Sparse Signal Representation in Digital and Biological Systems

Matthew Guay

University of Maryland, College Park
Department of Mathematics

Norbert Wiener Center
for Harmonic Analysis and Applications

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Introduction

This work focuses on the implications of signal sparsity in biology, from two very different perspectives.

**CS-ET**: in what sense are nanometer-scale images of biological structures sparse? Can that sparsity be exploited by compressed sensing?

**Sparse olfactory coding**: How, and why, do Kenyon cells in locust olfactory processing networks generate sparse sensory codes?
Electron tomography served as a focal point for understanding compressed sensing and sparse mathematical signal processing.

Signals are vectors in a space of voxel intensities, measurements and representations are linear transforms of the signal.

Question: Can we use compressed sensing to better recover tomograms from undersampled measurement data?
Sparse olfactory coding in locusts

- **Locust olfaction** serves as a common model system for studying **sparse sensory coding** in neuroscience.

- **Lifetime sparsity**: An active Kenyon cell spikes only at onset and possibly offset of a stimulus.

- **Population sparsity**: A small percentage of the Kenyon cell population emit spikes in response to an odor stimulus.

- **Question**: How do locust olfactory population dynamics give rise to this behavior?
Signal representation

- **Signal**: A vector $f \in \mathbb{R}^M$ for some $M$.

- A signal model describes the relationships between signals and their measurements and representations.

- **Linear signal model**: Used in the CS-ET project. Signals are represented as linear combinations of basis or frame vectors.

- **Dynamical system signal model**: Used in the locust olfaction project. Signal representations are time-varying states of populations of neurons, whose relationships to the signal are described by nonlinear ODEs.
A vector $x$ is **sparse** if its $\ell^0$ norm:

$$||x||_0 = \#\{x_i \in x | x_i \neq 0\}$$

is small.

Sparse linear signal representations aid machine learning by capturing statistical regularities within a class of signals of interest.

Sparse neural signal representations evidently aid organisms for this and additional reasons.
Compressed sensing

- **Compressed sensing (CS):** The recovery of a sparse signal \( f \in \mathbb{R}^M \) from appropriately-chosen measurements.

- **Measurement vectors:** A collection of \( D \) vectors \( \{\varphi_i\}_{i=1}^D \subseteq \mathbb{R}^M \). Each measurement \( i \) is \( \langle f, \varphi_i \rangle \).

- **Representation vectors:** A basis or frame \( \{\psi_j\}_{j=1}^N \) for \( \mathbb{R}^M \).

- **Stack measurement vectors** in rows of a measurement matrix \( \Phi \in \mathbb{R}^{D \times M} \). **Stack representation vectors** in rows of a representation matrix \( \Psi \in \mathbb{R}^{N \times M} \).
Compressed sensing

- **Sparse signal model**: An *a priori* assumption that $f = \Psi c$ for some $c \in \mathbb{R}^N$ with small $\ell^0$ norm.

- In the presence of noise or modeling error, signals are more likely compressible: $f \approx \Psi c$ to some suitable level of accuracy.

- $\epsilon$-compressibility ratio of a vector $x$ is the proportion of vector components with magnitude greater than $\epsilon \|x\|_\infty$.

- Most existing CS results focus on the cases where $\Psi$ is an orthonormal basis or tight frame, where $f = \Psi^T \Psi f$. 
Compressed sensing

- **Goal**: Given measurements $y = \Phi f$, recover $f$ even if $D \ll M$ as:

  $$f^* = \arg \min_{f \in \mathbb{R}^M} ||\Psi f||_0 \text{ such that } y = \Phi f. \quad (2)$$

- Equivalent for some choice of $\lambda$ to the more useful:

  $$f^* = \arg \min_{f \in \mathbb{R}^M} ||\Phi f - y||_2^2 + \lambda ||\Psi f||_0 \quad (3)$$

- Equation (3) is computationally intractible, we focus on the **convex relaxation** (Basis Pursuit Denoising):

  $$f^* = \arg \min_{f \in \mathbb{R}^M} ||\Phi f - y||_2^2 + \lambda ||\Psi f||_1 \quad (4)$$
Mutual coherence

- Mutual coherence can be used to obtain an upper bound on the number of measurements required for Equation (4) to recover an $s$-sparse signal $f$.

