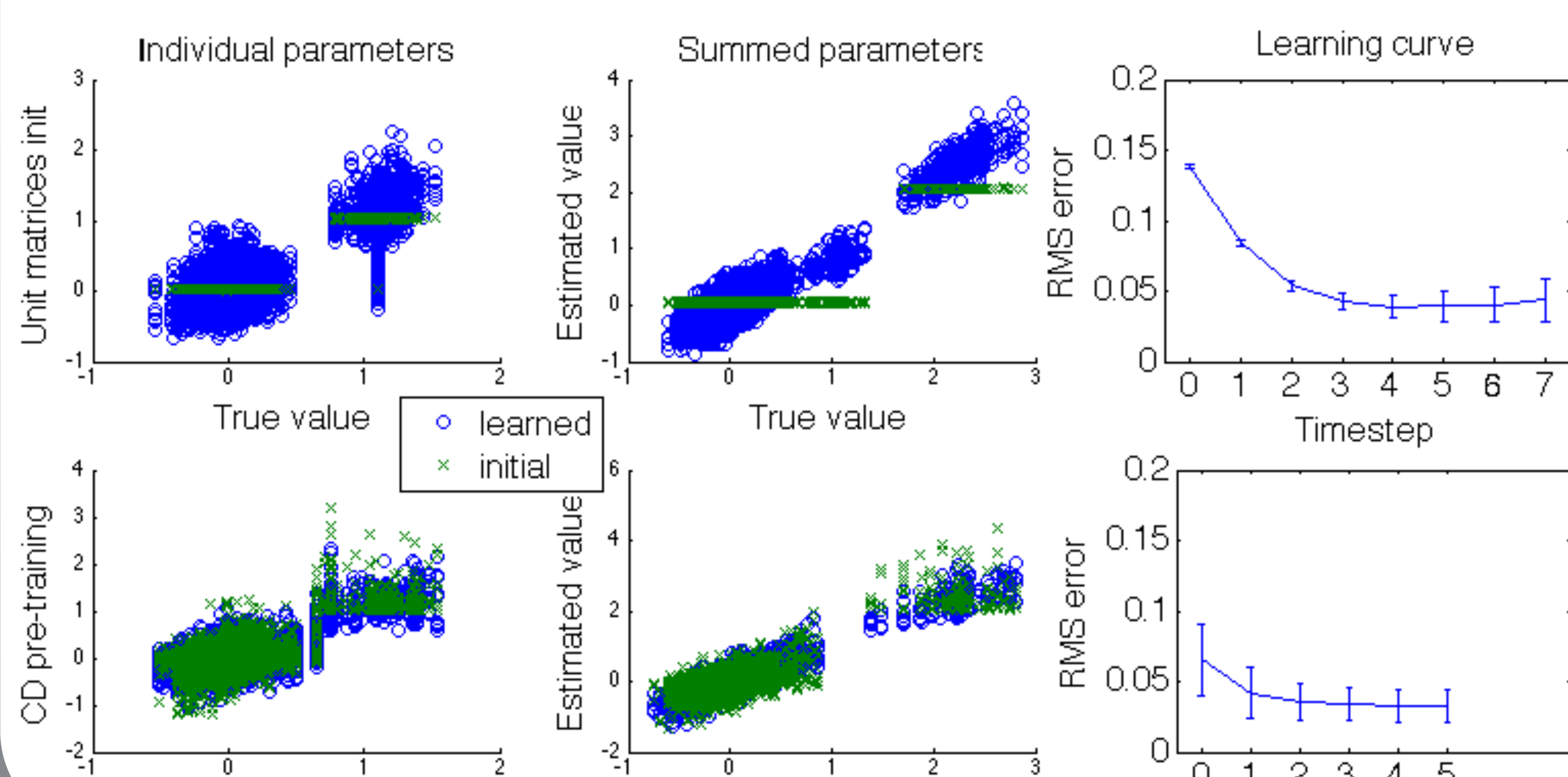
- Gradient descent as generalised M-step

$$[U_k]_{i,j}^{new} = [U_k]_{i,j}^{old} + \epsilon \frac{\partial \mathcal{L}}{\partial [U_k]_{i,j}}$$

