Sparse Signal Representation in Digital and Biological Systems

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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?

Compressed sensing for electron tomography

- 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 $\boldsymbol{f} \in \mathbb{R}^M$ 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.

Sparse signal representation

- A vector $\boldsymbol{x}$ is sparse if its ℓ^0 norm:

$$||\boldsymbol{x}||_0 = \#\{x_i \in \boldsymbol{x} \mid x_i \neq 0\} \tag{1}$$

  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 $\boldsymbol{f} \in \mathbb{R}^M$ from appropriately-chosen measurements.

- Measurement vectors: A collection of D vectors $\{\boldsymbol{\varphi}_i\}_{i=1}^D \subseteq \mathbb{R}^M$. Each measurement i is $\langle \boldsymbol{f}, \boldsymbol{\varphi}_i \rangle$.

- Representation vectors: A basis or frame $\{\boldsymbol{\psi}_j\}_{j=1}^N$ 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 $\boldsymbol{f} = \Psi \boldsymbol{c}$ for some $\boldsymbol{c} \in \mathbb{R}^N$ with small ℓ^0 norm.

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

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

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

Compressed sensing

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

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

- Equivalent for some choice of λ to the more useful:

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

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

$$f^* = \underset{f \in \mathbb{R}^M}{\arg\min} ||\Phi f - y||_2^2 + \lambda ||\Psi f||_1 \qquad (4)$$

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 Φ with $||\varphi_i||_2 = \sqrt{M}$ for all $i \in [1, D]$, and an orthonormal representation basis Ψ, the mutual coherence of Φ and Ψ is

$$\mu(\Phi, \Psi) = \max_{i,j} |\langle \varphi_i, \psi_j \rangle|. \qquad (5)$$

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

$$D \geq C \cdot s \cdot \mu^2(\Phi, \Psi) \cdot \log M, \qquad (6)$$

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
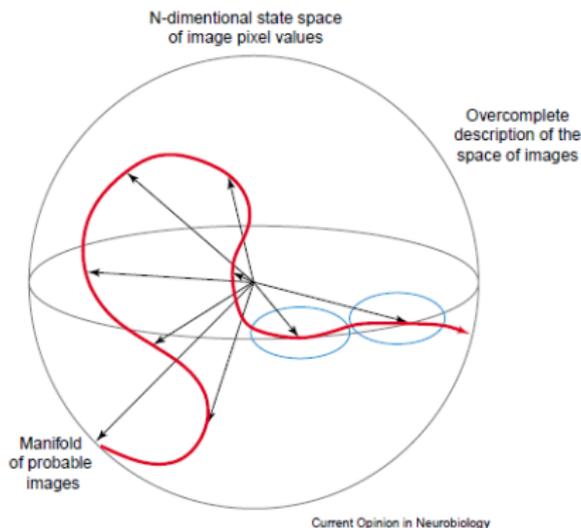
Figure: A stylized depiction of measurement state spaces and the subspace occupied by natural environments. Taken from (Olshausen, Field, 2004).

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Tomography

- 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 $f(\boldsymbol{x}) : \mathbb{R}^3 \to \mathbb{R}$ via the Beer-Lambert law:

$$\log\left(\frac{n}{n_0}\right) \propto \int_L f(\boldsymbol{x}) \, |d\boldsymbol{x}| \tag{7}$$

- The function f forms the tomogram recovered from the projection data.

From tomography to Radon transforms

- **Radon transform** - for $f : \mathbb{R}^2 \to \mathbb{R}$ and any line $L \subseteq \mathbb{R}^2$,

$$Rf(L) = \int_L f(\boldsymbol{x}) \, |d\boldsymbol{x}|. \qquad (8)$$

- This space of lines can be parametrized by a normal angle θ and a distance coordinate s:

$$Rf(\theta, s) = \int_{-\infty}^{\infty} f((t \sin\theta + s \cos\theta), (-t \cos\theta + s \sin\theta)) \, dt.$$

From tomography to Radon transforms

- 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 $\{Rf(\theta_i, s_j)\}_{i \in I, j \in J}$ for some finite sets I, J.

- Measurement limitations make tomogram recovery an ill-posed Radon transform inversion problem.

CS for tomography

- Each sample $Rf(\theta_i, s_j)$ corresponds to a measurement vector $\varphi_{ij} \in \mathbb{R}^D$, all stacked in a measurement matrix Φ.