- **Mutual coherence**: Given an orthogonal measurement matrix $\Phi$ with $||\varphi_i||_2 = \sqrt{M}$ for all $i \in [1, D]$, and an orthonormal representation basis $\Psi$, the mutual coherence of $\Phi$ and $\Psi$ is

\[
\mu(\Phi, \Psi) = \max_{i,j} |\langle \varphi_i, \psi_j \rangle| .
\]  

(5)

- **Theorem** (Candés, Romberg, 2007): Given $D$ measurements of an $s$-sparse signal $f$, Equation (4) recovers $f$ if

\[
D \geq C \cdot s \cdot \mu^2(\Phi, \Psi) \cdot \log M,
\]  

(6)

for some small constant $C$. 


The sparse coding hypothesis

- The **sparse coding hypothesis**: Information within a neural population is encoded in a small number of active neurons at each point in time.

- **Population sparsity**: At a fixed point in time, a small proportion of neurons in a population are active.

- **Lifetime sparsity**: A fixed neuron is active for a small proportion of time within an interval of interest.

- Sparse codes minimize overlap between representations of distinct stimuli, useful for associative memory. They are energy efficient, and exploit the statistics of sensory input.

- Found in sensory processing layers across the animal taxonomy, for all sensory modalities.
The sparse coding hypothesis

- Why can sparse codes represent natural stimuli?

- **Hypothesis**: Measurement vectors derived from natural environments lie along a low-dimensional subspace of the ambient measurement space.

- Sparse, overcomplete representations efficiently decompose signal information as a combination of a small number of features.

- In this work, I investigate the mechanisms which drive populations of nonlinear dynamical systems to produce sparse representations of olfactory sense data.
The sparse coding hypothesis

Figure: A stylized depiction of measurement state spaces and the subspace occupied by natural environments. Taken from (Olshausen, Field, 2004).
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Tomography - Producing a 3D reconstruction of a specimen by measuring changes in penetrating waves (or particles) which are sent through it.

- Computed tomography (CT), using X-rays.
- Electron tomography (ET), using electrons.

Electron tomography (ET) - 3D imaging using electron beams via a transmission electron microscope (TEM) or scanning transmission electron microscope (STEM).
Our ET data

- Each image is a projection of the rotated object, a sequence of images indexed by rotation angle is a tilt series.
- **Bright field** (BF) STEM imaging: detectors measure unscattered electrons passing through the specimen.
- **Dark field** (DF) STEM imaging: detectors measure electrons scattered by the specimen.
- Projection contrast comes from density-dependent differences in electron scattering within the specimen.
- Simulated phantom datasets were used to compare the efficacy of our CS-ET implementation with similar previous work.
From tomography to Radon transforms

- A beam of $n_0$ electrons travels along line $L$ through the specimen at each measurement location. Some $n$ electrons pass through undeviated.

- The ratio $\frac{n}{n_0}$ can be related to line integrals of an electron density function $f(x) : \mathbb{R}^3 \rightarrow \mathbb{R}$ via the Beer-Lambert law:

$$\log \left( \frac{n}{n_0} \right) \propto \int_L f(x) \, |dx|$$

- The function $f$ forms the tomogram recovered from the projection data.
Radon transform - for $f : \mathbb{R}^2 \to \mathbb{R}$ and any line $L \subseteq \mathbb{R}^2$,
\[
Rf(L) = \int_L f(x) |dx|.
\] (8)

This space of lines can be parametrized by a normal angle $\theta$ and a distance coordinate $s$:
\[
Rf(\theta, s) = \int_{-\infty}^{\infty} f((t \sin \theta + s \cos \theta), (-t \cos \theta + s \sin \theta)) \, dt.
\]
Parallel beam tomography used in ET decomposes 3D reconstruction into multiple independent 2D reconstruction problems.

For each plane normal to the rotation axis, tomographic measurements provide samples \( \{R_f(\theta_i, s_j)\}_{i \in I, j \in J} \) for some finite sets \( I, J \).

