Sensory Coding & Hierarchical Representations

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from Hedgé and Felleman, 2007



Palmer and Rock, 1994

### VI simple cells





Hubel and Wiesel, 1959

DeAngelis, et al, 1995





# Out of the retina

- > 23 distinct neural pathways, no simple function division
- Suprachiasmatic nucleus: circadian rhythm
- Accessory optic system: stabilize retinal image
- Superior colliculus: integrate visual and auditory information with head movements, direct eyes
- Pretectum: plays adjusting pupil size, track large moving objects
- Pregeniculate: cells responsive to ambient light
- Lateral geniculate (LGN): main "relay" to visual cortex; contains 6 distinct layers, each with 2 sublayers. Organization very complex



### VI simple cell integration of LGN cells







Hubel and Wiesel, 1963



### Anatomical circuitry in VI



from Callaway, 1998

#### Where is this headed?





Ramon y Cajal

A wing would be a most mystifying structure if one did not know that birds flew.

Horace Barlow, 1961

An algorithm is likely to be understood more readily by understanding the nature of the problem being solved than by examining the mechanism in which it is embodied.

David Marr, 1982

### A theoretical approach

- Look at the system from a functional perspective: What problems does it need to solve?
- Abstract from the details: Make predictions from theoretical principles.
- Models are bottom-up; theories are top-down.

### What are the relevant computational principles?









### VI simple cells





Hubel and Wiesel, 1959

DeAngelis, et al, 1995

#### Oriented Gabor models of individual simple cells



figure from Daugman, 1990; data from Jones and Palmer, 1987

### 2D Gabor wavelet captures spatial structure



- 2D Gabor functions
- Wavelet basis generated by dilations, translations, and rotations of a single basis function
- Can also control phase and aspect ratio
- (drifting) Gabor functions are what the eye "sees best"

#### Recoding with Gabor functions



Pixel entropy = 7.57 bits

Recoding with 2D Gabor functions Coefficient entropy = 2.55 bits

# How is the VI population organized?



## A general approach to coding: redundancy reduction



Redundancy reduction is equivalent to efficient coding.

Describing signals with a simple statistical model

#### Principle

Good codes capture the statistical distribution of sensory patterns.

How do we describe the distribution?

• Goal is to encode the data to desired precision

$$\mathbf{x} = \vec{a}_1 s_1 + \vec{a}_2 s_2 + \dots + \vec{a}_L s_L + \vec{\epsilon}$$
$$= \mathbf{A}\mathbf{s} + \boldsymbol{\epsilon}$$

• Can solve for the coefficients in the no noise case

$$\mathbf{\hat{s}} = \mathbf{A}^{-1}\mathbf{x}$$

### An algorithm for deriving efficient linear codes: ICA

Learning objective:

maximize coding efficiency

 $\Rightarrow$  maximize  $P(\mathbf{x}|\mathbf{A})$  over  $\mathbf{A}$ .

Probability of the pattern ensemble is:

$$P(\mathbf{x}_1, \mathbf{x}_2, ..., \mathbf{x}_N | \mathbf{A}) = \prod_k P(\mathbf{x}_k | \mathbf{A})$$

To obtain  $P(\mathbf{x}|\mathbf{A})$  marginalize over S:

$$P(\mathbf{x}|\mathbf{A}) = \int d\mathbf{s} P(\mathbf{x}|\mathbf{A}, \mathbf{s}) P(\mathbf{s})$$
$$= \frac{P(\mathbf{s})}{|\det \mathbf{A}|}$$

Using independent component analysis (ICA) to optimize A:

$$\Delta \mathbf{A} \propto \mathbf{A} \mathbf{A}^T \frac{\partial}{\partial \mathbf{A}} \log P(\mathbf{x} | \mathbf{A})$$
$$= -\mathbf{A} (\mathbf{z} \mathbf{s}^T - \mathbf{I})$$

where  $z = (\log P(s))'$ .

This learning rule:

- learns the features that capture the most structure
- optimizes the efficiency of the code

What should we use for P(s)?

# Modeling Non-Gaussian distributions

• Typical coeff. distributions of natural signals are *non-Gaussian*.



