



# Neural Coding: Generative Models

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Computational Neuroscience (Lecture 9, 2023/2024)

# Outline of Lecture

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- Natural image statistics
- Generative models
- Sparse Coding and independent components analysis
- Predictive Coding
- Convolutional Neural Networks

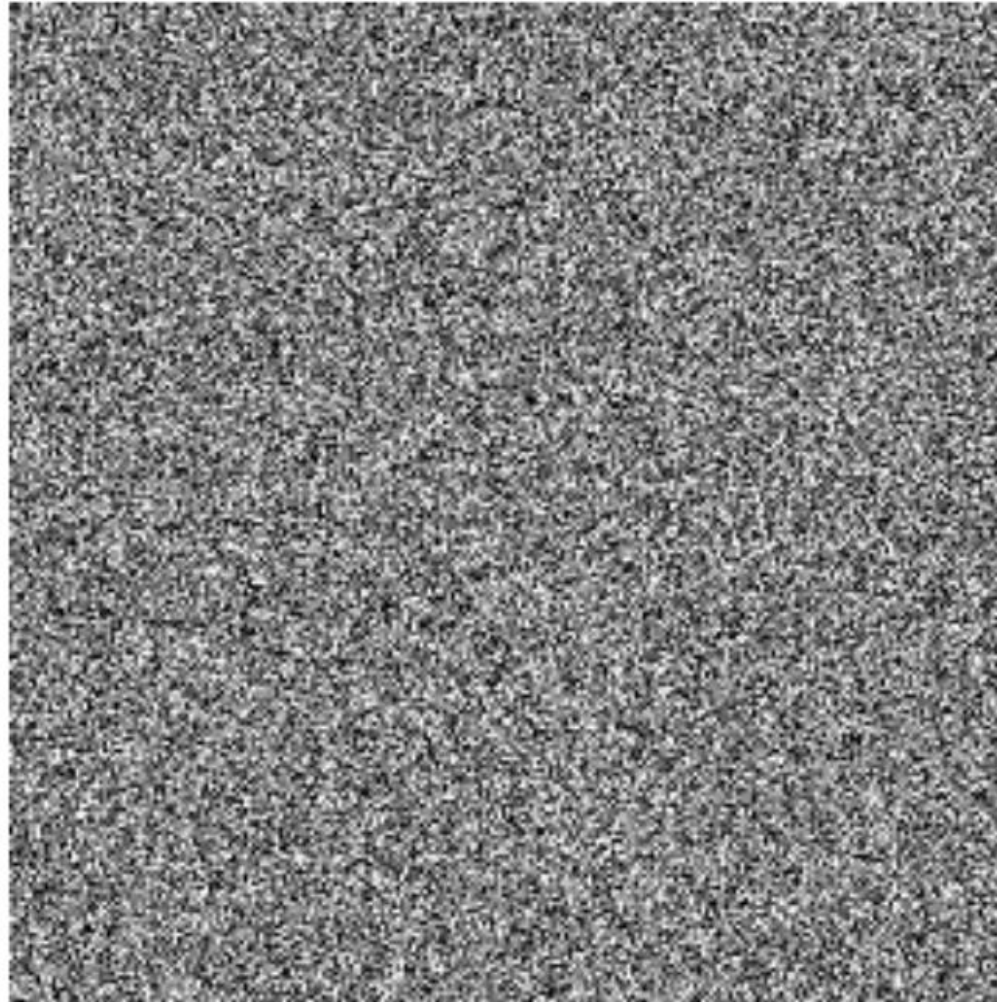
# Redundancy Reduction

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- Statistics of sensory input are highly **redundant**
- For example, neighbouring pixels of an image are highly correlated
- Horace Barlow (and earlier Attneave) hypothesised that sensory systems are designed to minimise redundancy (the **Efficient Coding Hypothesis**)
- One way to do this is to store a **generative model** for the underlying causes of sensory input
- Representing sensory input in terms of latent causes should result in an efficient code
- Basic idea goes back to Helmholtz (perception is “unconscious inference”)

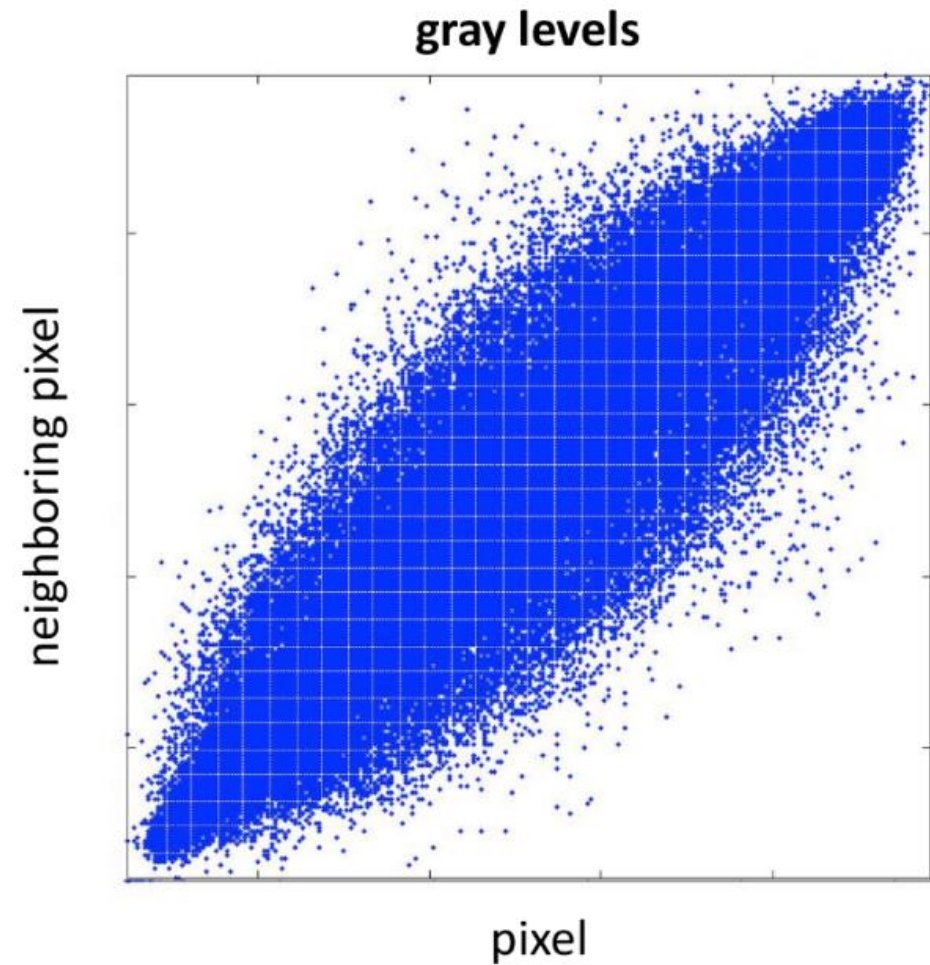
# Natural Image Statistics: First Order

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- An image with first order statistics of natural images but **higher order statistics** removed
- Natural images have an approximately log-normal distribution of pixel intensities

# Natural Image Statistics: Second Order

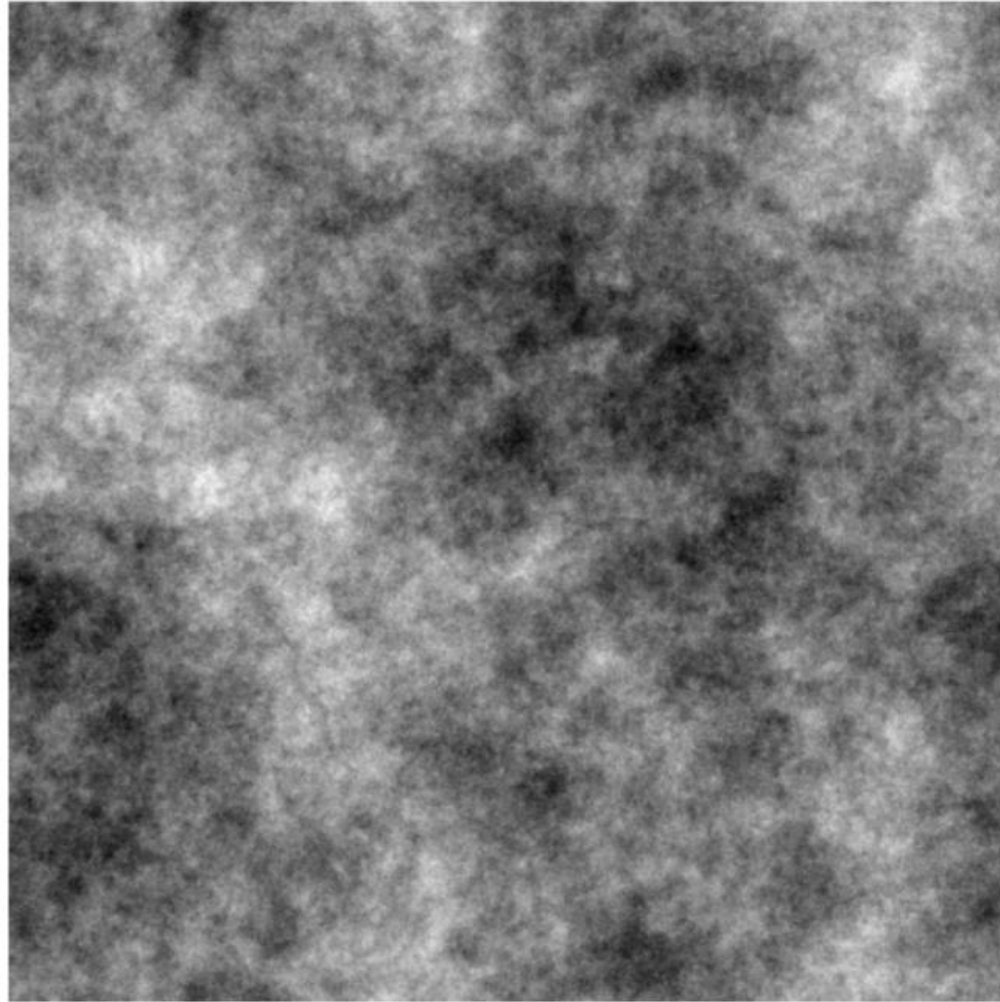


- Correlations between pixel values – can be removed by whitening (e.g. in retina)



# Natural Image Statistics: Second Order

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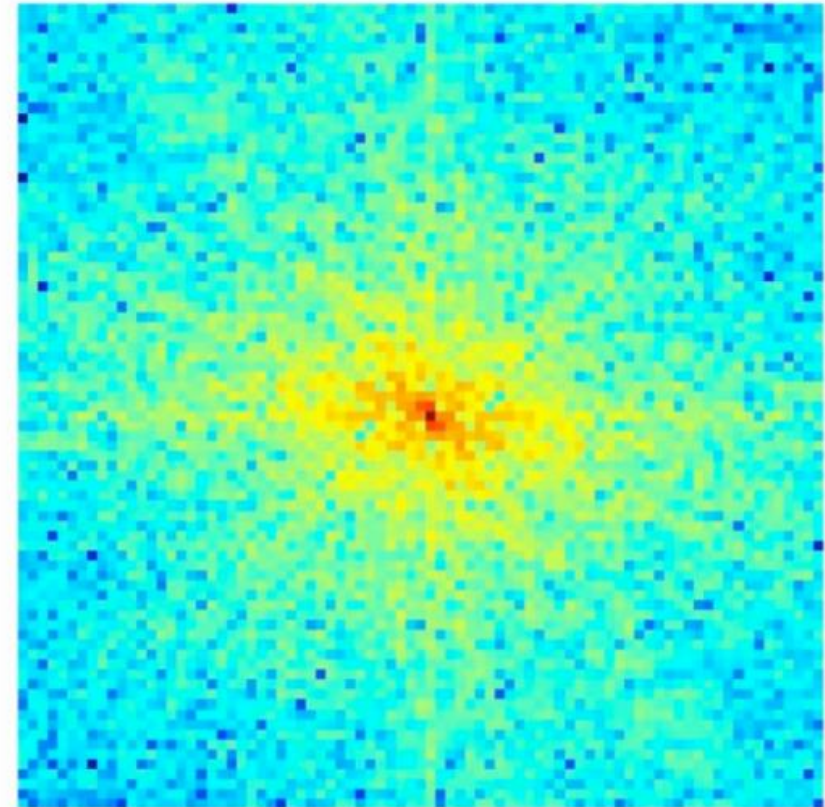