Measurement limitations make tomogram recovery an ill-posed Radon transform inversion problem.
Each sample $Rf(\theta_i, s_j)$ corresponds to a measurement vector $\varphi_{ij} \in \mathbb{R}^D$, all stacked in a measurement matrix $\Phi$.

Representation operators $\Psi$ used in this work: Identity mapping, discrete DB8 wavelet transform, or the total variation operator $TV$.

For a 2D discrete image $f$,

$$TV f \triangleq \sqrt{\Delta_x^+ f + \Delta_y^+ f}$$

for forward finite $x-$ and $y-$differences $\Delta^+$. 
Theoretical challenges

- There is little existing theory for CS recovery of signals with sparse images under nonlinear transforms (e.g. $TV$).

- ET measurement matrices $R$ are deterministic. $R$ and the sparsifying transforms studied here do not possess mutual coherences useful for theoretical analysis of the procedure.
CS-ET mutual coherence

Figure: A histogram of $\langle \varphi_i, \psi_j \rangle$ for $\varphi_i \in R$ and $\psi_j \in I$, an identity matrix. These values are equivalent to the components of Radon transform measurement vectors, taken from a Radon transform of a $256 \times 256$ image at angles from $-70^\circ$ to $70^\circ$ at $5^\circ$ increments.
CS-ET mutual coherence

Figure: A histogram of $\langle \varphi_i, \psi_j \rangle$ for $\varphi_i \in R$ and $\psi_j \in W$, the DB8 discrete wavelet transform on $\mathbb{R}^{256^2}$. Due to computational limitations, only 10% of the possible $\langle \varphi_i, \psi_j \rangle$ combinations were computed.
Numerical methods

- Our CS-ET algorithm computes each $x - z$ slice $f^*$ of a tomogram as

$$f^* = \arg \min_{f \in \mathbb{R}^D} \| Rf - y \|_2^2 + \lambda_1 \| f \|_1 + \lambda_2 \| TVf \|_1 + \lambda_3 \| Wf \|_1.$$  \hspace{1cm} (9)

- $R$ is a digital Radon transform, $y$ is measurement data, and the $\lambda_i$ are regularization weights.

- 1024 $x - z$ slices, each approximately $1024 \times 100$.

- We use the split Bregman algorithm, a GPU-based library for Radon transform computation, and concurrent computations for multiple $x - z$ slices to solve this problem efficiently.
Tomogram coordinate system

**Figure:** An illustration of the coordinate system used with 3D tomograms. A tomogram is assembled from independent 2D reconstructions parallel to the $x - z$ plane. An overhead view, parallel to the $x - y$ plane, is useful for visually inspecting tomogram structure.
Nanoparticle phantom reconstruction comparison
BF STEM reconstruction $x \rightarrow z$ comparison

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<tr>
<th></th>
<th>CS-ET</th>
<th>SIRT</th>
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DF STEM reconstruction $x - z$ comparison

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BF STEM reconstruction \( x - y \) comparison

- CS-ET
- SIRT
- WBP

1x

3x

6x
DF STEM reconstruction $x - y$ comparison

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The $x - z$ slices of the biological STEM datasets are markedly less sparse than the nanoparticle phantom.

This is a likely source for the disparity in CS-ET performance compared to other reconstruction methods, between the phantom and STEM datasets.

The correlation between application domain and the structural complexity of specimens is important for determining where CS-ET will be most relevant.
BF-STEM and DF-STEM dataset compressibility expressed as $\varrho$, defined as the STEM datasets’ compressibility ratios divided by the nanoparticle phantom’s sparsity ratios in each of the three transform domains studied.

All STEM dataset compressibility values were calculated separately for each $x - z$ slice and ordered by decreasing compressibility.
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Long-standing question: How do brains capture, filter, and integrate the information about the environment provided by the senses?

**Sensory receptors**: neurons whose membrane potentials are directly influenced by external (vision, olfaction) or internal (nociception, proprioception) environmental state.

Receptors form the first level in a hierarchy of sensory processing centers within brains.
Locust olfaction

- Olfactory systems in insects provide useful models for studying neuron population dynamics.