The generalized Gaussian distribution

$$P(x|q) \propto \exp(-\frac{1}{2}|x|^q)$$

• Or equivalently, and exponential power distribution (Box and Tiao, 1973):

$$P(x|\mu,\sigma,\beta) = \frac{\omega(\beta)}{\sigma} \exp\left[-c(\beta) \left|\frac{x-\mu}{\sigma}\right|^{2/(1+\beta)}\right]$$

•  $\beta$  varies monotonically with the kurtosis,  $\gamma_2$ :



## Modeling Gaussian distributions with PCA

- Principal component analysis (PCA) describes the principal axes of variation in the data distribution.
- This is equivalent to fitting the data with a multivariate Gaussian.





# Modeling non-Gaussian distributions

• What about non-Gaussian marginals?



 How would this distribution be modeled by PCA?



# Modeling non-Gaussian distributions

• What about non-Gaussian marginals?



 How would this distribution be modeled by PCA?

• How should the distribution be described?



### Efficient coding of natural images: Olshausen and Field, 1996



Network weights are adapted to maximize coding efficiency: minimizes redundancy and maximizes the independence of the outputs

### Model predicts local and global receptive field properties







Overlaid basis function properties

from Lewicki and Olshausen, 1999

## Algorithm selects best of many possible sensory codes



Theoretical perspective: Not edge "detectors." An efficient code for natural images.

### Comparing coding efficiency on natural images



Responses in primary visual cortex to visual motion



from Wandell, 1995
Sparse coding of time-varying images (Olshausen, 2002)



$$I(x, y, t) = \sum_{i} \sum_{t'} a_i(t') \phi_i(x, y, t - t') + \epsilon(x, y, t)$$
$$= \sum_{i} a_i(t) * \phi_i(x, y, t) + \epsilon(x, y, t)$$

#### Sparse decomposition of image sequences



# input sequence

from Olshausen, 2002

### Learned spatio-temporal basis functions



from Olshausen, 2002

### Animated spatial-temporal basis functions



from Olshausen, 2002

#### Theory

#### **Principle**

#### Idealization

Methodology

Prediction

• explains data from principles

- requires idealization and abstraction
- code signals accurately and efficiently
- adapted to natural sensory environment

• cell response is linear

• information theory, natural images

• explains individual receptive fields

• explains population organization

How general is the efficient coding principle?

Can it explain auditory coding?

#### Limitations of the linear model

- linear
- only optimal for block, not whole signal
- no phase-locking
- representation depends on block alignment



#### A continuous filterbank does not form an efficient code



#### Goal:

find a representation that is both time-relative and efficient

# Efficient signal representation using time-shiftable kernels (spikes)

Smith and Lewicki (2005) Neural Comp. 17:19-45



- Each spike encodes the precise time and magnitude of an acoustic feature
- Two important theoretical abstractions for "spikes"
  - not binary
  - not probabilistic
- Can convert to a population of stochastic, binary spikes

#### Coding audio signals with spikes





How do we compute the spikes?

"can" with filter-threshold



I. convolve signal with kernels



- I. convolve signal with kernels
- 2. find largest peak over convolution set



- I. convolve signal with kernels
- 2. find largest peak over convolution set
- 3. fit signal with kernel



- I. convolve signal with kernels
- 2. find largest peak over convolution set
- 3. fit signal with kernel
- 4. subtract kernel from signal, record spike, and adjust convolutions



- I. convolve signal with kernels
- ➡ 2. find largest peak over convolution set
  - 3. fit signal with kernel
  - 4. subtract kernel from signal, record spike, and adjust convolutions
  - 5. repeat



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  - 5. repeat



- I. convolve signal with kernels
- ➡ 2. find largest peak over convolution set
  - 3. fit signal with kernel
  - 4. subtract kernel from signal, record spike, and adjust convolutions
  - 5. repeat ...



- I. convolve signal with kernels
- ➡ 2. find largest peak over convolution set
  - 3. fit signal with kernel
  - 4. subtract kernel from signal, record spike, and adjust convolutions
  - 5. repeat ...
  - 6. halt when desired fidelity is reached



"can" 5 dB SNR, 36 spikes, 145 sp/sec



"can" 10 dB SNR, 93 spikes, 379 sp/sec



"can" 20 dB SNR, 391 spikes, 1700 sp/sec



"can" 40 dB SNR, 1285 spikes, 5238 sp/sec



### Efficient auditory coding with optimized kernel shapes

Smith and Lewicki (2006) *Nature* 439:978-982

What are the optimal kernel shapes?