- An image synthesised with 2<sup>nd</sup> order statistics of natural images

# Natural Image Statistics: Higher Order



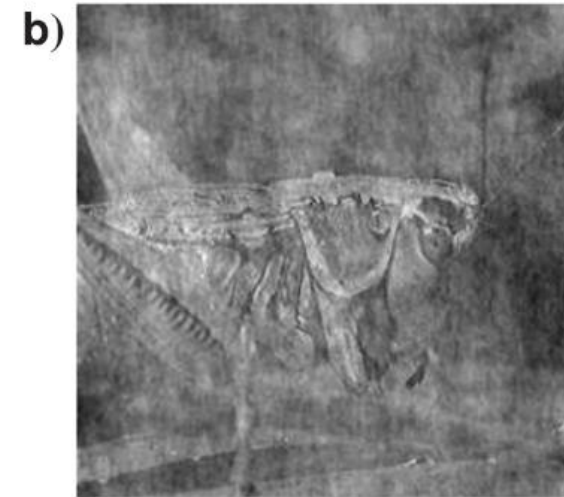
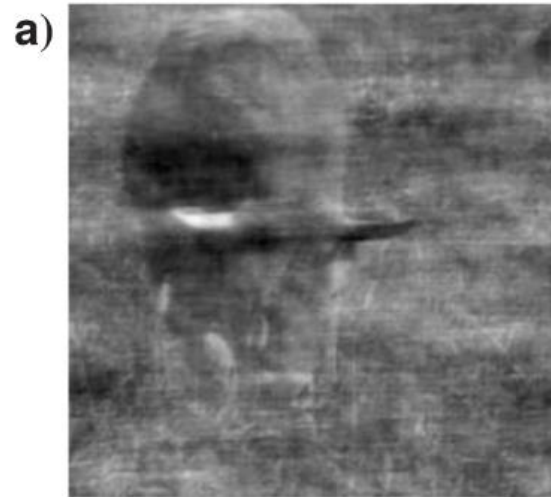
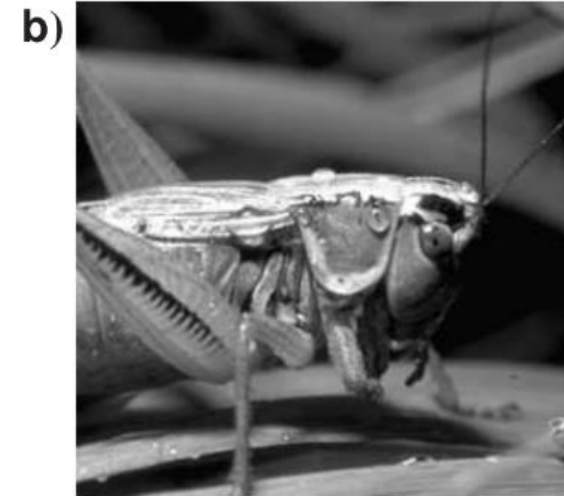
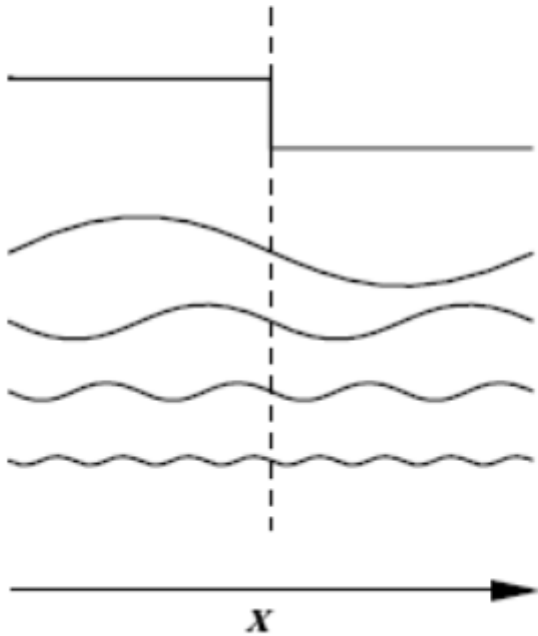
power spectrum



- Correlations between spatial frequencies (4<sup>th</sup> order statistics)

# Natural Image Statistics: Higher Order

Phase alignment



- Phases of different spatial frequencies are correlated



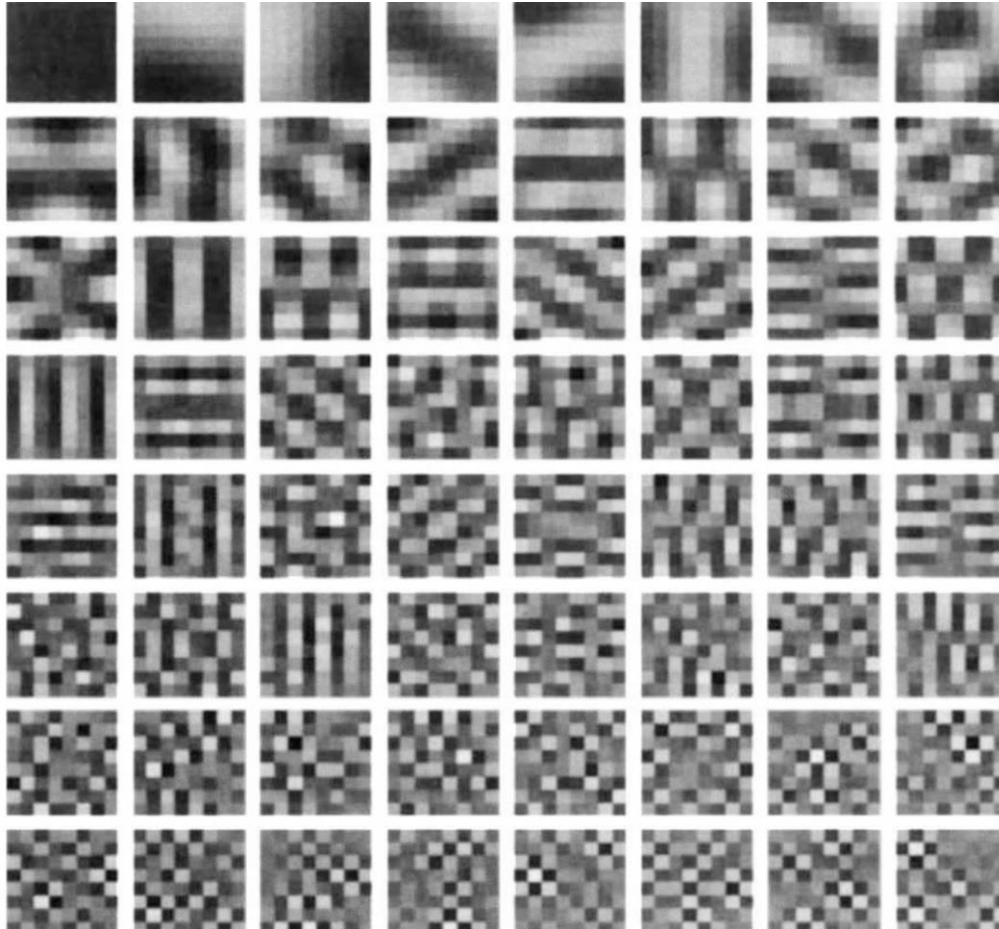
# Natural Image Statistics: Efficient Coding

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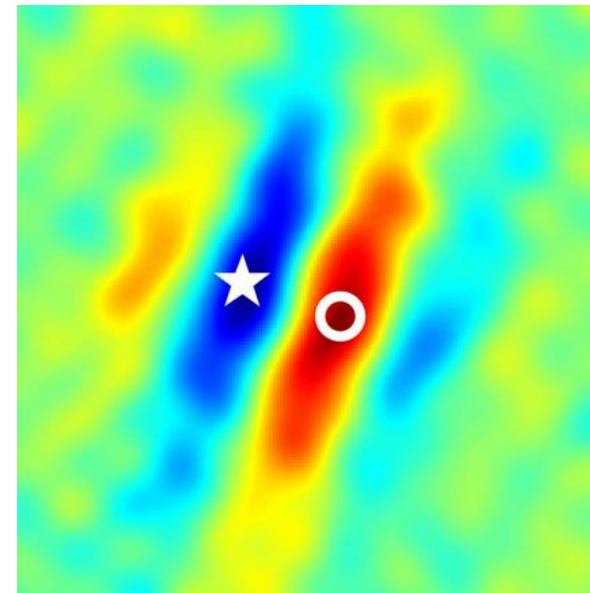
- First-order statistics: histogram equalisation (flatten distribution of pixel intensities)
- Second-order statistics: decorrelation/whitening (flatten power spectrum)
- Higher-order statistics: sparse coding, ICA, etc. can remove some of these
- We don't have any model which removes all statistical dependencies from natural images!

# Features Learned by Principal Components Analysis

Principal Components



V1 receptive field



- PCA captures 2<sup>nd</sup> order statistics of natural images - learned filters are combinations of plane waves at different spatial frequencies. V1 receptive fields look like Gabor filters.

# Natural Image Statistics and the Visual System

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- To efficiently encode natural image statistics, the visual system must find a representation where these statistical dependencies are eliminated
- One way is to store a generative model for natural images. In such a model, images are represented in terms of their underlying *causes*
- Given an image and a generative model, one can perform inference to find these latent causes – maybe this is what the visual system does?
- In addition to being statistically efficient, this should be useful for behaviour – causal elements are things that we need to act on (e.g., objects)

# Generative Models: Learning and Inference

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- Assume a model  $G$  where data  $\mathbf{u}$  are generated by a set of latent causes  $\mathbf{h}$ :  $p(\mathbf{u}|\mathbf{h}, G)$
- We can represent the likelihood of an observation  $\mathbf{u}$  given the generative model  $G$  as:

$$p(\mathbf{u}|G) = \sum_{\mathbf{h}} p(\mathbf{u}|\mathbf{h}, G)p(\mathbf{h}|G)$$



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- Given a model  $G$  and an observation  $\mathbf{u}$ , the probability of a set of latent causes  $\mathbf{h}$  is:

$$p(\mathbf{h}|\mathbf{u}, G) = \frac{p(\mathbf{u}|\mathbf{h}, G)p(\mathbf{h}, G)}{p(\mathbf{u}|G)}$$

- **Learning** of the generative model  $G$  involves maximising the likelihood given a set of observations  $\mathbf{u}$ , while **inference** involves finding the latent causes  $\mathbf{h}$  under a given model  $G$  for a single observation  $\mathbf{u}$

# Generative Models: Examples

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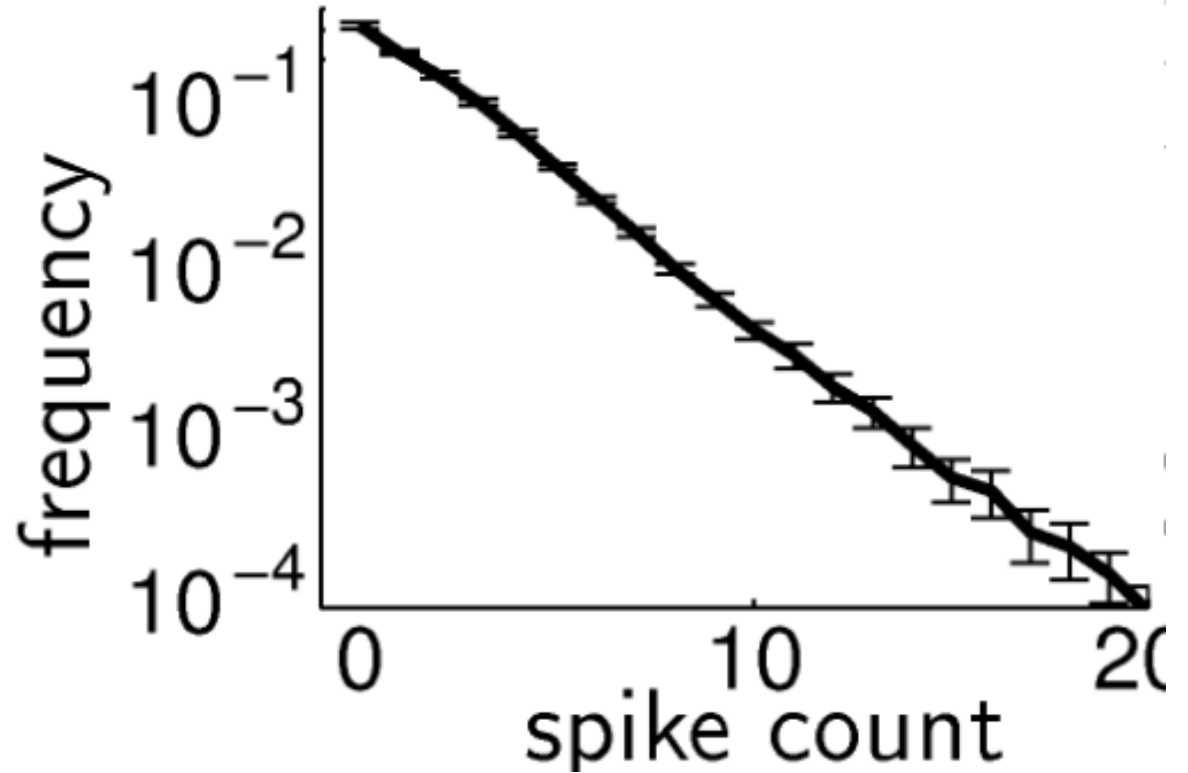
- Mixture of Gaussians
- Factor analysis, probabilistic PCA
- Sparse coding
- Independent components analysis

Note: learning and inference are typically hard problems. We often use approximate methods and/or algorithms like expectation-maximisation.

# Sparse Coding in V1

- **Overcompleteness:** There are many more neurons in V1 than LGN (25:1 in cat). Why?
- **Sparseness:** Neurons in V1 typically fire sparsely in response to natural images/movies  
(exponential firing rate distribution)

Note: Firing is sparser to natural images than to laboratory stimuli.