## Pre-training with contrastive divergence

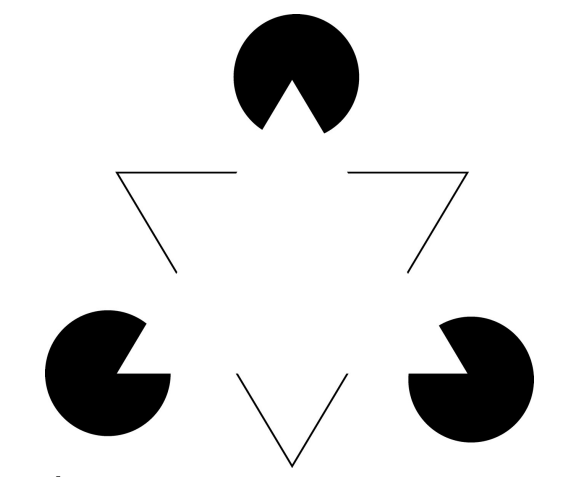
- Constructing a restricted Boltzmann machine of the two layers of hidden variables
- Sample  $v$  for each observation, and run CD1 between  $v$  and  $g$  layers
- Construct covariance components from learned weights between  $v$  and each  $g_k$

$$[C_k]_{i,j} = W_{i,k} W_{j,k}$$



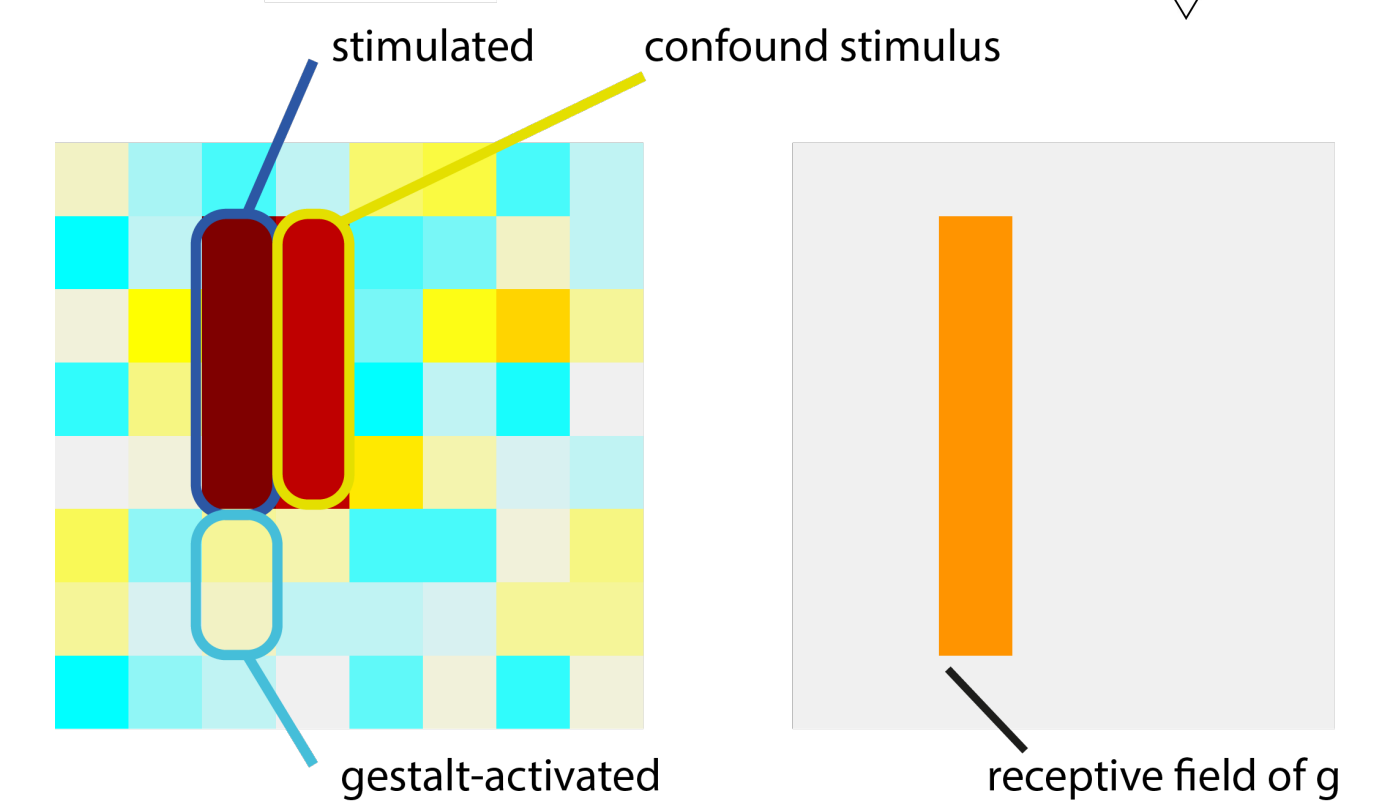
## Response to illusory contours

- We propose that IC responses are elicited by top-down Gestalt effects ( $g$  activations)
- The IC can be regarded as the non-stimulus-activated part of the receptive field of a covariance component partially activated by the stimulus