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

- For a 2D discrete image f,

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

for forward finite $x-$ and $y-$differences Δ^+.

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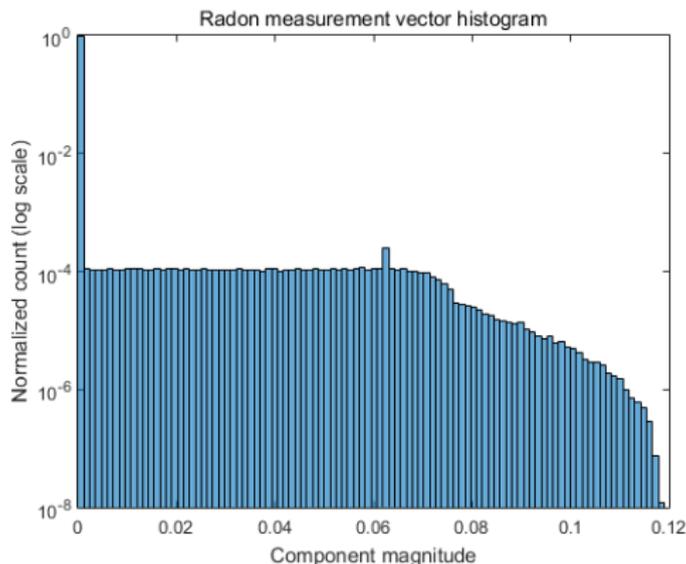
Figure: A histogram of $\langle \varphi_i, \psi_j \rangle$ for $\varphi_i \in R$ and $\psi_j \in I$, an identity matrix. These values are equivalent to the components of Radon transform measurement vectors, taken from a Radon transform of a 256×256 image at angles from $-70°$ to $70°$ at $5°$ increments.

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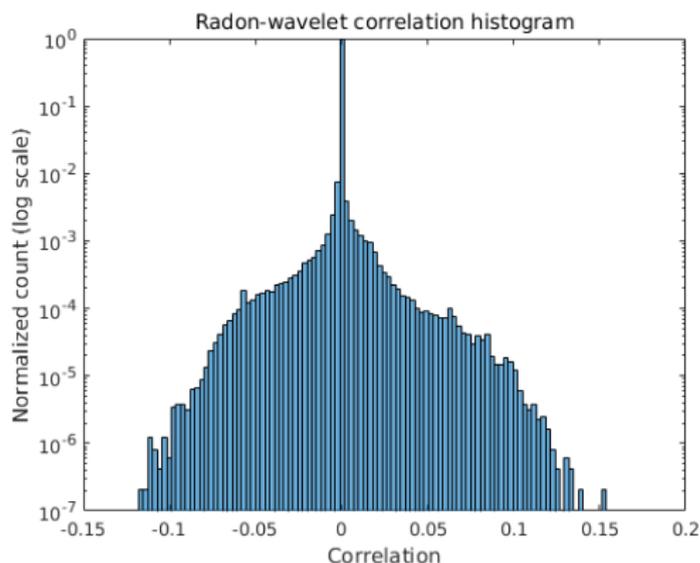
Figure: A histogram of $\langle \varphi_i, \psi_j \rangle$ for $\varphi_i \in R$ and $\psi_j \in W$, the DB8 discrete wavelet transform on $\mathbb{R}^{256^2}$. Due to computational limitations, only 10% of the possible $\langle \varphi_i, \psi_j \rangle$ combinations were computed.

Numerical methods

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

$$\boldsymbol{f}^* = \arg\min_{\boldsymbol{f} \in \mathbb{R}^D} ||R\boldsymbol{f} - \boldsymbol{y}||_2^2 + \lambda_1 ||\boldsymbol{f}||_1 + \lambda_2 ||TV\boldsymbol{f}||_1 + \lambda_3 ||W\boldsymbol{f}||_1. \tag{9}$$

- R is a digital Radon transform, $\boldsymbol{y}$ is measurement data, and the λ_i are regularization weights.

- 1024 $x - z$ slices, each approximately 1024×100.