# Measures of Sparseness

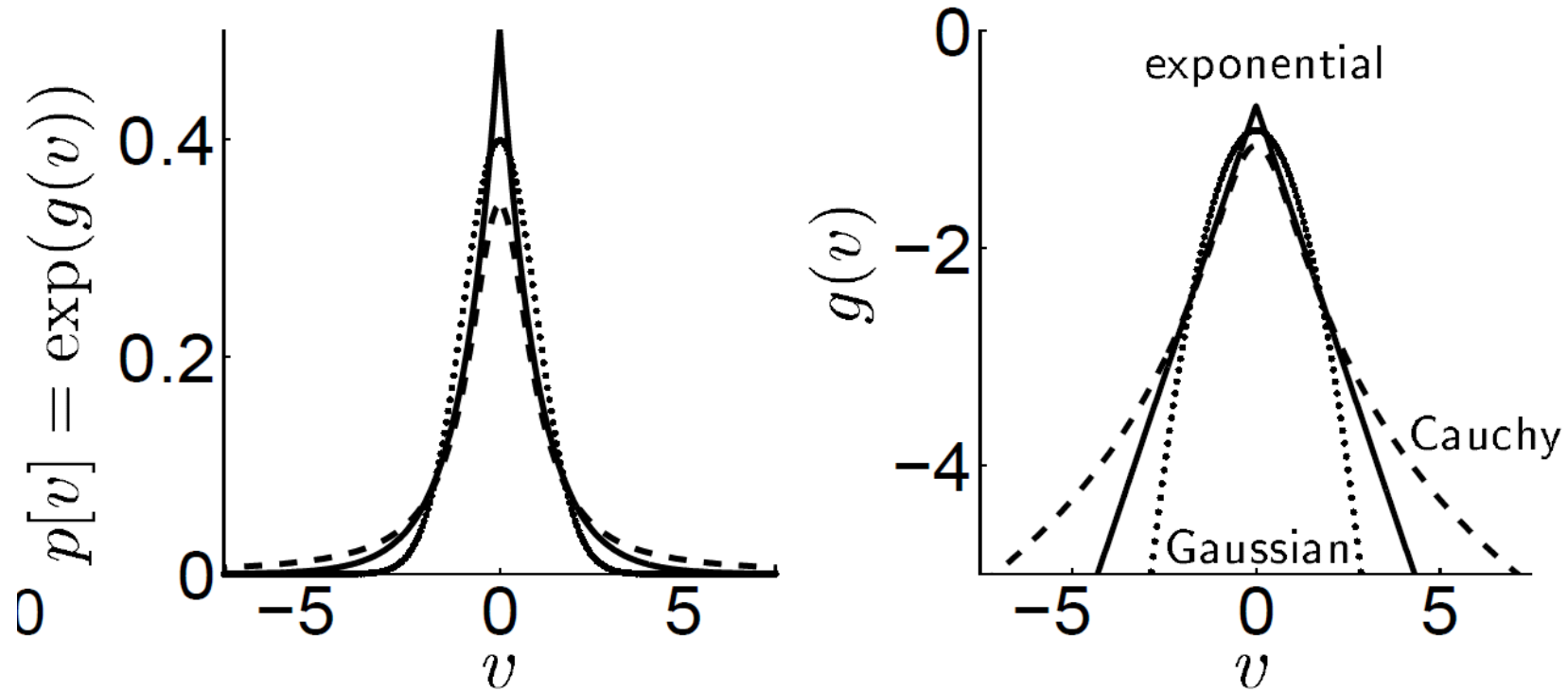
- Distributions that are close to zero most of the time but occasionally far from 0 are called **sparse**
- Sparse distributions are more likely than Gaussians to generate values near to zero and far from zero (heavy tailed)

$$\text{kurtosis} = \frac{\int p(x)(x - \bar{x})^4 dx}{([\int p(x)(x - \bar{x})^2 dx]^2)} - 3$$

- Gaussian has zero **kurtosis**, positive means sparser than Gaussian, negative means less sparse



# Measures of Sparseness



$$p(h) = \exp(g(h))$$

$$\text{exponential: } g(h) = -|h|$$

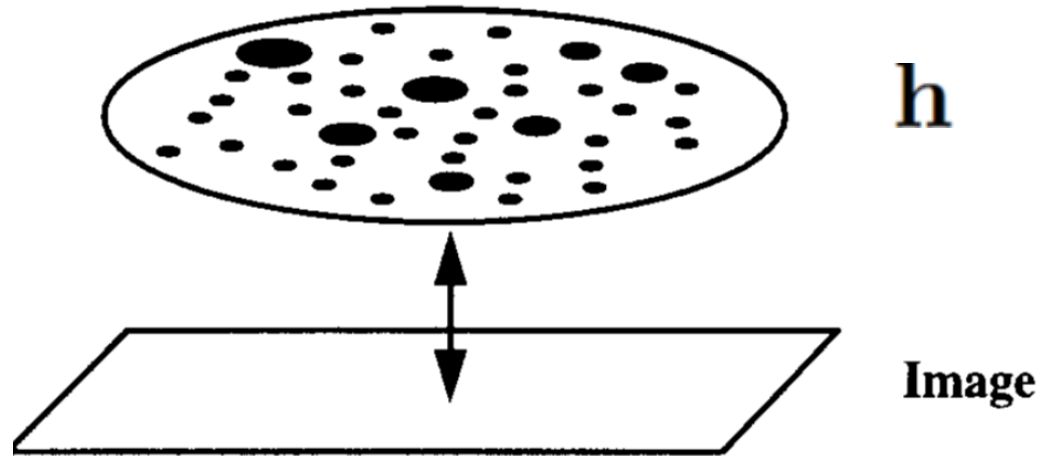
$$\text{Cauchy: } g(h) = -\log(1 + h^2)$$

$$\text{Gaussian: } g(h) = -h^2/2$$

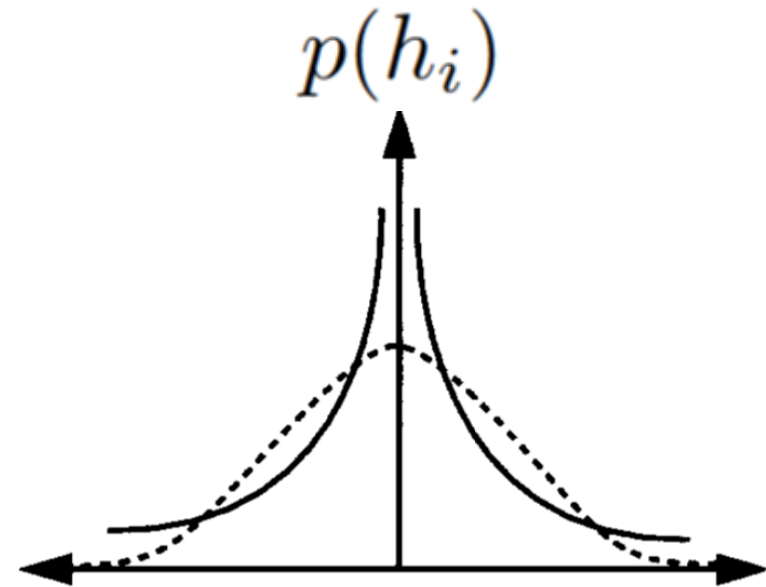
# Sparse Coding: Olshausen and Field

- Postulate a generative model for natural images – **sparse** and **independent** latent causes
- Assume many more latent causes than observed variables (i.e. pixels)
- Fit model to natural images – does anything that looks like V1 emerge?

## Sparse representation



$$\mathbf{u} = B\mathbf{h} + \mathbf{n}$$



# Sparse Coding: Olshausen and Field

**Prior:** 1) independent latent causes (factorial):  $p(\mathbf{h}) = \prod_i p(h_i)$

2) sparse latent causes (exponential or Cauchy)

$$p(h_i) \propto \exp(g(h_i))$$

$$g(h_i) = -|h_i| \qquad g(h_i) = -\log(1 + h_i^2)$$

# Sparse Coding: Olshausen and Field

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**Likelihood:** Linear-Gaussian, from high-D latent causes  $\mathbf{h}$  to lower-D image  $\mathbf{u}$ :

$$p(\mathbf{u}|\mathbf{h}, B) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left[ -\frac{1}{2\sigma^2} \|\mathbf{u} - B\mathbf{h}\|^2 \right]$$



# Learning and Inference

Given a set of images  $\mathbf{u}$ , need to learn a matrix  $B$  and infer coefficients for  $\mathbf{h}$  for each  $\mathbf{u}$ .

**Learning:**  $\langle p(\mathbf{u}|B) \rangle_{\mathbf{u}} = \left\langle \int p(\mathbf{u}|\mathbf{h}, B) p(\mathbf{h}) d\mathbf{h} \right\rangle_{\mathbf{u}}$

**Inference:**  $p(\mathbf{h}|\mathbf{u}, B) \propto p(\mathbf{u}|\mathbf{h}, B) p(\mathbf{h})$

Learning maximises the marginal likelihood of  $B$ , inference maximises the posterior probability of  $\mathbf{h}$  given  $B$  and a single  $\mathbf{u}$

# Inference

Given  $B$ , maximise posterior with respect to  $\mathbf{h}$ :

$$\log p(\mathbf{h}|\mathbf{u}, B) = -\frac{1}{2\sigma^2} \|\mathbf{u} - B\mathbf{h}\|^2 + \sum_i g(h_i) + \text{const}$$

$$\nabla \log p(\mathbf{h}|\mathbf{u}, B) = \frac{1}{\sigma^2} B^T [\mathbf{u} - B\mathbf{h}] + g'(\mathbf{h})$$

# Inference

Given  $B$ , maximise posterior with respect to  $\mathbf{h}$ :

$$\log p(\mathbf{h}|\mathbf{u}, B) = -\frac{1}{2\sigma^2} \|\mathbf{u} - B\mathbf{h}\|^2 + \sum_i g(h_i) + \text{const}$$

$$\nabla \log p(\mathbf{h}|\mathbf{u}, B) = \frac{1}{\sigma^2} B^T [\mathbf{u} - B\mathbf{h}] + g'(\mathbf{h})$$

Solve via “coordinate ascent”:  $\mathbf{h}_{t+1} = \mathbf{h}_t + \epsilon \nabla \log p(\mathbf{h}_t|\mathbf{u}, B)$

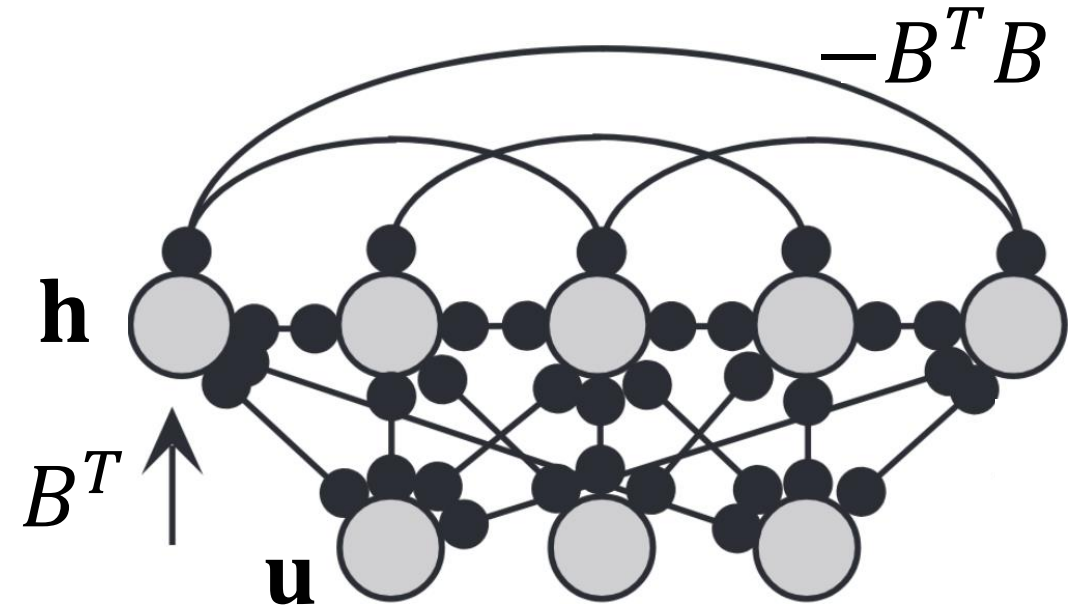
Converges to local minimum (or perhaps saddle point)

# Inference: Network Interpretation

Can also be written in terms of dynamics of a network of neurons:

$$\mathbf{h}_{t+1} = \mathbf{h}_t + \epsilon \nabla \log p(\mathbf{h}_t | \mathbf{u}, B)$$

$$\tau \frac{d\mathbf{h}}{dt} = \frac{1}{\sigma} B^T [\mathbf{u} - B\mathbf{h}] + g'(\mathbf{h})$$



Caption

[Figure: Dayan and Abbott]

The network can be interpreted as LGN and V1, with recurrent weights between V1 neurons enforcing the prior and causing convergence to the MAP solution via the network dynamics

# Learning

How do we learn the matrix  $B$  for a given set of images  $\mathbf{u}$ ?

$$\hat{B} = \operatorname{argmax} (\langle p(\mathbf{u}|B) \rangle_{\mathbf{u}}) = \operatorname{argmax} \left( \left\langle \int d\mathbf{h} p(\mathbf{u}|\mathbf{h}, B) p(\mathbf{h}) \right\rangle_{\mathbf{u}} \right)$$

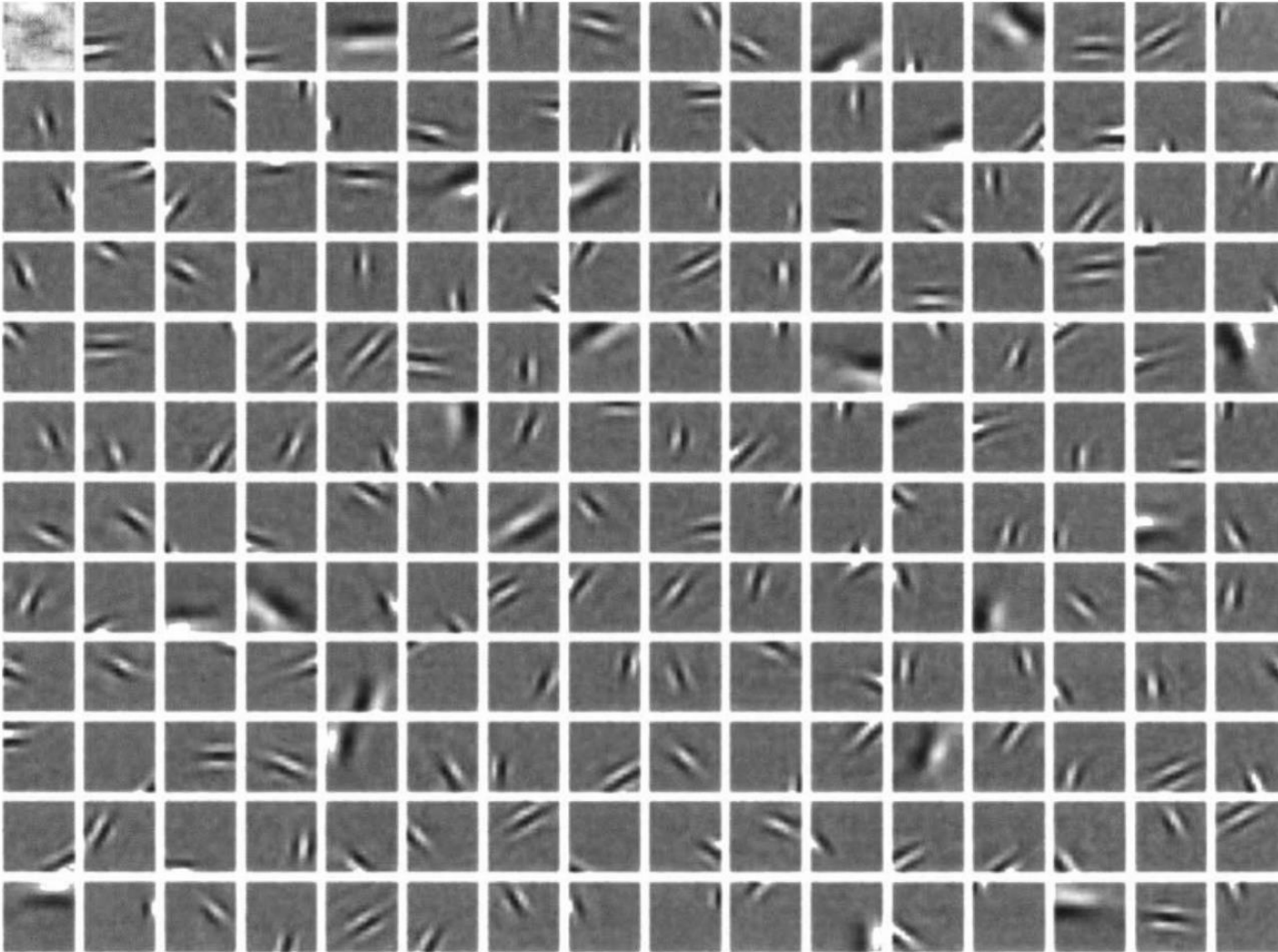
Optimising this is hard due to the integral over the high-dimensional vector  $\mathbf{h}$ . Learning can be slow to converge.