- Insect olfactory processing systems exhibit complex behavior, but contain relatively few ($\sim 10^6 - 10^7$) neurons and are well-characterized.

- This research focuses on locust olfaction as a model system.

- What network properties cause Kenyon cells (KCs) to exhibit both lifetime and population sparsity?
Figure: $\sim 50000$ olfactory receptor neurons (ORNs) synapse onto $\sim 830$ projection neurons (PNs) and $\sim 300$ local neurons (LNs). PNs synapse onto $\sim 50000$ KCs. Used with permission, (DiLorenzo et al., 2014) Chapter 11.
In the locust, an active KC emits a small number of spikes in response to changes in stimulus identity and concentration, i.e., onset spiking and offset spiking.

Sensory adaptation in ORNs drives ORN activity levels towards a baseline during prolonged exposure to a stimulus.

The time course of this adaptation creates a window of elevated PN activity after a stimulus change.

Relevant to insect behavior, e.g., for detecting boundaries in odor plumes.
Onset and offset spiking

Figure: PN activity data taken from (Mazor, Laurent 2005). All PN population statistics are calculated over time using activity binned into 50ms windows.
Onset and offset spiking

- During stimulation, increased LN→PN feedback inhibition creates oscillatory PN activity which enforces temporal synchrony among active PNs.

- At stimulus onset, increased PN firing rates and synchronous activity patterns lead to onset spiking in KCs.

- LN activity tracks stimulus offset closely, but some PNs continue to spike due to ORNs exhibiting offset activity.

- Stimulus offset creates increased PN firing rates, but decreased temporal coherence.
Modeling offset spiking

**Question**: What is the relationship between the temporal coherence of a KC’s active PN inputs, and the number of active PNs required to elicit a KC spike?

A suitably-accurate computational model can be used to describe this relationship.

**Modeling goal**: use a simulation of a KC and its PN synapses to determine how responsive KCs are to different numbers of PN spikes arriving in temporal windows of different lengths.

How to verify that the model is an accurate reflection of biological KCs?
Model overview

- One KC neuron with a variable number (0-430) of PN$\rightarrow$KC synapses.

- $N$ synapses activate randomly within a specified time window $[t_0, t + 0 + \Delta t]$ for varying values of $N$ and $\Delta t$.

- KC membrane potential is modeled by a Hodgkin-Huxley-type ODE. Synapses are modeled by a standard first-order ODE.

- Implemented in C++ using a 4-step Runge-Kutta (RK4) numerical integrator, time-step $h = 0.03\text{ms}$.
KC model

- **KC model**: A single-compartment Hodgkin-Huxley-type neuron.
- **KC membrane potential** $V$ is governed by the an ODE of the form:

$$C \frac{dV}{dt} = -(I_{\text{leak}} + I_{\text{int}} + I_{\text{syn}}) \quad (10)$$

- $C$ is a capacitance constant, $I_{\text{leak}}$ is a leakage current, $I_{\text{int}}$ is an intrinsic ionic current, $I_{\text{syn}}$ is a synaptic current.
KC model

- $I_{\text{leak}}$ consists of two components: a “general” leakage current $I_L = g_L(V - E_L)$ and a potassium leakage current $I_{KL} = g_{KL}(V - E_{KL})$.

- Each $g$ is a conductance variable and $E$ a reversal potential.

- $I_{\text{int}}$ has five components: $I_{\text{int}} = \sum_{i=1}^{5} g_i m_i^{M_i} h_i^{N_i} (V - E_i)$, with $g_i, E_i$ as before, $m_i(t)$ and $h_i(t)$ are activation and inactivation variables, and $M_i, N_i$ are experimentally-determined integers.
KC model

- Ionic current conductances:

<table>
<thead>
<tr>
<th>Current</th>
<th>Conductance</th>
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<tr>
<td>$I_{Na}$</td>
<td>$g_{Na} = 26.1 \mu S$</td>
</tr>
<tr>
<td>$I_{K(Ca)}$</td>
<td>$g_{K(Ca)} = 0.29 \mu S$</td>
</tr>
<tr>
<td>$I_{K,A}$</td>
<td>$g_{K,A} = 0.0145 \mu S$</td>
</tr>
<tr>
<td>$I_{K}$</td>
<td>$g_{K} = 2.9 \mu S$</td>
</tr>
<tr>
<td>$I_{Ca}$</td>
<td>$g_{Ca} = 0.029 \mu S$</td>
</tr>
</tbody>
</table>

