Representational learning in sensory cortices: connecting receptive fields to natural scene statistics

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Classical receptive field properties

Neurons in primary visual cortex are driven most strongly by oriented stimuli. Electrophysiological recordings made in cats show that neurons are tuned for orientation.

Hubel and Wiesel
Nobel Prize in Physiology or Medicine 1981

Optic nerve, lateral geniculate nucleus, primary visual cortex

Neuron (cat) Neuron (monkey)
Classical receptive field properties


Jones and Palmer 1987, The Two-Dimensional Spatial Structure of Simple

Moran spikes

Evans, 1961

Classical receptive field properties

Evans, 1961
Classical receptive field properties: Summary

- Two main cell types in primary visual cortex:
  - Simple cells
    - Orientation tuned
    - Phase tuned
  - Complex cells
    - Orientation tuned
    - Insensitive to phase

Classical receptive field properties (simple characteristics discovered first)

- Simple cells $\approx$ linear filter
- Complex cells $\approx$ sum of squared simple cell responses with different phases

But that's not all there is to the story...

Extra-classical receptive field properties

- Surround orientation/degrees

Jones et al. 2001 Surround suppression in primate V1, J. Neurophys.

Classical receptive field properties: Summary

- Two main cell types in primary visual cortex:
Core ideas

- A set of all possible images is enormous, but not all images are equally likely to be encountered in the environment.
- Finite neural resources: allocate according to sensory statistics (wasteful to devote resources to stimuli that are highly unlikely to occur, connection to information theory)
- Interpreting ambiguous stimuli: world is often noisy and uncertain and we use statistical knowledge to disambiguate.
- Neural processing is matched to statistics of the environment
- More direct evidence is required...

Representations

- Animals reared in a modified environment have different neural representations.
- Know that statistics shape neurobiology

Connecting neural responses to environmental statistics

How do we compute the statistics of natural scenes? How do we connect the statistics to neural processing? What computations is the brain performing which need to be calibrated to natural scene statistics?
Connecting neural responses to environmental statistics

- As the models become a better statistical match to natural images, the behavior of the latent variables corresponds more and more closely to biology.
- Build models to capture these statistical properties using latent variables.
- Modelling effort: unpeeling statistical regularities in natural images.

**Take home message**

- Modelling effort: unpeeling statistical regularities in natural images.
- Neuronal activities = functional of posterior.
- Image is made up of statistical primitives (plausible structural primitives).
- Image is made up of statistical description of how natural images are produced.
- Accurate inference requires calibration to natural scene statistics - learning.
Unpeeling the onion: Marginal statistics

Log transform makes pixel values symmetric: $y = \log(\text{pixel value})$

Ruderman, 1994
Unpeeling the onion: Marginal statistics

Summary of log-normal model for pixel values:

\[ p(y; \mu, \sigma) = \text{Norm}(y; \mu, \sigma) \]

- Captures the marginal distribution of pixel values
- Photoreceptors in the retina appear to use a log-like transform
- What about the dependencies between pixels?

Unpeeling the onion: Pixel correlations

Summary of log-normal model for pixel values:

\[ (\omega_i)_{\text{pixel-values}} \sim \text{exp} \]

\[ (\omega_i)_{\text{pixel-values}} \sim \text{Norm} = (P \gamma)d \]

What about the dependencies between pixels?

- Photoreceptors in the retina appear to use a log-like transform
- Captures the marginal distribution of pixel values
Unpeeling the onion: Marginal statistics

\[ \mathcal{L} = \mathbf{X} \]

[Diagram showing the unpeeling of the onion with marginal statistics]

**Generative model**

- Prior model
- Recognition
- Weight model
- Gaussian distribution

**Recognition model**

- Marginal
- Assume neural rates given by posterior mean/mode
- Likelihood can be maximized for learning: choose structural primitives \( \mathbf{W} \) that make the data most probable under the model

\[ \mathbf{X} \]

**Principal component analysis (PCA)**

\[ \mathbf{y} = \mathbf{W} \mathbf{x} \]

\[ \mathbf{y} \mathbf{y}' = \mathbf{W} \mathbf{x} \mathbf{x}' \mathbf{W}' = \mathbf{x} \mathbf{x}' \mathbf{x}' \mathbf{x} = \mathbf{y} \mathbf{y}' \]

\[ 0 = \mathbf{W} \mathbf{x} \mathbf{x}' \mathbf{x}' \mathbf{x} = \mathbf{y} \mathbf{y}' = \mathbf{y} \mathbf{y}' \]

\[ \mathbf{y} \mathbf{y}' = \mathbf{y} \mathbf{y}' \]

\[ \mathbf{y} \mathbf{y}' = \mathbf{y} \mathbf{y}' \]

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PCA receptive fields - with artificial locality constraint

PCA receptive fields
PCA Conclusions

- Captures correlational statistics of images
- Non-local receptive fields are non-biological
- Can be restricted to be local which makes them look more biological: but this doesn't arise from the statistics of natural scenes
- Instead of hacking the solution: look at higher order statistics

Unpeeling the onion: pixel correlations
Unpeeling the onion: sparsity

Filtered images

PCA

More mass near 0 than a Gaussian

More mass in the tails than a Gaussian
Sparsecoding

Assume neural rates computed using optimization

\[ [(\lambda|x)d]_{\text{max}} = [(\lambda|x)d]_{\text{mode}} = r \]

\[ (\lambda|x)d \prod \times \]

\[ (\lambda|x)d_{\text{prior}} \propto (\lambda|x)d \]

\[ (x)d_{\text{IC}} \frac{(\lambda|x)d}{1} = (\lambda|x)d \]