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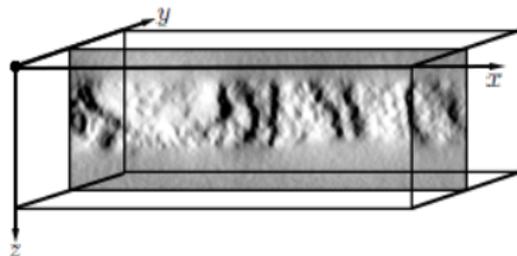
Figure: An illustration of the coordinate system used with 3D tomograms. A tomogram is assembled from independent 2D reconstructions parallel to the $x - z$ plane. An overhead view, parallel to the $x - y$ plane, is useful for visually inspecting tomogram structure.

Nanoparticle phantom reconstruction comparison
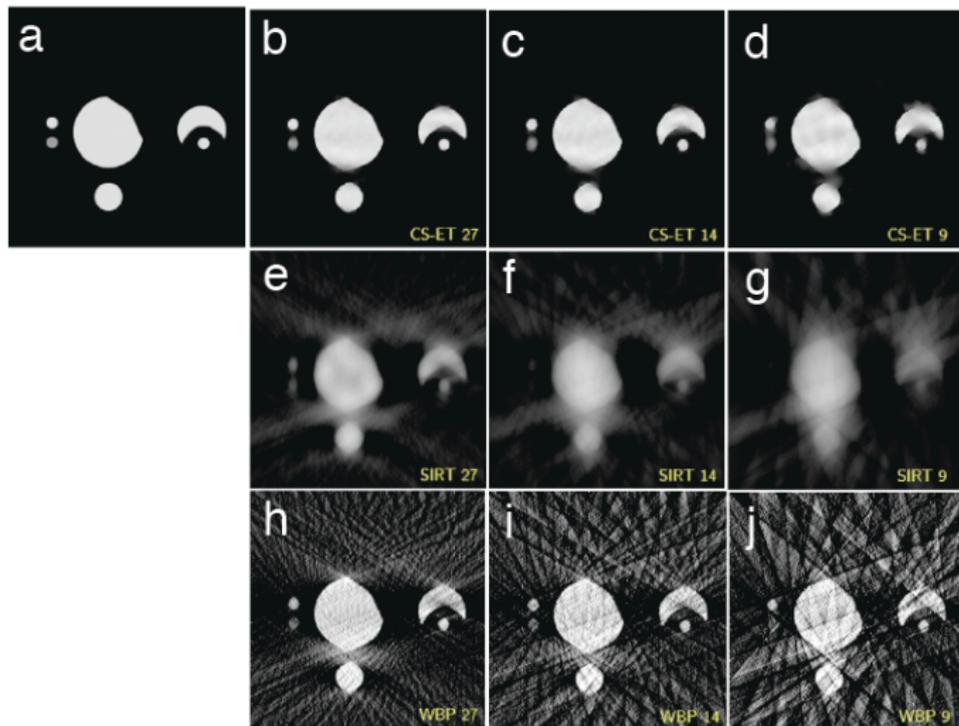
BF STEM reconstruction $x - z$ comparison
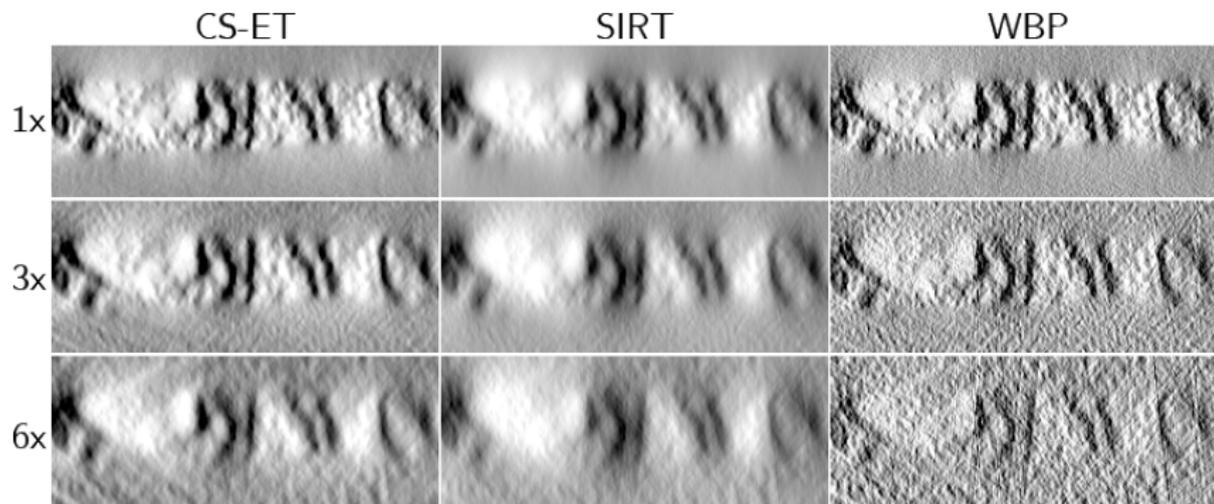
DF STEM reconstruction $x - z$ comparison
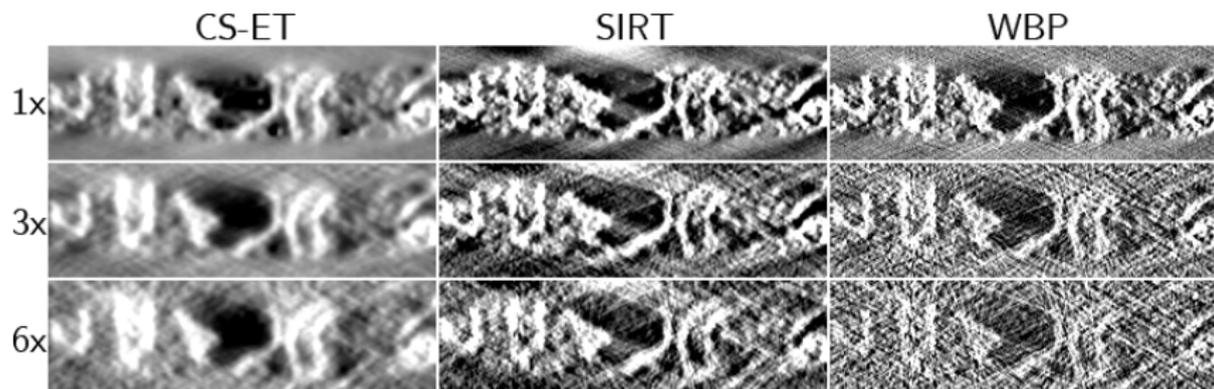
BF STEM reconstruction $x - y$ comparison
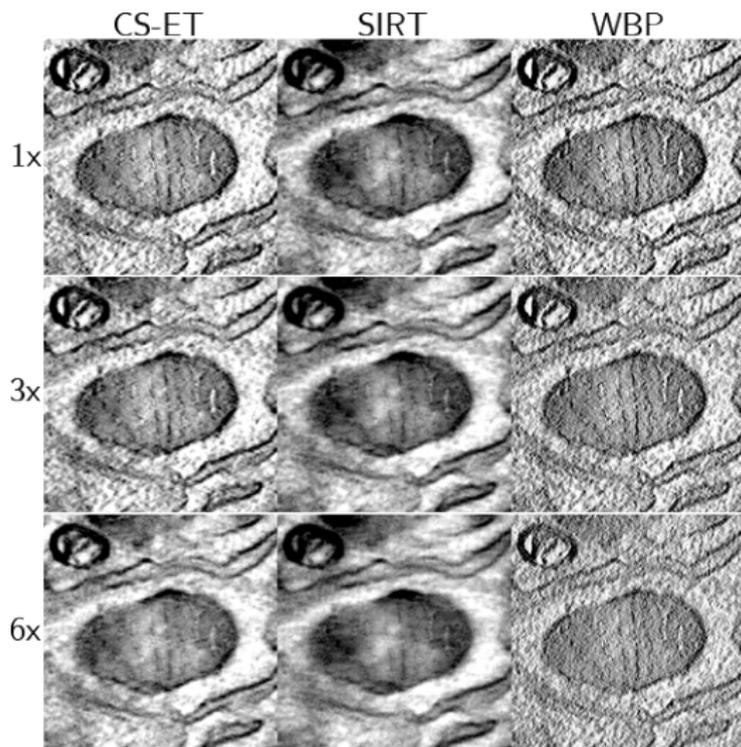
DF STEM reconstruction $x - y$ comparison
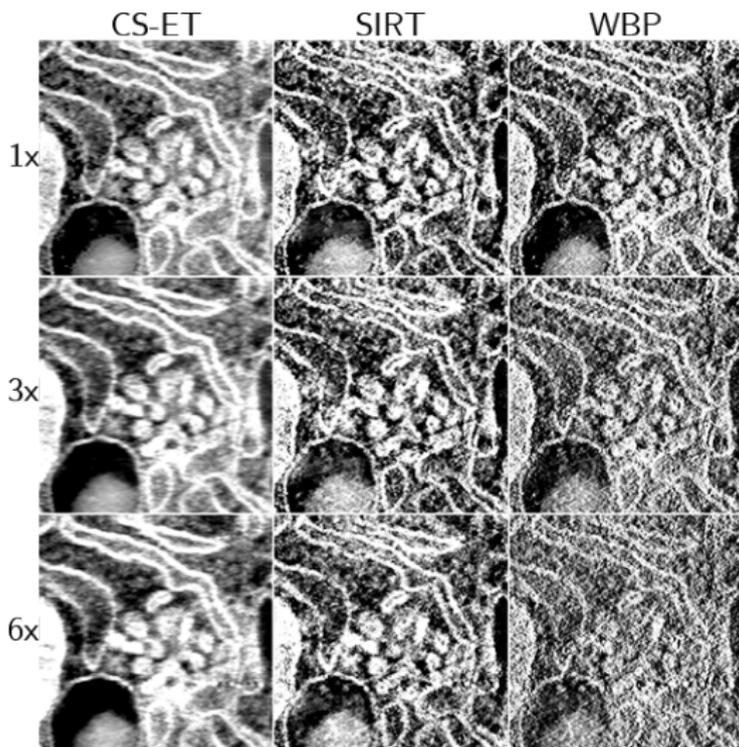
CS-ET and structural sparsity