- $I_{syn}$ is a sum of individual synaptic currents of the form $g[O](V - E)$, one for each PN$\rightarrow$KC synapse. Here, $g$ and $E$ are the same as before, and $[O](t)$ is a proportion of open synaptic channels.
[\mathcal{O}(t)] for each PN→KC synapse is updated as

\[
\frac{d[\mathcal{O}]}{dt} = \alpha(1 - [\mathcal{O}])[T] - \beta[\mathcal{O}].
\] (11)

\([T](t)\) measures transmitter concentration, \(\alpha\) is a synaptic current rise rate parameter, and \(\beta\) is a synaptic current decay rate parameter.

Synapse strength \(g\) is not uniform across PN→KC connections.
Synaptic model

- To test the effect of coordinated PN spiking on the KC, each of $N$ synapses is set to activate at a time drawn uniformly at random from the interval $[t_0, t_0 + \Delta t]$.

- Biological PNs exhibit nonzero baseline firing rates ($\sim 2.5\text{Hz}$) which may be important for tuning the KC’s responsiveness to coordinated spikes.

- Model this by adding $415 - N$ synapses with no coordinated spiking time, to all $415$ synapses assign random spiking events with exponentially-distributed interarrival times ($\lambda = 0.0025$).
Simulation protocol

- For each $N$ in $\{50 : 10 : 200\}$ and each $\Delta t$ in
  $\{10 : 10 : 60\} \cup \{100 : 15 : 400\}$, simulate $N$ synapses with
  activation times in $[t_0, t_0 + \Delta t]$. Run the simulation for
  $K = 100$ trials.

- Using the $K$ trials, for each parameter configuration construct
  a KC peristimulus time histogram (PSTH).

- PSTH: For each trial, bin spike counts in time, then average
  the binned counts across all trials.
KC PSTHs

 KC PSTH, 20.0 ms input window
 100 trials per plot, 2.0 ms bins
 50 synapses
 60 synapses
 70 synapses
 80 synapses
 90 synapses
 100 synapses
 110 synapses
 120 synapses

 KC PSTH, 50.0 ms input window
 100 trials per plot, 2.0 ms bins
 50 synapses
 130 synapses
 60 synapses
 140 synapses
 70 synapses
 150 synapses
 80 synapses
 160 synapses
 90 synapses
 170 synapses
 100 synapses
 180 synapses
 110 synapses
 190 synapses
 120 synapses
 200 synapses

Time (ms)
KC PSTHs

KC PSTH, 100.0 ms input window
100 trials per plot, 2.0 ms bins
50 synapses

KC PSTH, 130.0 ms input window
130 synapses

Time (ms)
Model validation

- Computational modeling indicates that the 150-200 PNs spiking across a 150-300ms interval (like at stimulus offset) are unlikely to trigger a KC spike.

- Is this modeling error? How do we assess the biological relevance of this model?

- **Goal**: Model should conform with known activity statistics for PN→KC interactions and KC behavior.

- Focuses so far: parameter selection, synaptic conductance distribution, KC resting potential and firing threshold, KC membrane time constant.
Explaining KC population sparsity

- Useful KC population analysis is difficult to analyze as a large nonlinear ODE model.
- To what extent can KC population activity be explained more simply?
- **Goal:** Produce activity statistic distributions for KCs, in a simplified PN and KC network.
- Choose statistics to explain how KC activity is sparse, and how KC activity is a representation of sensory information.
**Simple model:** KC activity is binned over time. Within each time bin, use a binary active/silent model for each PN and KC.

A KC is connected to $K = 415$ of the 830 PNs. The PN target set is chosen uniformly at random from the possible subsets of PNs.

A KC is active in a time bin if $\tau = 100$ or more PNs are active.
Derive that

\[
\varrho(M) = P(\text{active KC}| M \text{ active PNs}) = \sum_{k=\tau}^{M} \binom{M}{k} \binom{830-M}{K-k} \binom{830}{k}. 
\]  

(12)

For this model, 150 active PNs marks a transition from a low probability of KC activity to a high probability.