Olshausen and Field used an approximate posterior to speed up learning (see Dayan and Abbott Ch. 10).

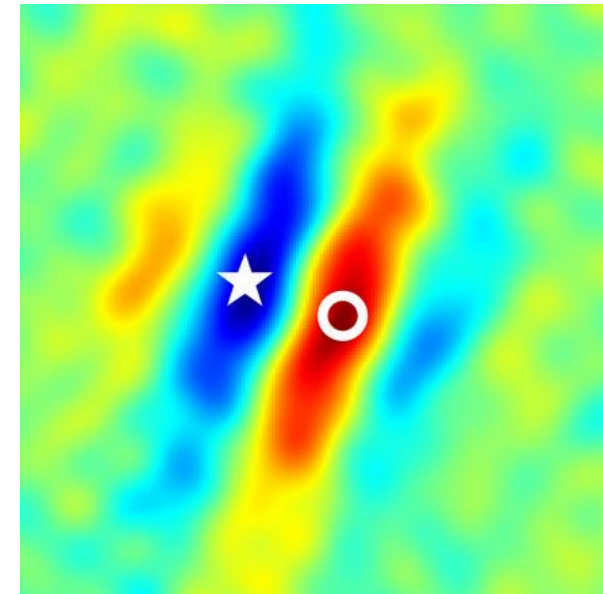
# Gabor Receptive Fields via Sparse Coding

- V1-like receptive fields emerge naturally when this algorithm is trained on natural images.

Rows of  $B$  matrix



V1 receptive field

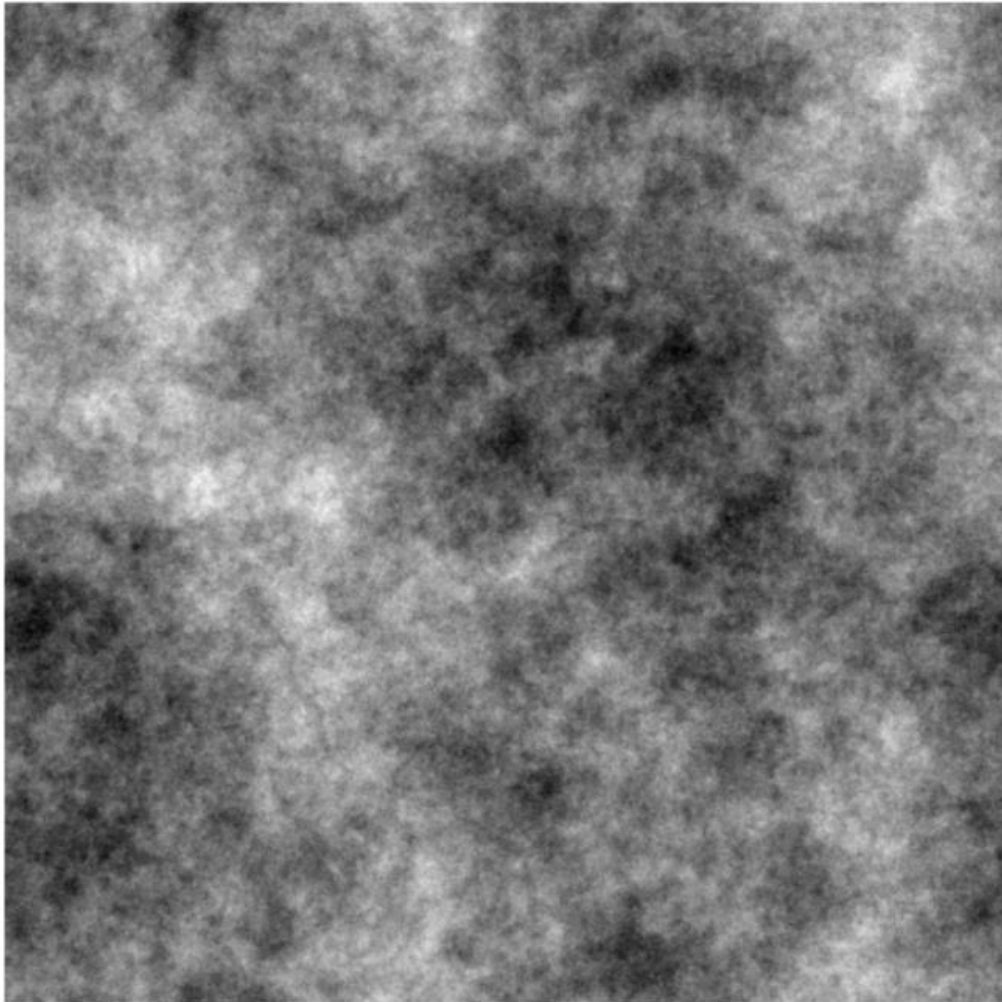


*[Figure Olshausen and Field (1996)]*

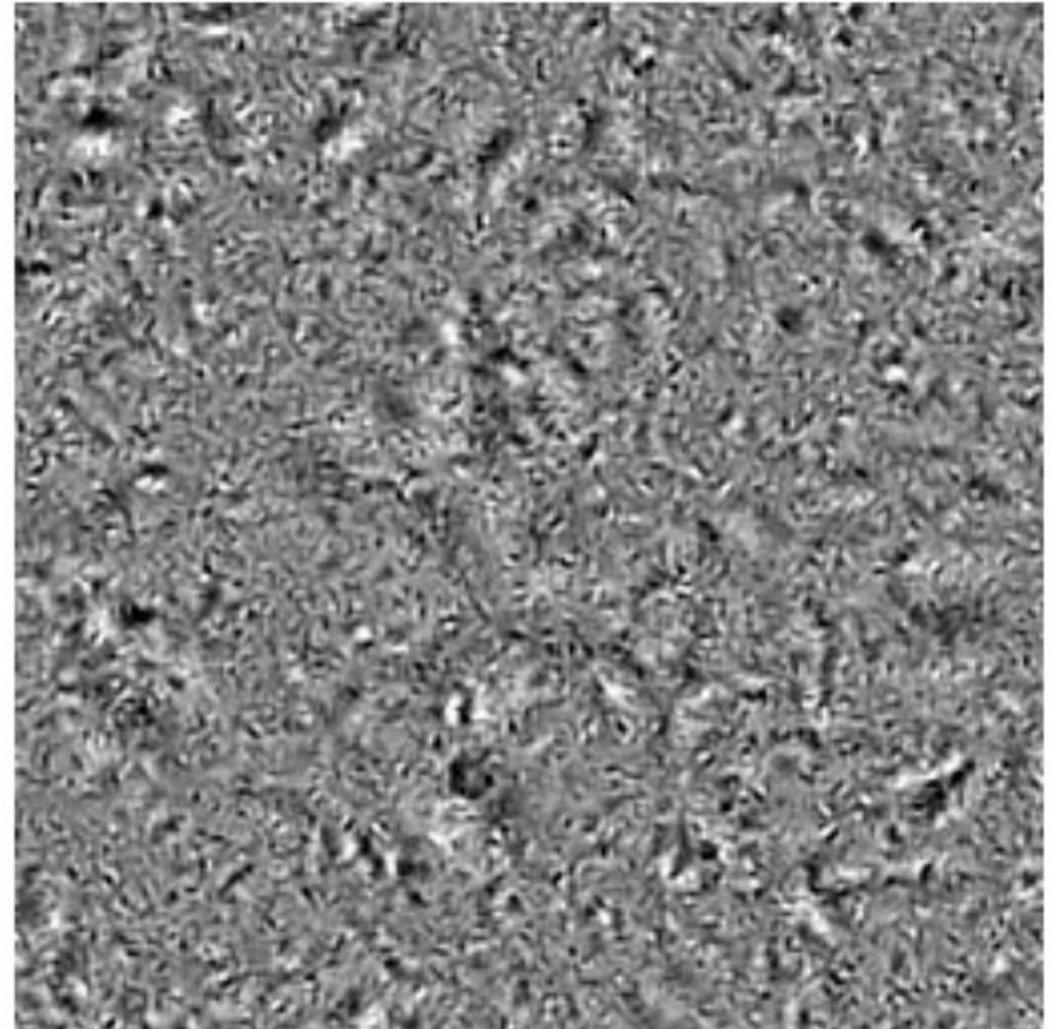


# Image Synthesis via Sparse Coding

2<sup>nd</sup> Order Statistics Model



Sparse Coding Model





# Limitations of Sparse Coding

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- Model assumptions are ad hoc (why sparse?)
- Learned causes are not independent (e.g., edges), violating assumption of model
- Converges to local minimum, sometimes learns multiple copies of same filter
- Choice of number of latent variables, and other hyperparameters is also ad hoc
- Have to whiten images first, otherwise just learns PCA
- Better models involve hierarchies of latent causes (objects, occlusion, luminance, etc.)

# Summary: Sparse Coding

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- A linear-Gaussian generative model for natural images
- Assumes overcomplete representation (more latents than observed), similar to LGN-V1 cell numbers
- Assumes sparse and independent latent causes
- Gabor filters emerge when trained on natural images
- First model to derive a computational account of V1 receptive fields

# Independent Components Analysis

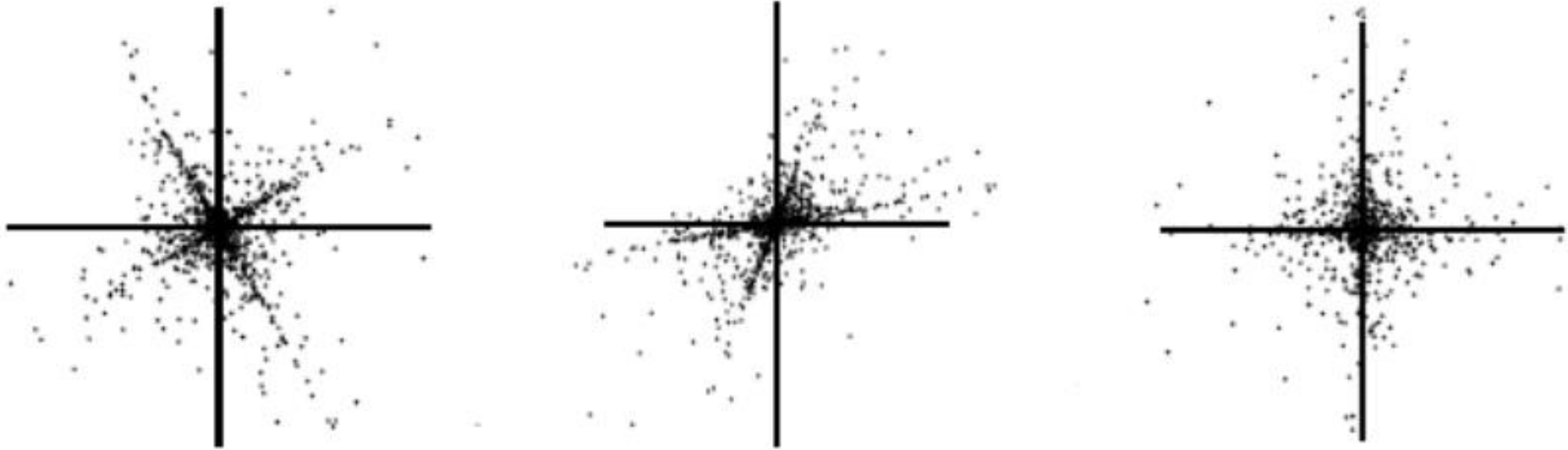
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- A similar approach to sparse coding: use a linear generative model (this time with no noise)

$$\mathbf{u} = B\mathbf{h}$$

- Assume that there are sparsely active latent variables  $\mathbf{h}$  that mix to form the observed signal  $\mathbf{u}$  – goal is to unmix them
- General idea – adding independent random variables yields something more Gaussian (central limit theorem).
- A number of objectives can be used: maximise mutual information between  $\mathbf{u}$  and  $\mathbf{h}$  (infomax); maximise non-Gaussianity (e.g., Kurtosis), etc.

