# **Efficient Coding of Natural Sounds**

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# How does the brain encode complex sensory signals?

#### Outline

Motivations Efficient coding theory Application to natural sounds Interpretation of experimental data

Efficient coding in population spike codes

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

Horace Barlow, 1961

#### Natural signals are redundant



Efficient coding hypothesis (Attneave, 1954; Barlow, 1961; et al):

Sensory systems encode only non-redundant structure

# Why code efficiently?

Information bottleneck of sensory coding:

- restrictions on information flow rate
  - channel capacity of sensory nerves
  - computational bottleneck
  - $-5 \times 10^6 \rightarrow 40 50$  bits/sec
- facilitate pattern recognition
  - independent features are more informative
  - better sensory codes could simply further processing
- other ideas
  - efficient energy use
  - faster processing time

How do we use this hypothesis to predict sensory codes?

#### A simple example: efficient coding of a single input



(from Atick, 1992)

#### How to set sensitivity?

- too high  $\Rightarrow$  response saturated
- too low  $\Rightarrow$  range under utilized

- inputs follow distribution of sensory environment
- encode so that output levels are used with equal frequency
- each response state has equal area (⇒ equal probability)
- continuum limit is cumulative pdf of input distribution

For 
$$y = g(c)$$

$$\frac{y}{y_{max}} = \int_{c_{min}}^{c} P(c') dc' \mathbf{I}$$

## Testing the theory: Laugin, 1981

Laughlin, 1981:

- predict response of fly LMC (large monopolar cells)
  - interneuron in compound eye
- output is graded potential



- collect natural scenes to estimate stimulus pdf
- predict contrast response function
  ⇒ fly LMC transmits information
  efficiently

What about complex sensory patterns?

#### V1 receptive fields are consistent with effcient coding theory









V1 receptive fields are well-fit by 2D Gabor functions (Jones and Palmer, 1987).

Does this yield an efficient code?

#### Coding images with pixels (Daugman, 1988)



Lena

histogram of pixel values Entropy = 7.57

High entropy means high redundacny  $\Rightarrow$  a very *inefficient* code

### **Recoding with Gabor functions (Daugman, 1988)**



Pixel entropy= 7.57 bits

Recoding with 2D Gabor functions Filter output entropy = 2.55 bits.

#### Can these codes be predicted?

# Sparse coding of natural images (Olshausen and Field, 1996)



Adapt population of receptive fields to

- accurately encode an ensembe of natural images
- maximizing the sparseness of the output, i.e. minimizing entropy.

#### Theory predicts entire population of receptive fields

(Lewicki and Olshausen, 1999)



Population of receptive fields. (black = inhibitory; white = exicitatory)



Overlayed response property schematics.

## Algorithm selects best of many possible sensory codes

#### Learned



Haar







**PCA** 

Gabor





(Lewicki and Olshausen, 1999) Theoretical perspective: Not edge "detectors" but an efficient way to describe natural, complex images.



Efficient coding of natural sounds

#### Efficient coding: focus on coding waveform directly



#### Goal:

Predict optimal transformation of acoutsic waveform from statistics of the acoustic environment.

#### Why encode sound by frequency?



Auditory tuning curves.

#### A simple model of waveform encoding

Data consists of waveform segments sampled randomly from a sound ensemble:



Filterbank model:

$$a_i(t) = \sum_{\tau=0}^{N-1} x(t-\tau)h_i(\tau)$$

How do derive the filter shapes  $h_i(t)$  that optimize coding efficiency?

# Model only describes signals within the window of analysis.

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#### Information theoretic viewpoint

Use Shannon's source coding theorm.

$$\mathcal{L} = E[l(X)] \geq \sum_{x} p(x) \log \frac{1}{q(x)}$$
$$= \sum_{x} p(x) \log \frac{p(x)}{q(x)} + \sum_{x} p(x) \log \frac{1}{p(x)}$$
$$= D_{KL}(p||q) + H(p)$$

If model density q(x) equals true density p(x) then  $D_{KL} = 0$ .  $\Rightarrow q(x)$  gives *lower bound* on average code length.

greater coding efficiency  $\Leftrightarrow$  more learned structure

#### Principle

Good codes capture the statistical distribution of sensory patterns.

How do we describe the distribution?

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#### Describing signals with a simple statistical model

Goal is to encode the data to desired precision

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

Can solve for  $\hat{\mathbf{s}}$  in the no noise case

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

Want algorithm to choose optimal A (i.e. the basis matrix).

#### Algorithm for deriving efficient codes

Learning objective:

maximize coding efficiency

 $\Rightarrow$  maximize  $P(\mathbf{x}|\mathbf{A})$  over  $\mathbf{A}$  (basis for analysis window, or filter shapes).