For a fixed \( M \) and 50000 KCs, we compute that

\[
P(s \text{ total KC spikes}) = \binom{50000}{s} \varrho(M)^s (1 - \varrho(M))^{50000-s}.
\]  

(13)
Figure: Single time bin plot of $P(s$ total KC spikes) for several values of $M$, the number of active PNs.
KC response distinguishability

- Define $B_i$ as the binary time series of a KC population in response PN population time series $A_i$.

- **Goal:** Compute the distribution of $\|B_1 - B_2\|_1$, for two PN activity series $A_1, A_2$.

- $A_1$ and $A_2$ have a fixed number of active PNs in each time bin, chosen uniformly at random from the population.

- **Result:** $\|B_1 - B_2\|_1$ is large with high probability, but specifics are dependent on a number of parameters.
Thank you!
Emmanuel Candes and Justin Romberg.

Sparsity and incoherence in compressive sampling.


Patricia M DiLorenzo and Jonathan D Victor.

*Spike timing: mechanisms and function.*

CRC Press, 2014.
Works cited II

Ron A Jortner, S Sarah Farivar, and Gilles Laurent.

A simple connectivity scheme for sparse coding in an olfactory system.


Ofer Mazor and Gilles Laurent.

Transient dynamics versus fixed points in odor representations by locust antennal lobe projection neurons.

Works cited III

Bruno A Olshausen and David J Field.
Sparse coding of sensory inputs.


Javier Perez-Orive, Maxim Bazhenov, and Gilles Laurent.
Intrinsic and circuit properties favor coincidence detection for decoding oscillatory input.

Appendix: Model parameter selection

- (Perez-Orive et al. 2004) describes a Hodgkin-Huxley model of the locust KC. Our model is based on this one.

- Errors in the paper required communication with Maxim Bazhenov to obtain their model source code.

- Our model uses an $I_{Ca}$ current and calcium dynamics described in the source code, differing from the paper.

- Leakage conductance $g_L$ has been increased from $2.9 \times 10^{-3}$ to $2.9 \times 10^{-2}$, fixing the KC resting potential and making the KC less quiescent.
Appendix: Synaptic conductance distribution

- PN→KC synaptic conductances are not uniform across the population. Their distribution may be estimated from the EPSP amplitude distributions recorded in (Jortner et al. 2007).

- I created a conductance distribution function matching this distribution, then computed a simulated EPSP amplitude distribution to verify its match with the Jortner et al. data.
Figure: A comparison of a simulated peak EPSP distribution (left) and the equivalent data from (Jortner et al., 2007) (right).
Appendix: KC firing threshold

Figure: A comparison of a simulated KC’s firing threshold with a firing threshold distribution measured in (Jortner et al., 2007). A neuron’s firing threshold is defined here as the difference between resting potential and the point with largest second derivative during a spike response.
Appendix: KC membrane time constant

- **Membrane time constant**: Amount of time required for a neuron to transition \((1 - 1/e) \approx 63.2\%\) of the distance from a membrane potential depolarized by a square current pulse, back to equilibrium.

<table>
<thead>
<tr>
<th>Current (nA)</th>
<th>0.025</th>
<th>0.05</th>
<th>0.1</th>
<th>0.2</th>
<th>0.25</th>
</tr>
</thead>
<tbody>
<tr>
<td>STC (ms)</td>
<td>6.89</td>
<td>6.83</td>
<td>6.77</td>
<td>6.89</td>
<td>7.37</td>
</tr>
</tbody>
</table>

**Table**: Simulated KC membrane time constant measurements from square current pulses of several amplitudes. Comparisons with biological experiments are forthcoming.
Appendix: Future validation work

- Current validation procedures give little explicit comparison between simulated ionic current behaviors and their biological counterparts.

- A **voltage clamp** experiment gives more detailed information about the magnitude of ionic current flowing through a neuron at a variety of membrane potentials.

- Voltage clamps can be simulated - code is currently written, awaiting electrophysiological data to use for comparison.