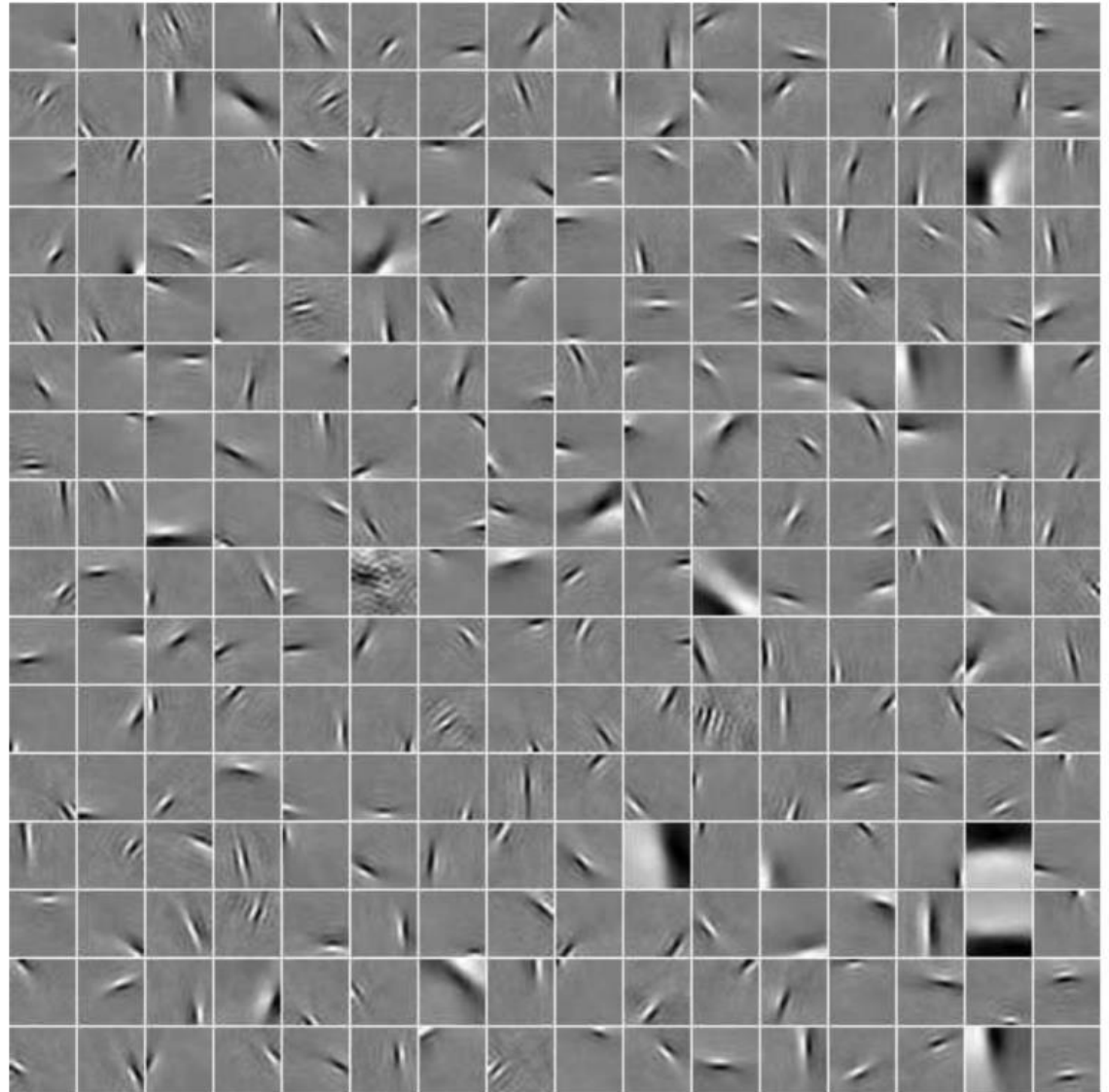
# Independent Components Analysis



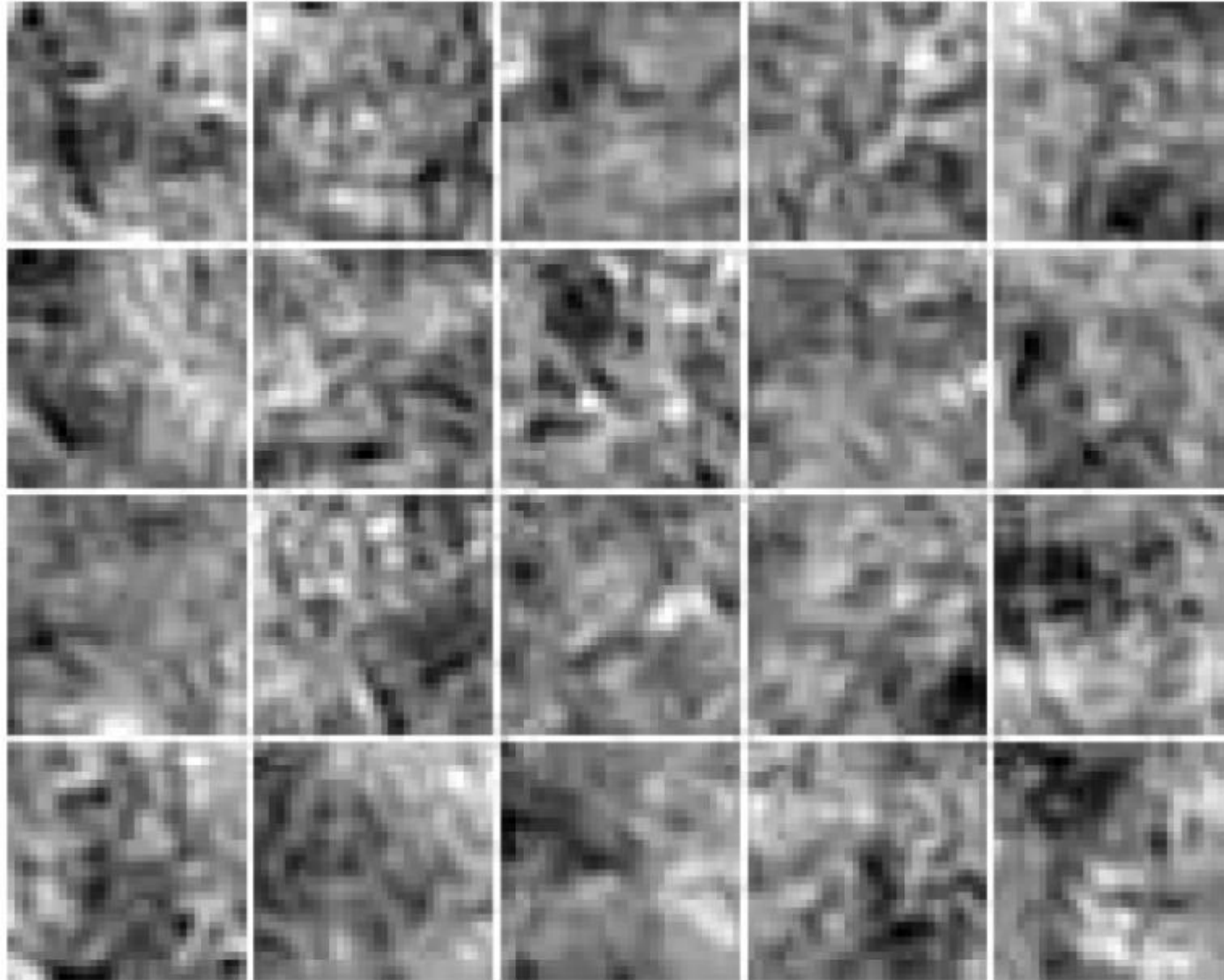
- Middle: observed data, constructed by two mixed independent components
- Left: apply PCA, whitens the data via rotation and scaling (x and y uncorrelated but still dependent)
- Right: apply ICA, x and y are now independent (but not Gaussian)

# ICA: Learned Receptive Fields

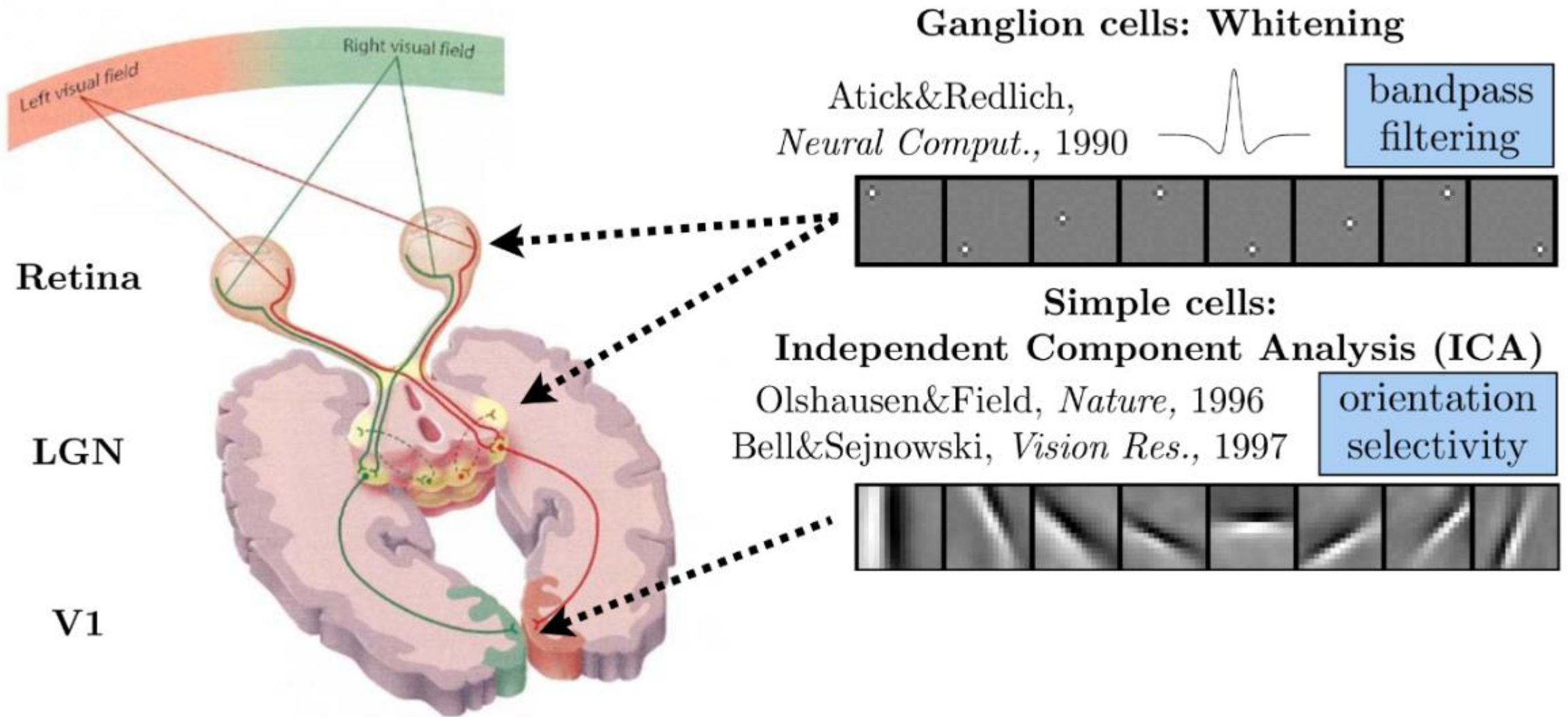
- ICA filters also match V1 receptive fields