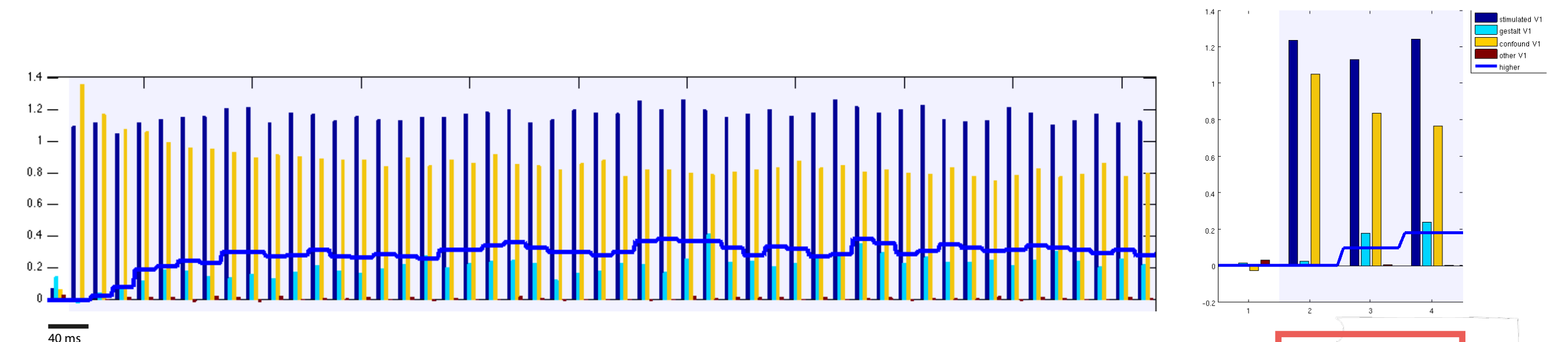
## Stimulus

- To compare model responses to experimental results with IC a test stimulus is constructed
- Left: mean stimulus in the  $v$  space
- Right: receptive field of one of the covariance component in the  $v$  space

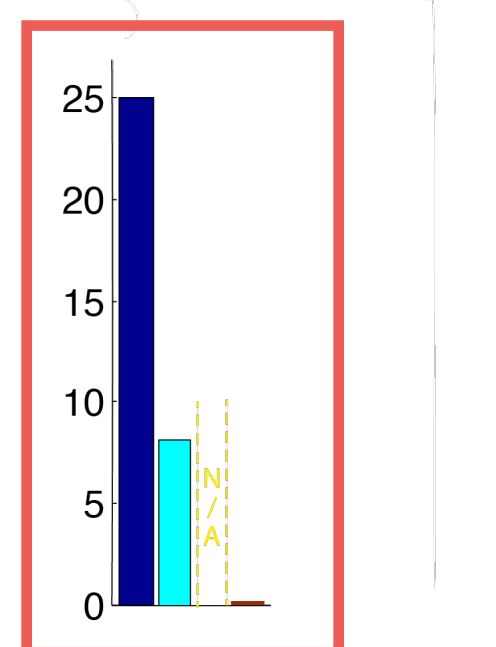


## Firing rates

- Alternating sampling from  $v$  and  $g$  conditioned on the observation, starting with  $v$
- Non-stimulus-evoked activity in  $v$  follows the activation of higher-level areas