- 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.

CS-ET and structural sparsity
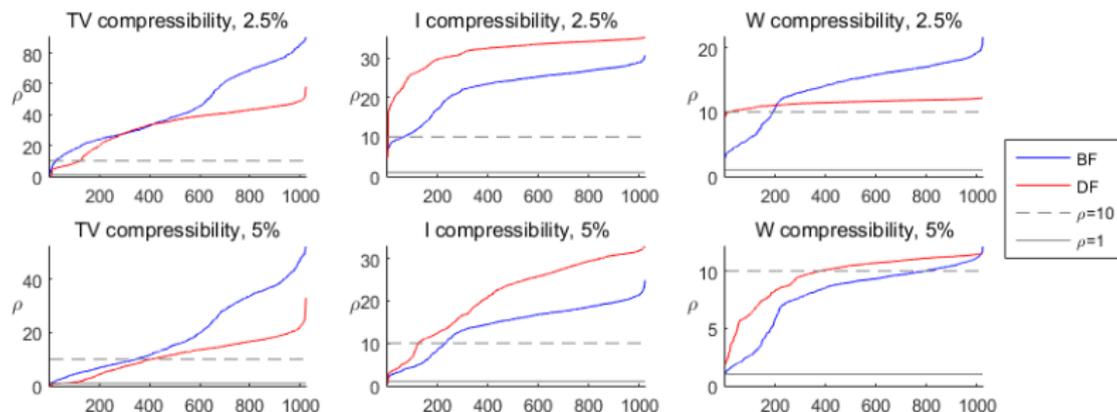
- BF-STEM and DF-STEM dataset compressibility expressed as ϱ, defined as the STEM datasets' compressibility ratios divided by the nanoparticle phantom's sparsity ratios in each of the three transform domains studied.

- All STEM dataset compressibility values were calculated separately for each $x - z$ slice and ordered by decreasing compressibility.

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Compressed Sensing for Electron Tomography
Sparse Olfactory Coding in the Locust

Background
Modeling offset spiking
KC population sparsity

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Sensory processing

- 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.

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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?

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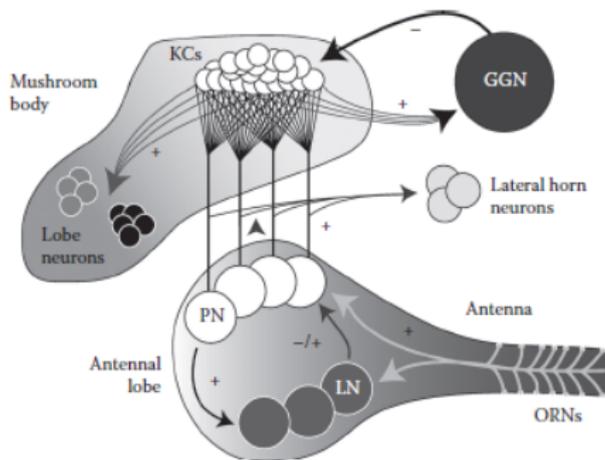
Locust olfaction

Figure: ~ 50000 olfactory receptor neurons (ORNs) synapse onto ~ 830 projection neurons (PNs) and ~ 300 local neurons (LNs). PNs synapse onto ~ 50000 KCs. Used with permission, (DiLorenzo et al., 2014) Chapter 11.