# ICA: Synthesised Images



# The Early Visual System: Whitening + ICA/Sparse Coding



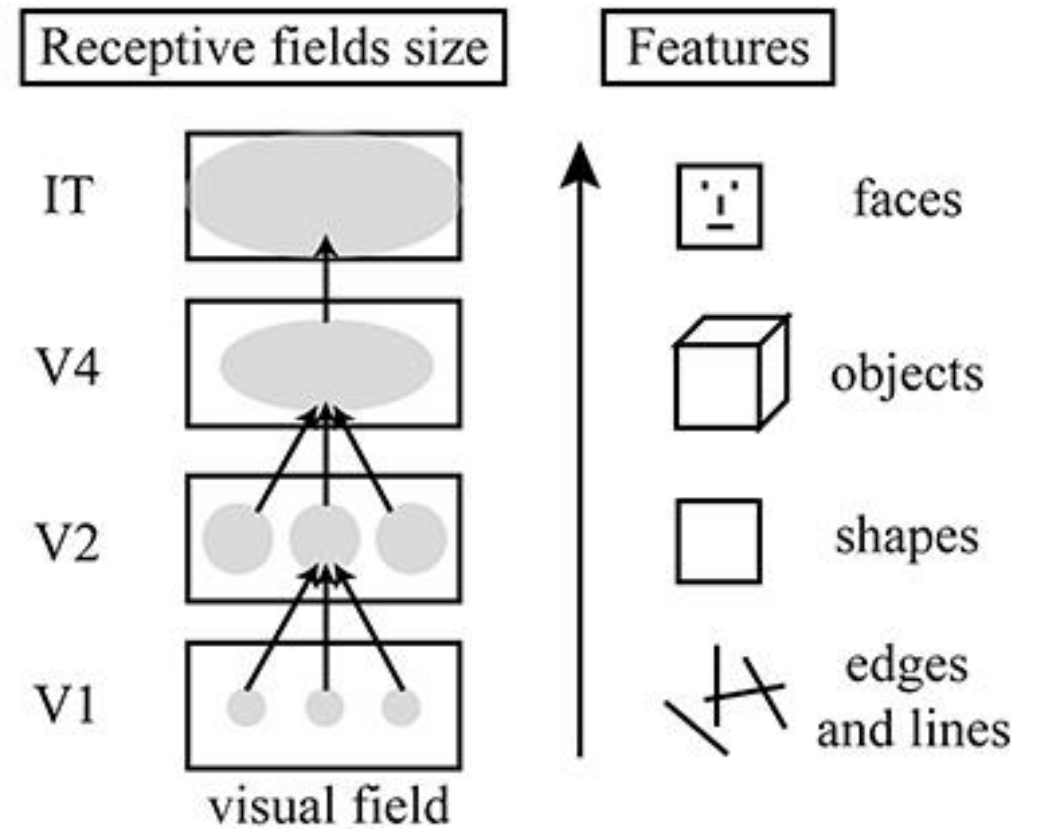
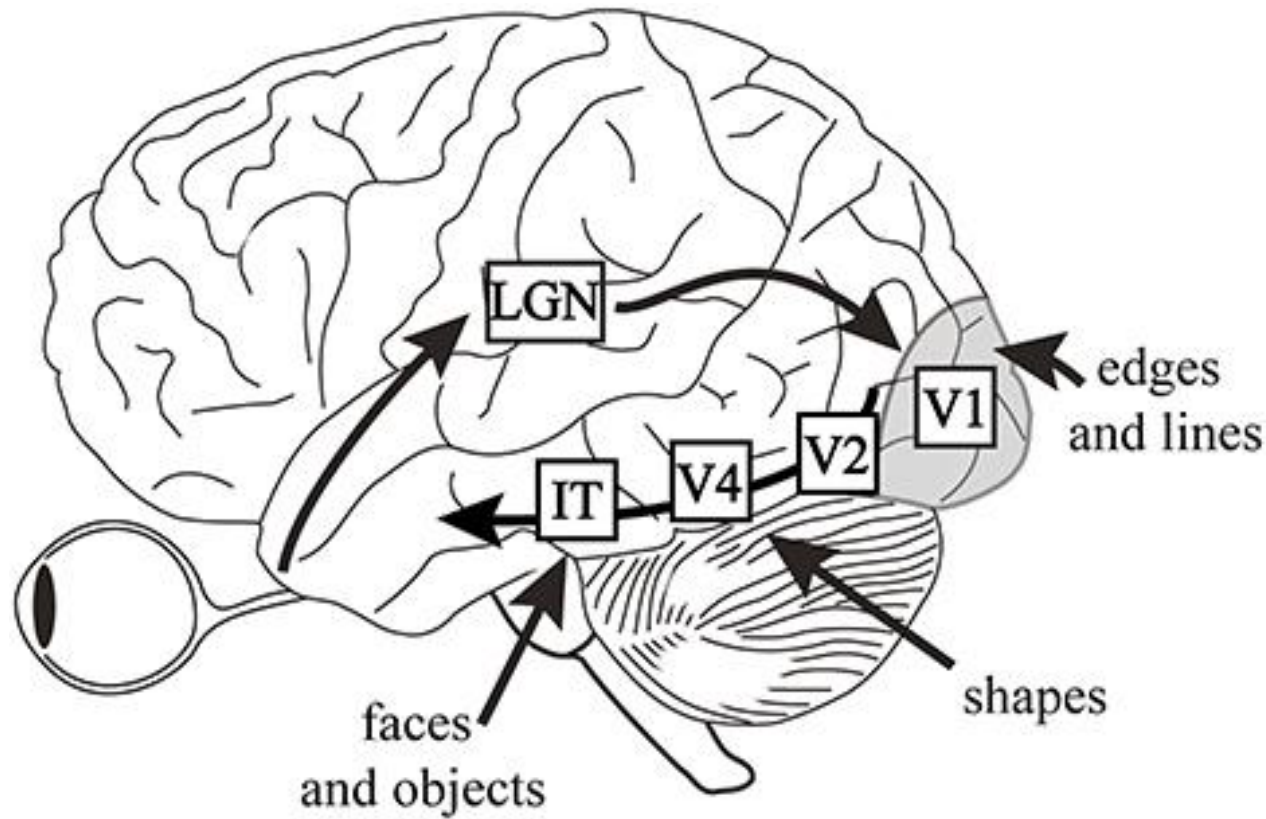


# Sparse Coding vs ICA

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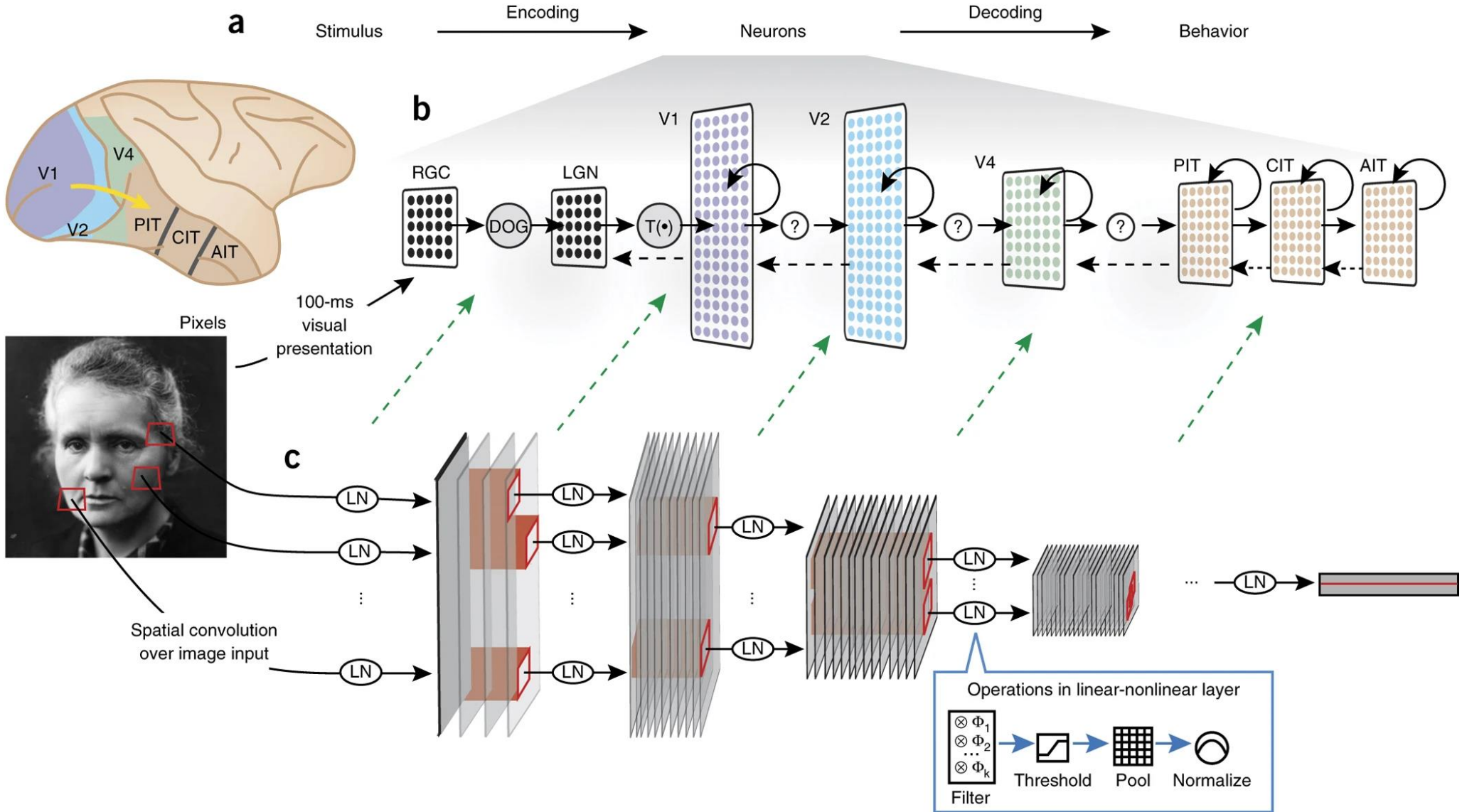
- Both are linear generative models
- Both reproduce V1-like receptive fields (as do various other algorithms)
- Both generate sparse output for natural images
- Different objectives/algorithms (ICA: maximise information/non-Gaussianity, SC: sparse overcomplete representation)
- Both fail to capture representations in higher visual brain areas - independent components aren't independent! (but some work has been done to address this...)

# Higher Visual Processing



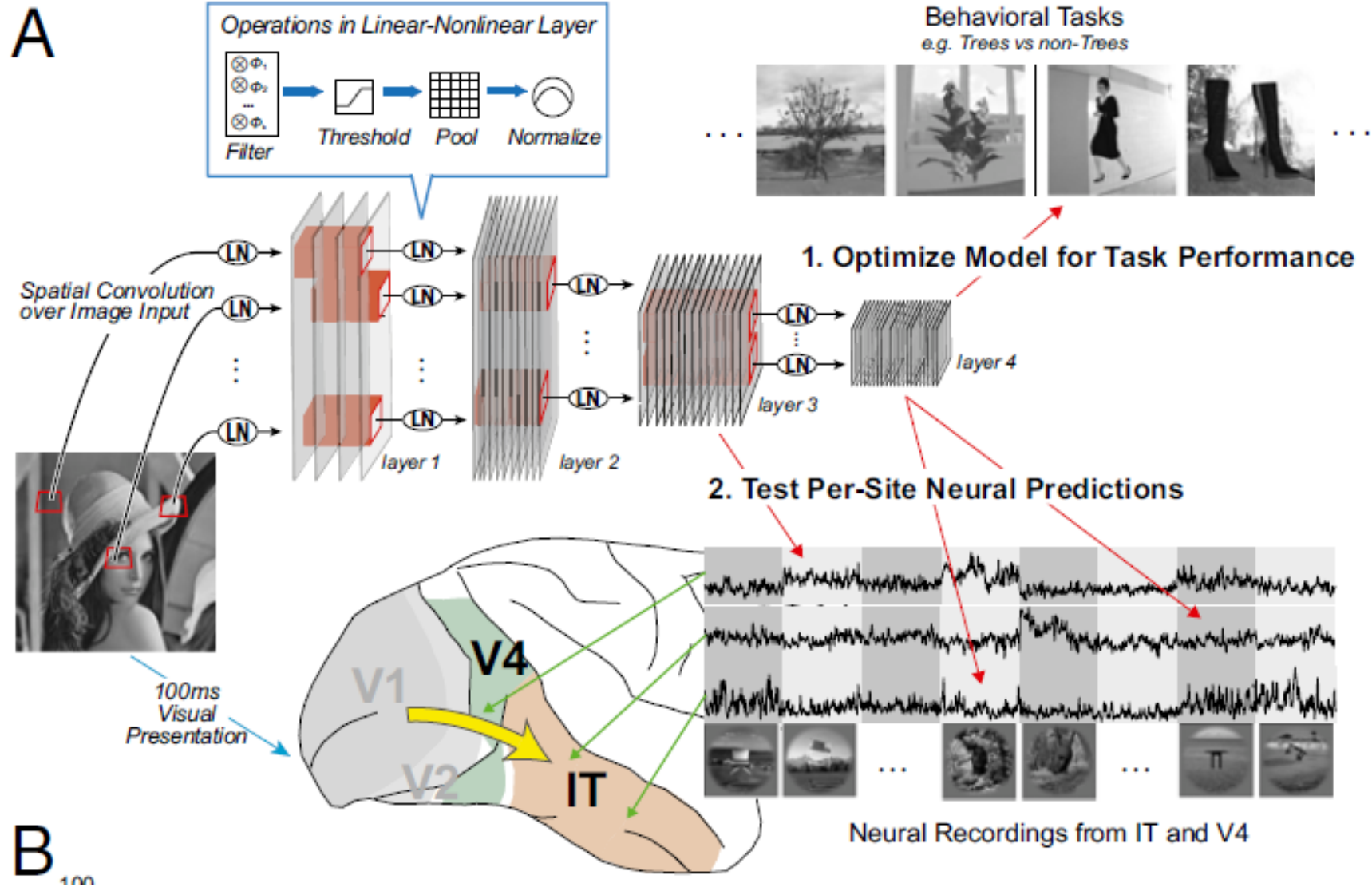
# Convolutional Neural Networks

Do CNNs resemble the visual system?



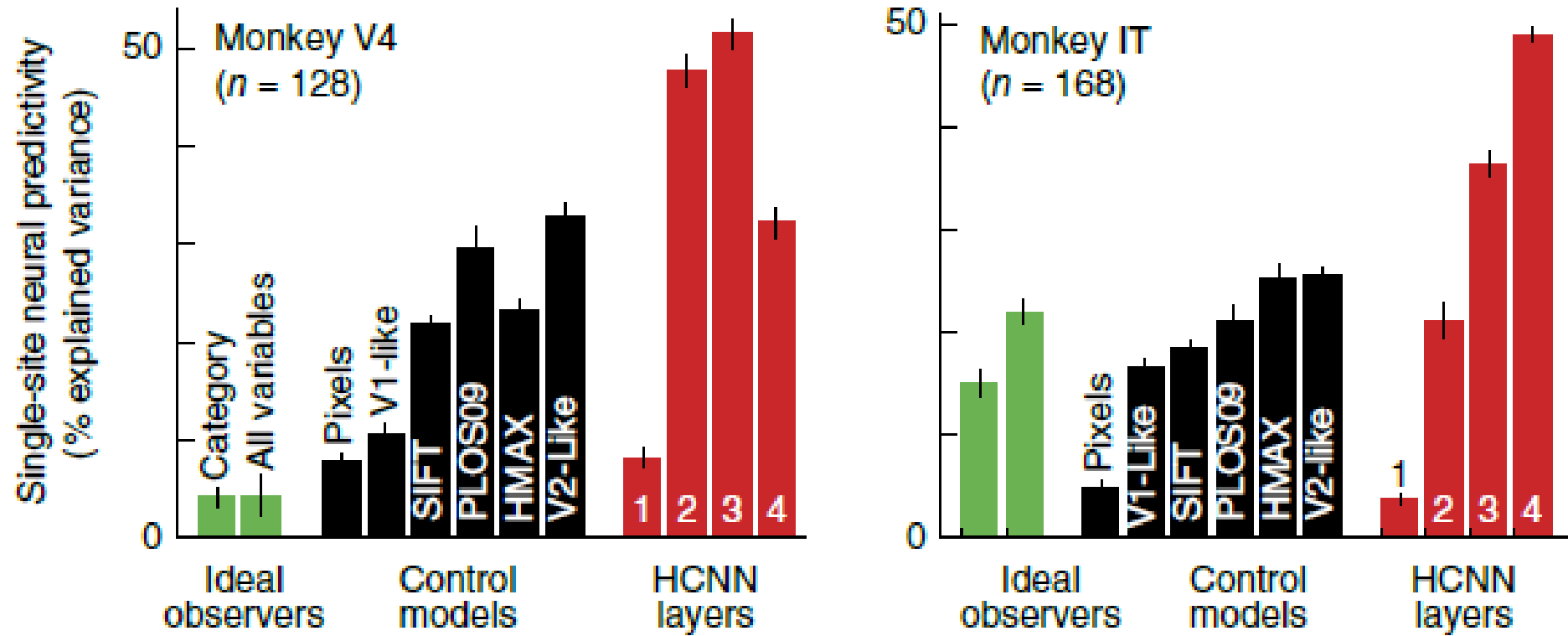
# Convolutional Neural Networks

Train CNNs to categorise images, compare learned representations to visual system