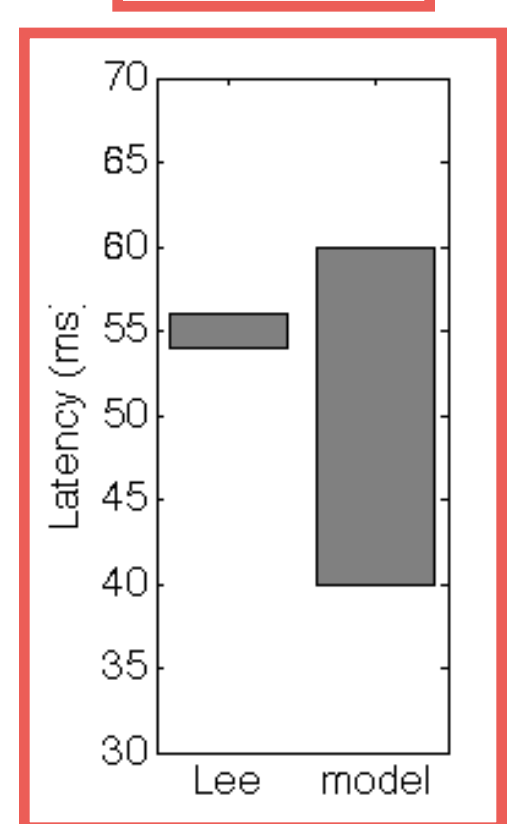


- The model reproduces the magnitude ratio of response rates to real contours, ICs and background
- Mean spike count in V1 as a response to different stimuli in receptive field from Lee & Nguyen, PNAS, 2001.



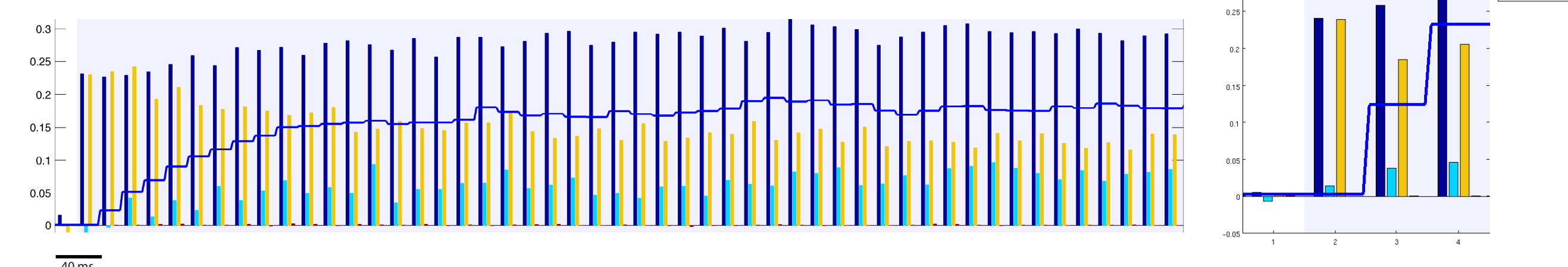
## Latencies

- Lee & Nguyen (2001) report that the response to ICs arrives with an additional latency of 55 ms compared to real contours
- In the model, rates of Gestalt-activated  $v$  units increase 2-3 Gibbs steps later
- Membrane potential autocorrelation typically diminishes after 20 ms, taking this as the duration of a sampling step, the model predicts 40-60 ms latency



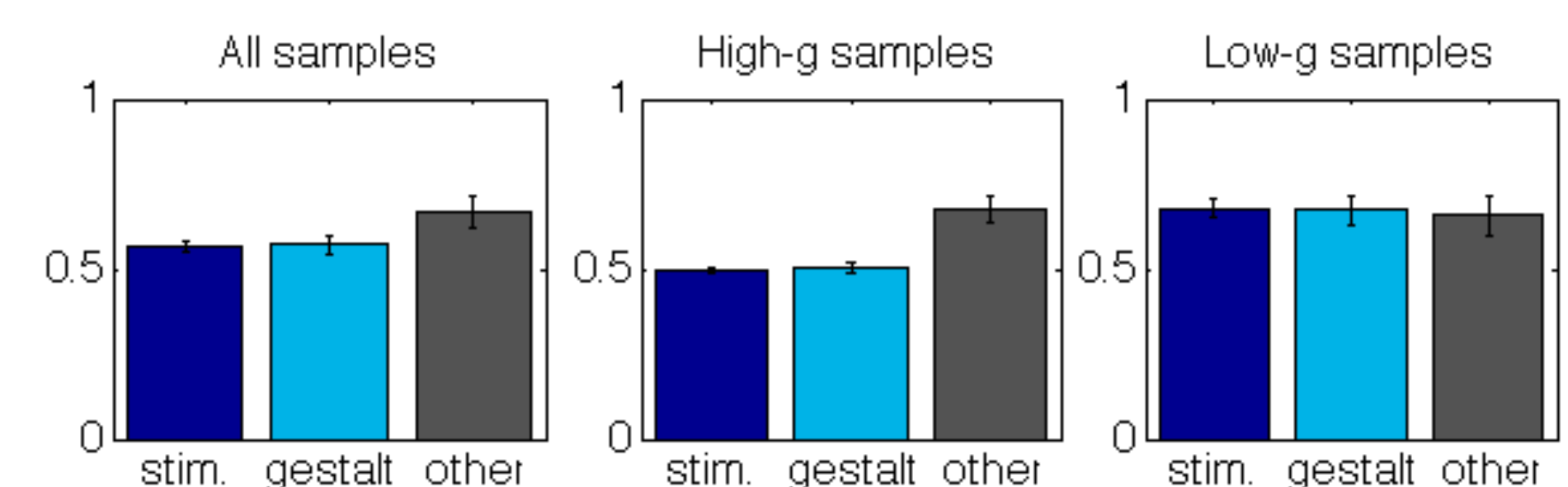
## Predicted correlations

- The model predicts that noise correlations increase with  $g$  activations
- Correlations appear between only congruently activated cells too