Probability of 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 
$$\mathbf{z} = (\log P(\mathbf{s}))'$$
. Use  $P(s_i) \sim \mathsf{ExPwr}(s_i | \mu, \sigma, \beta_i)$ .

This learning rule:

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

#### Modeling Non-Gaussian distributions with ICA



- Typical coeff. distributions of natural signals are *non-Gaussian*.
- Independent component analysis (ICA) describes the statistical distribution of non-Gaussian distributions
- The distribution is fit by optimizing the filter shapes.
- Unlike PCA, vectors are not restricted to be orthogonal.
- This permits a much better description of the actual distribution of natural signals.

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#### Efficient coding of natural sounds: Learning procedure

To derive the filters:

- select sound segments randomly from sound ensemble
- optimize filter shapes to maximize coding efficiency

What sounds should we use?

What are auditory systems adapted for?

- localization / environmental sounds?
- communication / vocalizations?
- specific tasks, e.g sound discrimination?

We used the following sound ensembles:

- non-harmonic environmental sounds (e.g. footsteps, stream sounds, etc.)
- animal vocalizations (rainforest mammals, e.g chirping, screeching, cries, etc.)
- speech (samples from 100 male and female speakers from the TIMIT corpus)

#### Results of adapting filters to different sound classes



Efficient filters for speech:



Efficient filters for environmental sounds: Efficient filters for animal vocalizations:



- Each result shows only a subset
- Auditory nerve filters best match those derived from environmental sounds and speech
- learning movie

#### Upsampling removings aliasing due to periodic sampling



#### A combined ensemble: env. sounds and vocalizations



Efficient filters for speech:



Can vary along the continuum by changing relative proportion, best match is 2:1  $\Rightarrow$  speech is well-matched to the auditory code

#### Can decorrelating models also explain data?

Redundancy reduction models that adapt weights to decorrelate output activies assume a Gaussian model:

 $\mathbf{x} \sim \mathcal{N}(\mathbf{x}|\boldsymbol{\mu}, \boldsymbol{\sigma})$ 

Under this model, the filters can be derived with principal component analysis. PCs of Environmental Sounds: Corresponding Power Spectra:

 $\Rightarrow$  just decorrelating the outputs does not yield time-frequency localized filters.

#### Why doesn't PCA work?

Check assumptions:

 $\mathbf{x} = \mathbf{As} \text{ and } \mathbf{x} \sim \mathcal{N}(\mathbf{x} | \boldsymbol{\mu}, \sigma)$ 

 $\Rightarrow$  distribution of  ${\bf s}$  should also be Gaussian.

Actual distribution of filter coefficients:



### Efficient coding of sparse noise



Efficient filters are delta functions that represent different time points in the analysis window.

...but what about the auditory system?

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#### Auditory filters estimated by reverse correlation



Cat auditory "revcor" filters:



#### **Revcor filter predictions of auditory nerve response**



- stimulus is white noise
- histogram: measured auditory nerve response
- smooth curve: predicted response

#### Conclusion:

Shape and distribution of revcor filters account for a large part of the auditory sensory code.

We want to match more than just individual filters:

How do we characterize the population?



#### Schematic time-frequency distributions



time

time



#### Animal vocalizations:



#### Tiling trends follow power law



#### **Does equalization of power explain these data?**



#### Comparison to auditory population code



Filter sharpness characterizes how bandwidth changes as a function of frequency

$$Q_{10\mathrm{dB}} = f_c / w_{10dB}$$



# Summary

Information theory and efficient coding:

- can be used to *derive* optimal codes for different pattern classes.
- explains important properties of sensory codes in both the auditory and visual system.
- gives insight into how our sensory systems are adapted to the natural environment.

Caveats

- Codes can only be derived within a small window
- Does not explain non-linear aspects of coding
- Models do not capture higher order structure

Coding natural sounds with spikes

#### Addressing some limitations of the current theory

The current model assumes the sound waveform is dividing into blocks:



Problems with block coding:

- signal structure is arbitrarily aligned
- code depends on block alignment
- difficult to encode non-periodic structure, e.g. rapid onsets

#### An efficient, shift-invariant model

The signal is modeled by a sum of events plus noise:

$$x(t) = s_1\phi_1(t-\tau_1) + \dots + s_M\phi_M(t-\tau_M) + \epsilon(t).$$

The events  $\phi_m(t)$ :

- can be placed at arbitrary time points  $au_m$
- are scaled by coefficients  $s_m$

#### Solution after optimization: 105 dB SNR



#### Time shifting