Adapt algorithm of Olshausen (2002)

#### Optimizing the probabilistic model

$$x(t) = \sum_{m=1}^{M} \sum_{i=1}^{n_m} s_i^m \phi_m(t - \tau_i^m) + \epsilon(t),$$

$$\begin{array}{ll} p(x|\Phi) &=& \int p(x|\Phi,s,\tau)p(s)p(\tau)dsd\tau\\ &\approx& p(x|\Phi,\hat{s},\hat{\tau})p(\hat{s})p(\hat{\tau})\\ &\quad \epsilon(t)\sim\mathcal{N}(0,\sigma_{\epsilon}) \end{array}$$

Learning (Olshausen, 2002):

$$\begin{aligned} \frac{\partial}{\partial \phi_m} \log p(x|\Phi) &= \frac{\partial}{\partial \phi_m} \log p(x|\Phi, \hat{s}, \hat{\tau}) + \log p(\hat{s}) p(\hat{\tau}) \\ &= \frac{1}{2\sigma_{\varepsilon}} \frac{\partial}{\partial \phi_m} [x - \sum_{m=1}^M \sum_{i=1}^{n_m} \hat{s}_i^m \phi_m (t - \tau_i^m)]^2 \\ &= \frac{1}{\sigma_{\varepsilon}} [x - \hat{x}] \sum_i \hat{s}_i^m \end{aligned}$$

Also adapt kernel lengths

### Adapting the optimal kernel shapes



#### Kernel functions optimized for coding speech



## Quantifying coding efficiency

- 1. fit signal
- 2. quantize time and amplitude values
- 3. prune zero values
- 4. measure coding efficiency using the entropy of quantized values
- 5. reconstruct signal using quantized values
- 6. *measure fidelity* using signal-to-noise ratio (SNR) of residual error
- identical procedure for other codes (e.g. Fourier and wavelet)

$$x(t) = \sum_{m=1}^{M} \sum_{i=1}^{n_m} s_{m,i} \phi_m(t - \tau_{m,i}) + \epsilon(t)$$



### Coding efficiency curves



# Using efficient coding theory to make the cetical predictions



### Learned kernels share features of auditory nerve filters



Auditory nerve filters from Carney, McDuffy, and Shekhter, 1999

Optimized kernels scale bar = 1 msec

#### Learned kernels closely match individual auditory nerve filters



for each kernel find closet matching auditory nerve filter in Laurel Carney's database of ~100 filters.

#### Learned kernels overlaid on selected auditory nerve filters



For almost all learned kernels there is a closely matching auditory nerve filter.
## Coding of a speech consonant



## How is this achieving an efficient, time-relative code?



### Theory

### **Principle**

Idealization

Methodology

Prediction

• explains data from principles

- requires idealization and abstraction
- code signals accurately and efficiently
- adapted to natural sensory environment

analog spikes

- information theory, natural sounds
- optimization

- explains individual receptive fields
- explains population organization



## Redundancy reduction for noisy channels (Atick, 1992)



Mutual information

$$I(x,s) = \sum_{s,x} P(x,s) \log_2 \left[ \frac{P(x,s)}{P(s)P(x)} \right]$$

I(x,s) = 0 iff P(x,s) = P(x)P(s), i.e. x and s are independent.

## Profiles of optimal filters



- high SNR
  - reduce redundancy
  - center-surround

- Iow SNR
  - average
  - low-pass filter
- matches behavior of retinal ganglion cells

### An observation: Contrast sensitivity of ganglion cells



Luminance level decreases one log unit each time we go to lower curve.