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KC lifetime sparsity

- 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.

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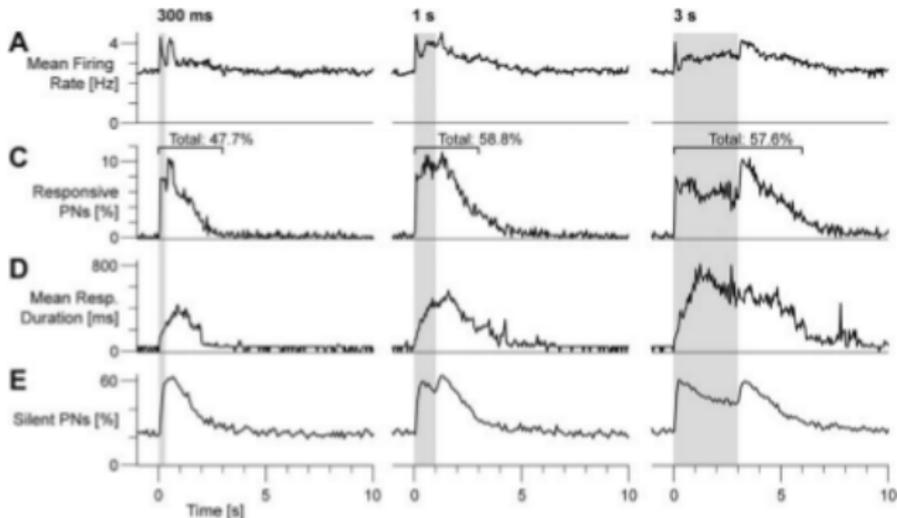
Figure: PN activity data taken from (Mazor, Laurent 2005). All PN population statistics are calculated over time using activity binned into 50ms windows.

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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.

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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?

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Model overview

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

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

- 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 $h = 0.03$ms.

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KC model

- KC model: A single-compartment Hodgkin-Huxley-type neuron.

- KC membrane potential V is governed by the an ODE of the form:

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

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

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KC model

- I_{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_{int} has five components: $I_{int} = \sum_{i=1}^{5} g_i m_i^{M_i} h_i^{N_i} (V - E_i)$, 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.

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KC model

- Ionic current conductances:

I_{Na}	$g_{Na} = 26.1\,\mu S$	I_K	$g_K = 2.9\,\mu S$
$I_{K(Ca)}$	$g_{K(Ca)} = 0.29\,\mu S$	I_{Ca}	$g_{Ca} = 0.029\,\mu S$
$I_{K,A}$	$g_{K,A} = 0.0145\,\mu S$		

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

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Synaptic model

- $[O](t)$ for each PN$\rightarrow$KC synapse is updated as

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

- $[T](t)$ measures transmitter concentration, α is a synaptic current rise rate parameter, and β is a synaptic current decay rate parameter.

- Synapse strength g is not uniform across PN$\rightarrow$KC connections.

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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 (~ 2.5Hz) 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 ($\lambda = 0.0025$).

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Simulation protocol

- For each N in $\{50 : 10 : 200\}$ and each Δt 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.

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KC PSTHs

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KC PSTHs

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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.

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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.

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Binary time series model

- 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.

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KC population sparsity

- Derive that

$$\varrho(M) = P(\text{active KC}|M \text{ active PNs}) = \sum_{k=\tau}^{M} \frac{\binom{M}{k}\binom{830-M}{K-k}}{\binom{830}{k}}. \tag{12}$$

- 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

$$P(s \text{ total KC spikes}) = \binom{50000}{s}\varrho(M)^s(1 - \varrho(M))^{50000-s}. \tag{13}$$