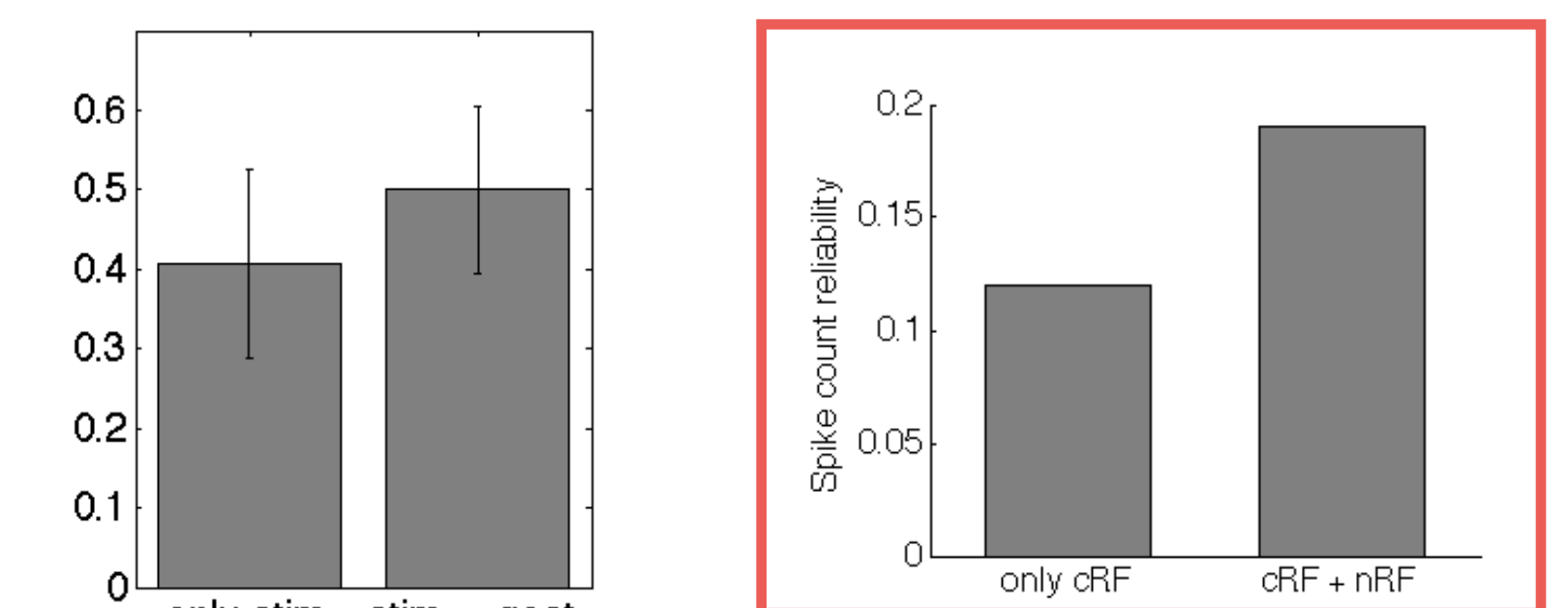
## Variances

- Within-trial variance of stimulated and Gestalt-activated  $v$  units decrease in the model as the  $g$  activation of the covariance component that has them in its receptive field increases



- Haider et al. Neuron, 2010.

report that the spike train reliability of V1 cells increase with non-classical RF activation when added to classical RF stimuli.



## Conclusions

- Gestalt principles can be formalised in a probabilistic generative model
- Inference on the model can be realised as Gibbs sampling
- Firing rates during sampling reproduces the temporal order and the magnitude ratio of activation in cortical areas responding to illusory contours
- The model predicts diminishing variance in cells with Gestalt-activated receptive fields
- Top-down effects may contribute to non-classical receptive field activations
- The model can be trained on a set of stimuli with an EM algorithm
- Contrastive divergence can approximate model parameters and speed up learning

## Acknowledgement

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