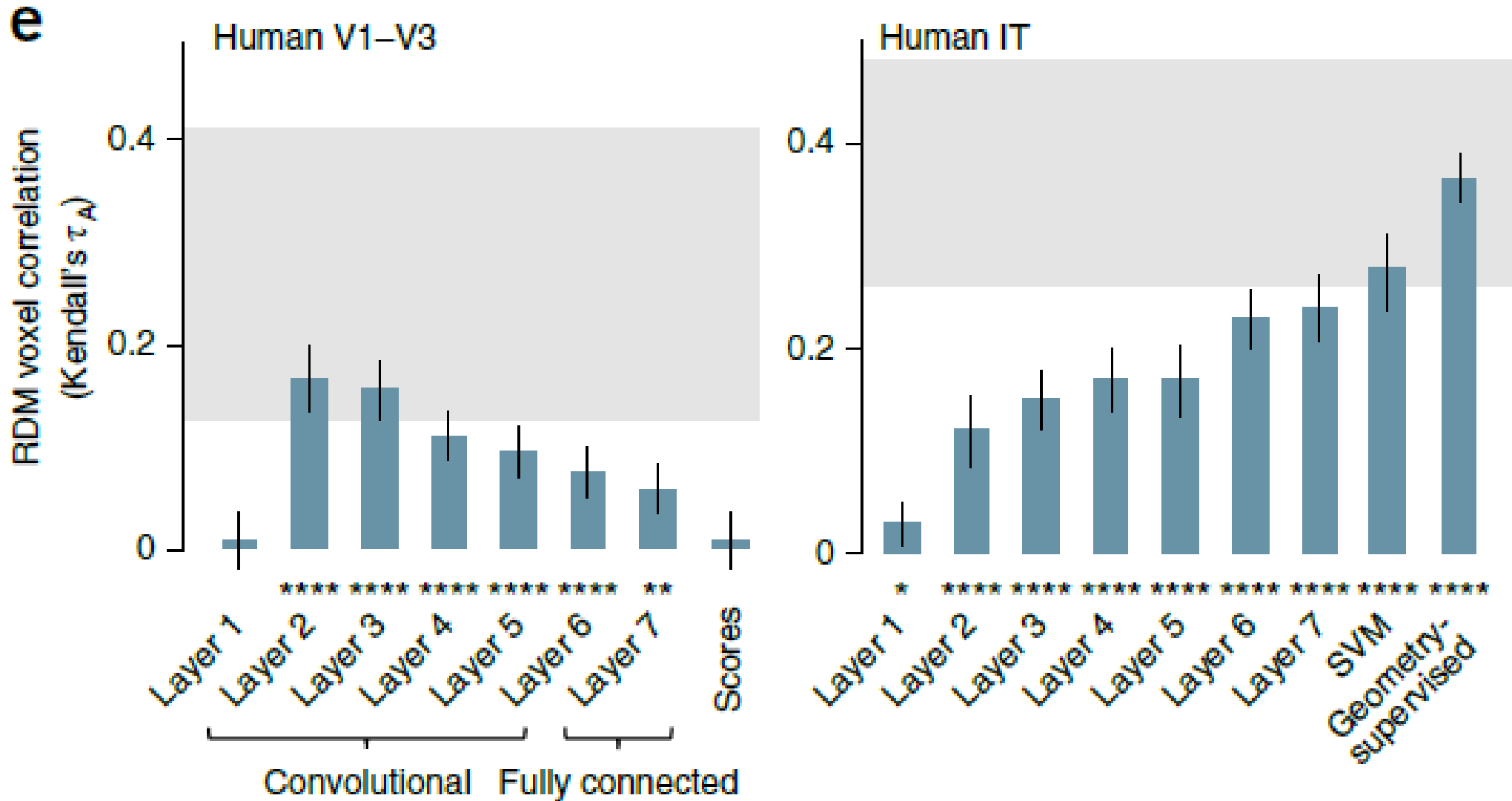
# Convolutional Neural Networks

CNN responses better resemble higher visual system layers than other models



# Convolutional Neural Networks

Layers of the CNN roughly correspond to the layers of the visual system



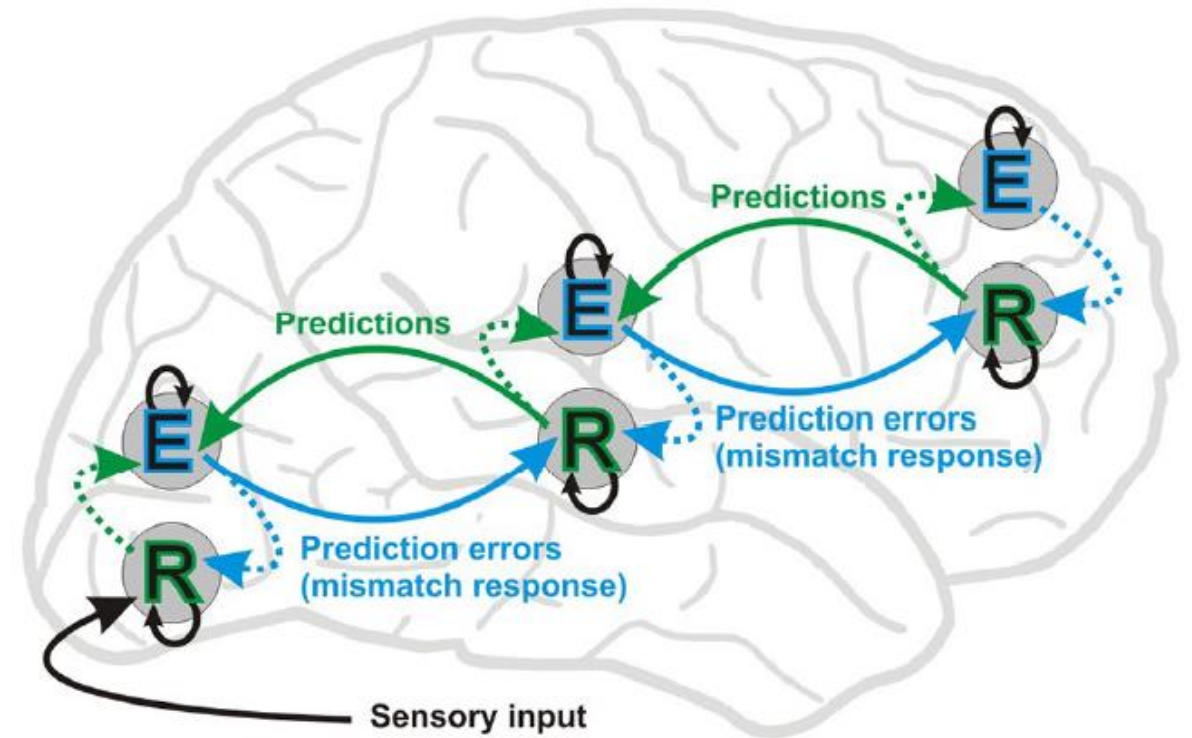
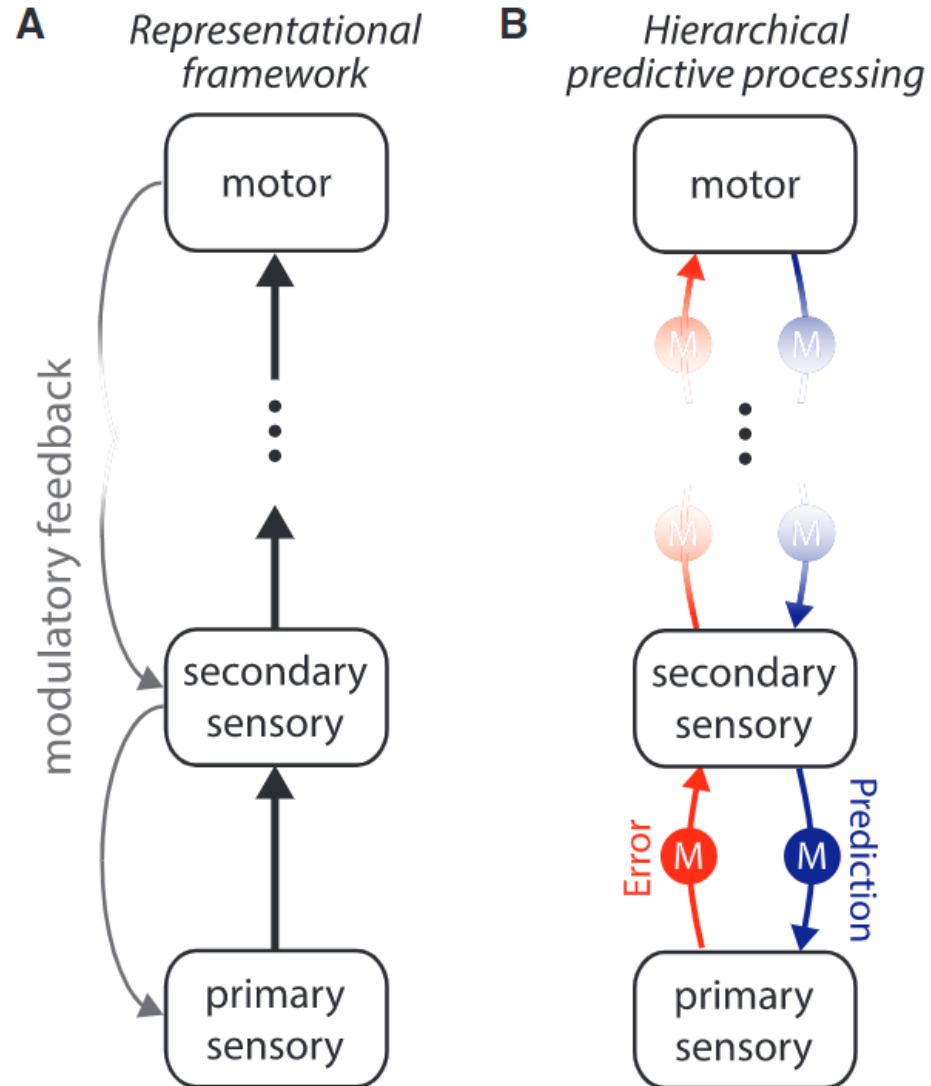
# Convolutional Neural Networks: Summary

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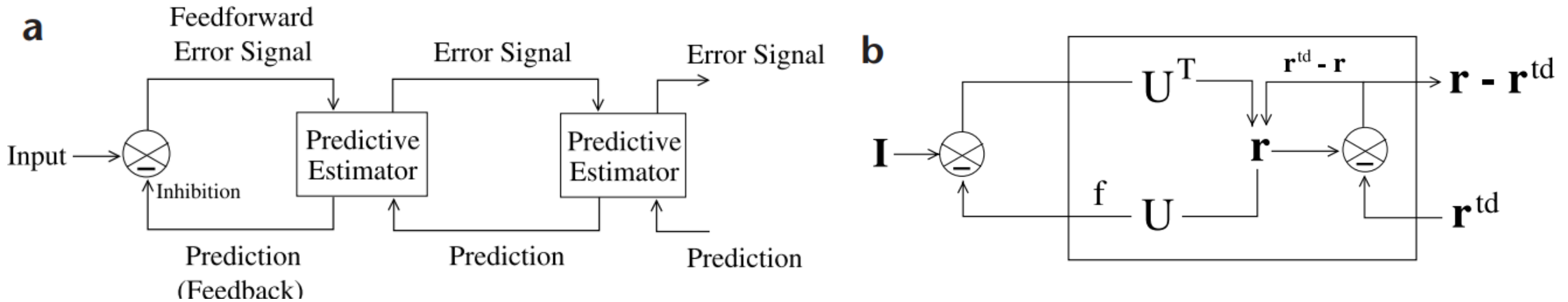
- CNNs are discriminative, not generative models
- CNNs are supervised, the brain doesn't get much supervision (mostly reward/punishment)
- CNNs use backprop, the brain can't use backprop (backprop is non-local)
- Nonetheless, when trained on natural images, CNNs reproduce aspects of the visual system, including deeper layers
- A less principled approach than generative models, and less biologically plausible in terms of learning, but generative models struggle to capture deeper layers of the visual system



# Role of Feedback: Predictive Coding



# Predictive Coding: Generative Model



Predictive coding uses the following Hierarchical Generative Model

$$\mathbf{I} = f(\mathbf{U}\mathbf{r}) + \mathbf{n} \quad \mathbf{r} = \mathbf{r}^{td} + \mathbf{n}^{td} \quad \mathbf{r}^{td} = f(\mathbf{U}^h \mathbf{r}^h)$$

$\mathbf{I}$  is the image,  $\mathbf{U}$  is a learned matrix, and  $\mathbf{n}$  is Gaussian noise.

This represents a single layer of the hierarchy, which can be stacked to create more layers.

# Predictive Coding: Learning and Inference

The generative model has the following negative log likelihood:

$$E_1 = \frac{1}{\sigma^2} (\mathbf{I} - f(\mathbf{U}\mathbf{r}))^T (\mathbf{I} - f(\mathbf{U}\mathbf{r})) + \frac{1}{\sigma_{td}^2} (\mathbf{r} - \mathbf{r}^{td})^T (\mathbf{r} - \mathbf{r}^{td})$$

Adding a prior gives the negative log posterior:  $E = E_1 + g(\mathbf{r}) + h(\mathbf{U})$

Where  $g$  and  $h$  set the priors on  $\mathbf{r}$  and  $\mathbf{U}$  respectively. A sparse prior can be used for  $\mathbf{r}$ .