Maximum-likelihood intractable

Approximate by maximising joint over structural primitives \( W \) and activities \( x \)

Neural rates computed using optimisation

\[ \hat{\lambda} \]

Generative model

Recognition model

Sparsecoding
• train filters on a large number of natural images $Y = \{y^n_i\}_{n=1}^N$

• compute neural responses to white noise stimuli $y^m \sim \text{Norm}(0, I)$

$$r^m = \mathbb{X} \left( p(x^m | y^m, W) \right) = \arg\max x^m \left( p(x^m | y^m, W) \right)$$

• use reverse correlation to estimate receptive fields $R$

$$u^x \mathbb{X} R \approx u^w.$$  

• compare neural responses to white noise stimuli to \( u^x \mathbb{X} \) \( \sim \text{Norm}(0, I) \)

$$\mathbb{X} \left( \mathbb{X} \right) = \mathbb{W}$$

$$\mathbb{X} \left( \mathbb{X} \right) = \mathbb{W}$$

Train filters on a large number of natural images $\mathbb{Y}$.  

Comparison to biology.
Unpeeling the onion: sparsity

Sparse coding fails to capture sparsity in all directions.

Sparse coding captures sparsity in direction of filters.

Unpeeling the onion: sparsity
Sparse Coding Conclusions

- Computational interpretation for simple cells
- Doesn’t capture the sparsity of images correctly
- What about complex cells?

Unpeeling the onion: power-correlations

- Let’s look at higher order statistics
- Doesn’t capture the sparsity of images correctly

Computational Interpretation for Simple Cells

Sparse Coding Conclusions
Summary

- When any local oriented filter is applied to natural images the power in the outputs is correlated (not captured by sparse coding).
- Filters which are nearby in location/orientation/spatial-scale have strong correlation.
- When oriented filters are applied to natural images, the marginals are sparse (sparse coding only captures sparsity in some directions).

- Idea: Introduce another latent variable which represents "power" and correlates with the activity variables.
Gaussian Scale Mixture (GSM) Model

Sparse coding
Sparse coding can be viewed as comprising a scale mixture of Gaussians. Power variables control the variance in a single activity component. Sparse coding can be viewed as comprising a scale mixture of Gaussians.

\[
\{(\mathbf{x}^o_1, \theta^1, \xi^1, \phi_1^1, \psi_1^1) \mid \text{N} = (\mathbf{x}|\mathbf{\phi})d \}
\]

\[
(\mathbf{x}^o_1, \theta^1, \xi^1, \phi_1^1, \psi_1^1) \mid \text{N} = (\mathbf{x}|\mathbf{\phi})d
\]

Sparse Coding: a new perspective.

\[
(\mathbf{x}^o_1, \theta^1, \xi^1, \phi_1^1, \psi_1^1) \mid \text{N} = (\mathbf{x}|\mathbf{\phi})d
\]

Sparse Coding: a new perspective.
Gaussian scale mixture

Model parameters - independent variance components

power dependencies

Share power variables across activity variables in order to capture

\[
\begin{align*}
\mathbf{x} & \sim \mathcal{N}(d) \\
\mathbf{o} & \sim \mathcal{N}(\mathbf{x}) \\
\end{align*}
\]

generative model

Gaussian scale mixture
Unpeeling the onion: power-correlations

Simoncelli 1997

Turner et al. submitted

Unpeeling the onion: power-correlations
Model parameters - independent variance components

Unpeeling the onion: sparsity

Sparse coding fails to capture sparsity in all directions
Classical receptive field properties

Simple cell

Orientation / degrees

Neural response

$-60 \quad -30 \quad 0 \quad 30 \quad 60$

Complex cell

Orientation / degrees

Neural response

$-60 \quad -30 \quad 0 \quad 30 \quad 60$

Movshon et al. 1978a, 1978b and Jones et al. 2001

Surround orientation / degrees

Surround orientation / degrees

Normalised neural response

Simple cell

Orientation / degrees

Normalised neural response

Complex cell

Orientation / degrees

Normalised neural response

Jones et al. 2001 Surround suppression in primate V1, J. Neurophys.
Computational perspective: what are complex cells coding?

Variance units (complex cells) code for texture types
proj1 proj2
Look at 2D projection of model complex cell responses to different texture classes
Textures well clustered in this space

Neuron-Variable identifications
Karklin & Lewicki 2008, Nature
Ranzato & Hinton 2010
Schwartz, Dayan & Sejnowski 2009
Berkes, Turner and Salama 2009
Schwartz, Hayman & Sivilotti 2009
Karklin & Lewicki 2003
Karklin and Lewicki 2005
Osindero, Welling and Hinton 2006
Hyvarinen and Hoyer 2000
Hyvarinen and Hoyer 2001

Textures well clustered in this space

Texture classes complex cell responses to different look at 2D projection of model
for texture types
Variance units (complex cells) code

Computational perspective: what are complex cells coding?
Many computational models of cortical processing are instances of a single model. They statistically match lower order statistics of images and provide a zoo of responses. GSMs: computational interpretation of simple and complex cells.

Conclusions

- GSMs: computational interpretation of simple and complex cells
- Provide a zoo of responses
- Statistically a good match to lower order statistics of images
- Many computational models of cortical processing are instances of a single model

Neuron-Variable Identifications