### Natural images have a 1/f amplitude spectrum



Log<sub>10</sub> spatial frequency (cycles/picture)

## Components of predicted filters



### Predicted contrast sensitivity functions match neural data



from Atick, 1992

## Robust coding of natural images

- Theory refined:
  - image is noisy and blurred
  - neural population size changes
  - neurons are noisy



from Hubel, 1995



from Doi and Lewicki, 2006

## Problem I: Real neurons are "noisy"

Estimates of neural information capacity

system (area)	stimulus	bits / sec	bits / spike
fly visual (HI)	motion	64	~
monkey visual (MT)	motion	5.5 - 12	0.6 - 1.5
frog auditory (auditory nerve)	noise & call	46 & 133	1.4 & 7.8
Salamander visual (ganglinon cells)	rand. spots	3.2	I.6
cricket cercal (sensory afferent)	mech. motion	294	3.2
cricket cercal (sensory afferent)	wind noise	75 - 220	0.6 - 3.1
cricket cercal (10-2 and 10-3)	wind noise	8 - 80	avg. = 1
Electric fish (P-afferent)	amp. modulation	0 - 200	0 - 1.2

Limited capacity  $\Rightarrow$  neural codes need to be *robust*.

## Traditional codes are not robust

encoding neurons



sensory input

Original



## Traditional codes are not robust

encoding neurons

sensory input

Original



**Ix** efficient coding

I bit precision

Add noise equivalent to I bit precision







## Redundancy plays an important role in neural coding



Response of salamander retinal ganglion cells to natural movies

From Puchalla et al, 2005

## Robust coding (Doi and Lewicki, 2005, 2006)



## Generalizing the model: sensory noise and optical blur





### Can also add sparseness and resource constraints

## Robust coding is distinct from "reading" noisy populations



### Here, we want to learn an optimal image code using noisy neurons.

## How do we learn robust codes?



#### **Objective**:

Find W and A that minimize reconstruction error.

• Channel capacity of the i<sup>th</sup> neuron:

$$C_i = \frac{1}{2}\ln(\mathrm{SNR}_i + 1)$$

• To limit capacity, fix the coefficient signal to noise ratio:

$$\mathrm{SNR}_i = \frac{\langle u_i^2 \rangle}{\sigma_n^2}$$

Now robust coding is formulated as a constrained optimization problem.

## Robust coding of natural images

encoding neurons

sensory input

Original



**Ix** efficient coding

I bit precision

Add noise equivalent to I bit precision

reconstruction (34% error)





## Robust coding of natural images

encoding neurons

sensory input

Original



**I x** robust coding

I bit precision

Weights adapted for optimal robustness

reconstruction



LACORNOLD

(3.8% error)

## Reconstruction improves by adding neurons



## Adding precision to 1x robust coding

original images

l bit: 12.5% error

2 bit: 3.1% error



Can derive minimum theoretical average error bound

$$\mathcal{E} = \frac{1}{\frac{M}{N} \cdot SNR + 1} \frac{1}{N} \left[ \sum_{i=1}^{N} \sqrt{\lambda_i} \right]^2 \quad \text{if } SNR \ge SNR_c$$

 $\lambda_i$  - ith eigenvalue of the data covariance

N - input dimensionality

M - # of coding units (neurons)

Algorithm achieves theoretical lower bound

	Results	Bound
0.5x	19.9%	20.3%
lx	12.4%	12.5%
8x	2.0%	2.0%

Balcan, Doi, and Lewicki, 2007; Balcan and Lewicki, 2007

## Sparseness localizes the vectors and increases coding efficiency



robust sparse coding

## Non-zero resource constraints localize weights



#### Theory

### **Principle**

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### Prediction

- explains data from principles
- requires idealization and abstraction
- code signals accurately, efficiently, robustly
- adapted to natural sensory environment
- cell response is linear, noise is additive
- simple, additive resource constraints
- information theory, natural images
- constrained optimization
- explains individual receptive fields
- explains non-linear response
- explains population organization



## What happens next?



### Joint statistics of filter outputs show magnitude dependence



from Schwartz and Simoncelli (2001)

## Using sensory gain control to reduce redundancy

#### Schwartz and Simoncelli (2001)



# Model accounts for several non-linear response properties

Schwartz and Simoncelli (2001)



## What about image structure?

- Bottom-up approaches focus on the non-linearity.
- Our aim here is to focus on the *computational* problem:

How do we learn the intrinsic dimensions of natural image structure?

• Idea: characterize how the local image distribution changes.