# Predictive Coding: Learning and Inference

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Adding a prior gives the negative log posterior:  $E = E_1 + g(\mathbf{r}) + h(\mathbf{U})$

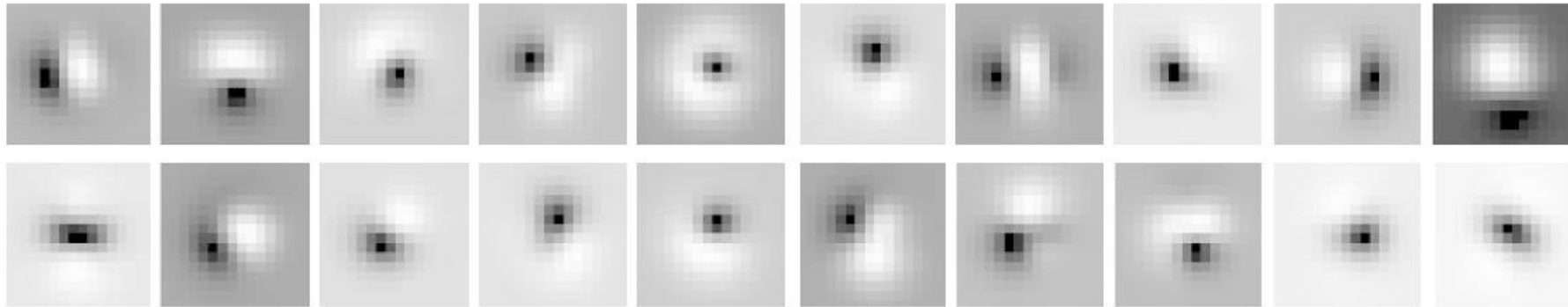
Where  $g$  and  $h$  set the priors on  $\mathbf{r}$  and  $\mathbf{U}$  respectively. A sparse prior can be used for  $\mathbf{r}$ .

Gradient descent on  $E$  can be written in terms of the dynamics of  $\mathbf{r}$ :

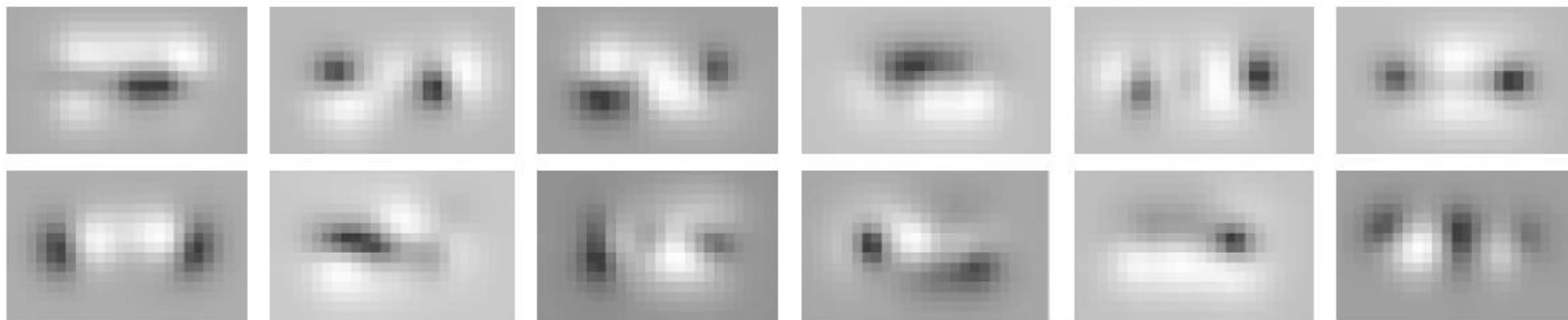
$$\frac{d\mathbf{r}}{dt} = -\frac{k_1}{2} \frac{\partial E}{\partial \mathbf{r}} = \frac{k_1}{\sigma^2} \mathbf{U}^T \frac{\partial f^T}{\partial \mathbf{x}} (\mathbf{I} - f(\mathbf{U}\mathbf{r})) + \frac{k_1}{\sigma_{td}^2} (\mathbf{r}^{td} - \mathbf{r}) - \frac{k_1}{2} g'(\mathbf{r})$$

# Predictive Coding: Learned Representations

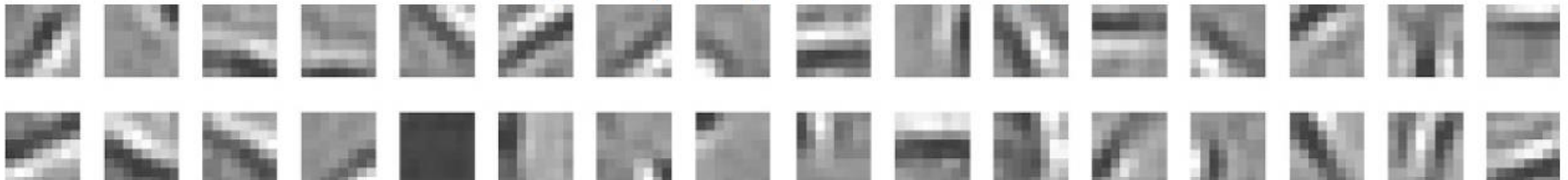
Level 1



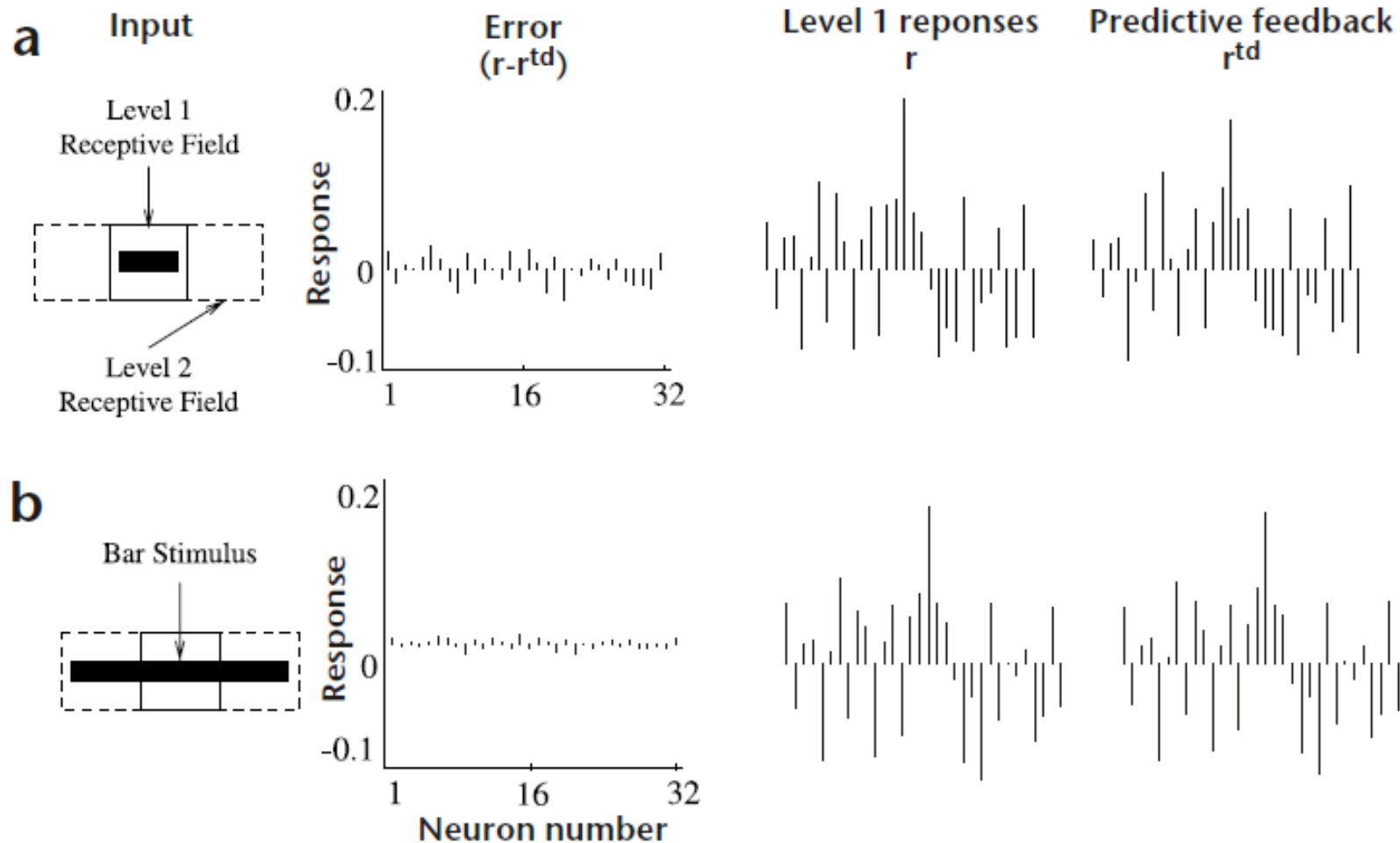
Level 2



Level 1 (with sparse prior distribution)

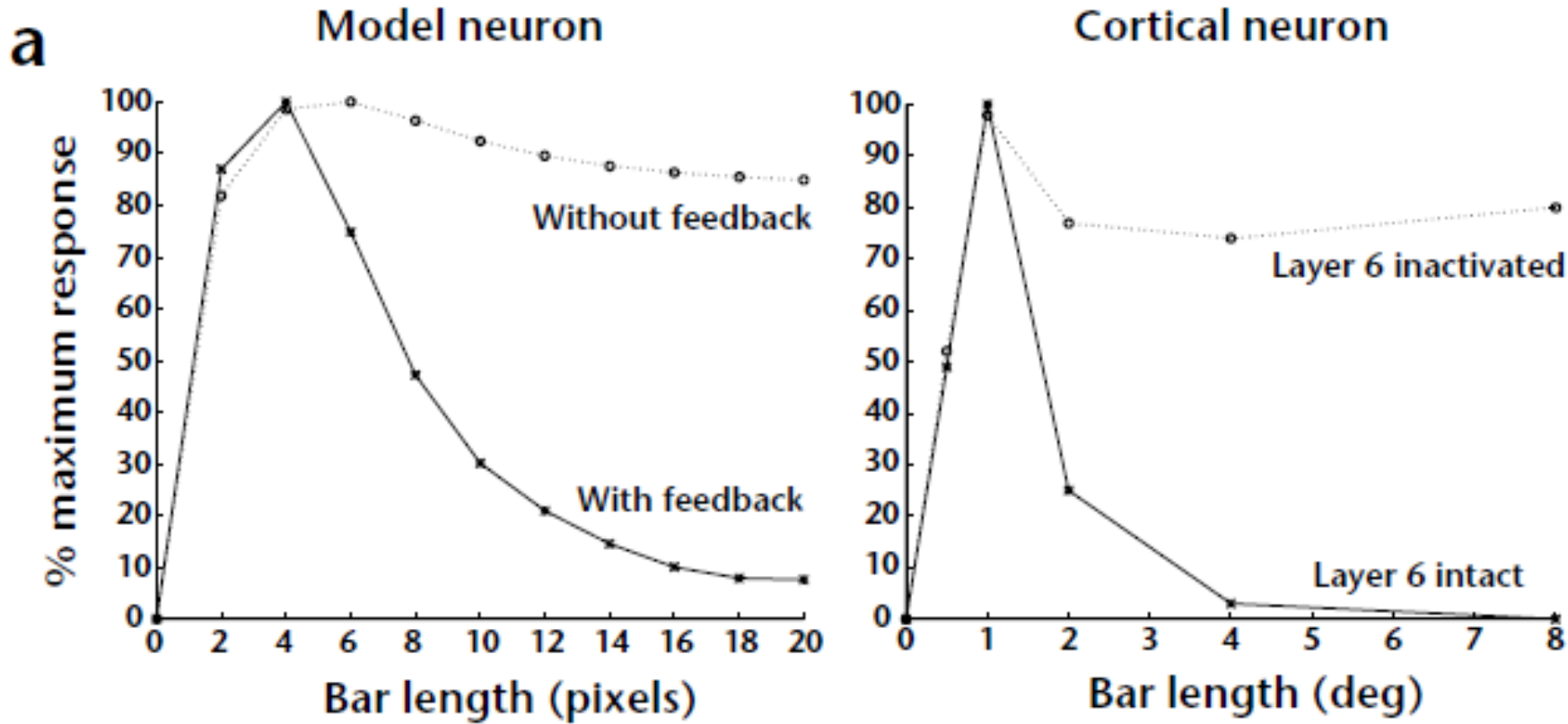


# Predictive Coding: Nonclassical Receptive Fields



Bars which are smaller than a neuron's receptive field generate a prediction error  
=> Prediction error neurons should exist that signal this in their firing rate.

# Predictive Coding: Nonclassical Receptive Fields



Such neurons are found in V1. Silencing top-down input reveals impact of predictive feedback from higher visual areas. Same effect occurs in model.



# Summary: Predictive Coding

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- Predictive coding is a hierarchical generative model for natural images
- Top-down predictions are compared to bottom-up prediction errors
- Reproduces classical V1 receptive fields and non-classical responses related to prediction errors
- Provides a computational account of feedback from higher to lower visual areas
- More recent variants can account for many more properties of visual system (Lotter and Cox, 2020)

# Summary: Generative Models

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- Generative models attempt to explain data via their underlying causes
- Typically unsupervised: can learn representations from data
- Sensory systems are hypothesised to learn a generative model for the statistics of sensory input, and perform inference to find latent causes
- Sparse coding, ICA, and predictive coding learn V1-like receptive fields
- Convolutional neural networks are not generative models, but can replicate aspects of the visual system
- Generative models address representation but not the goals of sensory systems – sensory systems evolved to guide behaviour, and do not passively represent the world

# Bibliography

- Hyvarinen, Hurri and Hoyer (Natural Image Statistics)
- Dayan and Abbott Ch 10
- Olshausen and Field (1996, 1997, 2004)
- Rao and Ballard (1999) (and Mumford 1992)
- Bell and Sejnowski (1995) (and Linsker 1988)