## Perceptual organization in natural scenes



image of Kyoto, Japan from E. Doi

## Palmer and Rock's theory of perceptual organization



Palmer and Rock, 1994

## Gestalt grouping principles


Malik and Perona's (1991) model of texture segregation



Visual Features

## Malik and Perona algorithm can find texture boundaries



Painting by Gustav Klimt

texture boundaries from Malik and Perona algorithm

#### Can we apply these to natural scenes?



natural scenes are more complex, and the structures more subtle

A different representation of a natural scene (Kersten and Yuille, 2003)



## A representation we're more familiar with



## A representation we're more familiar with



#### This is what our brain does



## How do neurons in the visual cortex generalize?



Conjecture I: Two regions are similar if they come from the same statistical distribution.

Conjecture 2: Neurons encode the local distribution of natural images.

(image data from Doi et al, 2003)

# Perceptual generalization in natural scenes



# Perceptual generalization in natural scenes



## Linear representations do not separate the image classes

• bushes



• hillside



• tree edge



• tree bark





# Modeling local natural scene statistics

- need to model *local* scene structure, not average scene statistics
- need to model all structure
  - want a "complete" code
  - a universal "texture" model
- code should be *distributed* and statistically *efficient*



# ICA mixtures for similar images





from Lee, Lewicki, and Sejnowski 2000

#### Limitations:

- can only have a small number of classes
- representations are not shared
- cannot learn *intrinsic* dimensions













# Generalizing the standard ICA model

Karklin and Lewicki (2003; 2005)



# Generalizing the standard ICA model

Karklin and Lewicki (2003; 2005)

$$\begin{array}{c} \mathbf{v} = -\log p(\boldsymbol{u}|\mathbf{B}, \boldsymbol{v}) \propto \sum_{i} \left| \frac{u_{i}}{\exp([\mathbf{B}\boldsymbol{v}]_{i})} \right|^{q_{i}} \\ \mathbf{B} = P(u_{i}|\lambda_{i}) \propto \exp\left[ - \left| \frac{u_{i}}{\lambda_{i}} \right|^{q_{i}} \right] \\ \mathbf{A} = P(u_{i}|\lambda_{i}) \propto \exp\left[ - \left| \frac{u_{i}}{\lambda_{i}} \right|^{q_{i}} \right] \\ \log \lambda_{i} = [\mathbf{B}\boldsymbol{v}]_{i} \\ p(u_{i}|\lambda_{i}) = \frac{P(u_{i}|\lambda_{i})}{\log \lambda_{i}} \end{array}$$

#### Independent density components



#### Illustration of inference in the model using synthesized data



# Learning higher-order structure of natural images

• A is learned with ICA • B is learned by maximizing B the posterior distribution U X Train on natural images

raw weights **B**<sub>i</sub> V. B U Gabor function fits X































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## Learned density components of natural images



(30 out of 100 shown)

## Full set of natural image density components



# What about a feed-forward non-linearity?

Isn't this the same?

- 3. Do ICA again on output:
- 2. Add non-linearity:
- I. Take standard ICA model:



## ICA on non-linearity reveals no structure



subset of ICA basis functions on log |s|

## Inferred v forms a sparse distributed code




## Most typical images for selected density components



## Distributed representation of natural image densities







Comparing the degree of abstraction



# Winner maps: Maximum $|u_i|$ for each pixel



Winner maps: Maximum  $|v_i|$  for each pixel



## A distributed code for visual surfaces



## Smooth changes in representation for texture gradients



higher-level output

First 3 PCs

# Smooth changes in representation for texture gradients



higher-level output

First 3 PCs

## Clustering the higher-order representation yields segmentation



clustering v's



clustering color



# Model can be extended to model local covariance structure



# Linear code of image regions



distributions in simple cell space (VI)



2D projection of 400D space

# Distributed covariance model of image regions



distributions in higher-order space



2D projection of 150D space

For more, see workshop talk

#### Theory

#### **Principle**

Idealization

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• explains data from principles

- requires idealization and abstraction
- code signals accurately and efficiently
- adapted to natural sensory environment
- neurons encode local image distributions
- information theory, natural images
- hierarchical, probabilistic models

- good generalization in natural images
- functional explanation of non-simple cells?

# Thank you!