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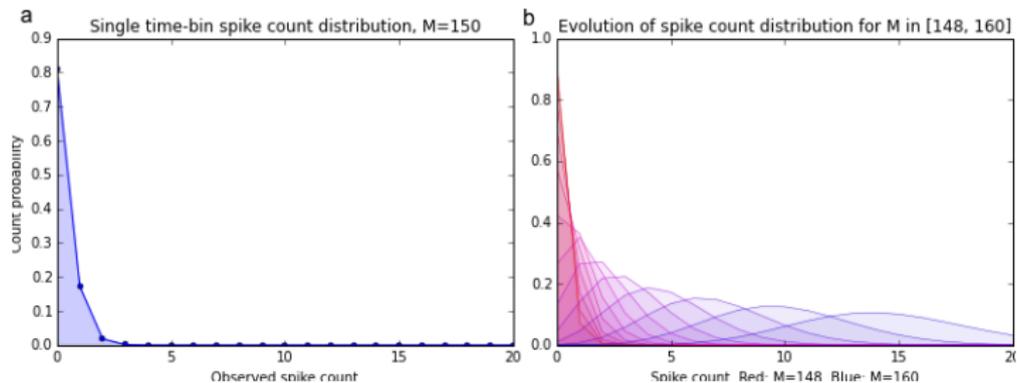
Figure: Single time bin plot of $P(s$ total KC spikes$)$ for several values of M, the number of active PNs.

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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.

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End

Thank you!

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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 2.9×10^{-3} to 2.9×10^{-2}, fixing the KC resting potential and making the KC less quiescent.

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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.

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Appendix: Synaptic conductance distribution
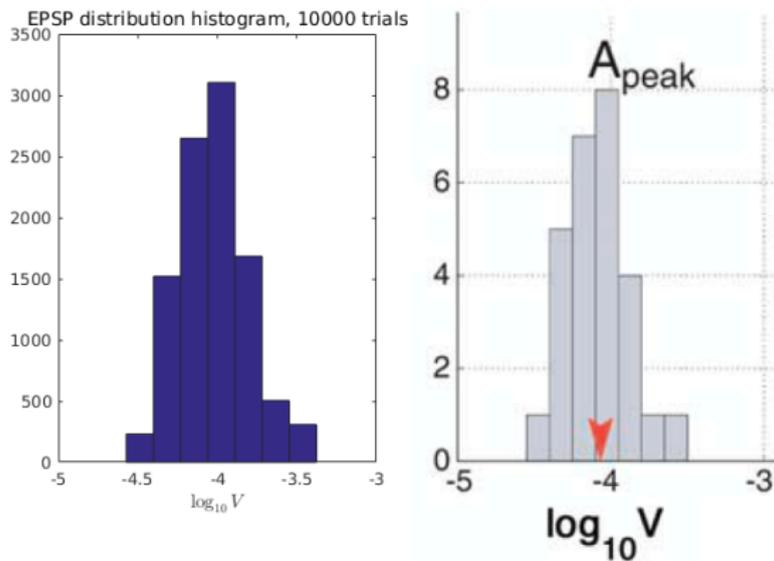
Figure: A comparison of a simulated peak EPSP distribution (left) and
the equivalent data from (Jortner et al., 2007) (right).

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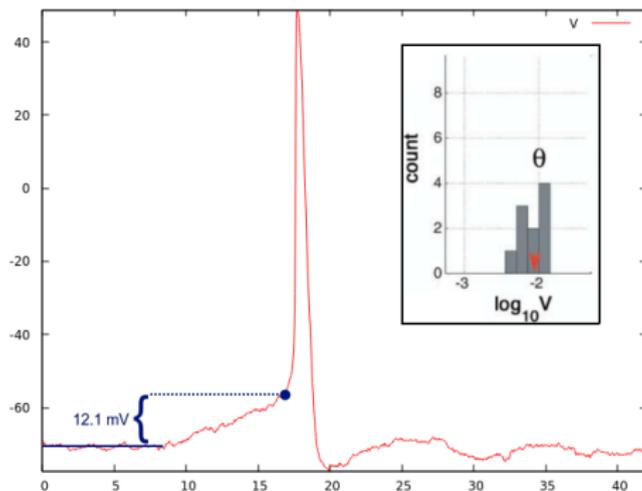
Figure: A comparison of a simulated KC's firing threshold with a firing threshold distribution measured in (Jortner et al., 2007). A neuron's firing threshold is defined here as the difference between resting potential and the point with largest second derivative during a spike response.

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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 as quare current pulse, back to equilibrium.

Current (nA)	0.025	0.05	0.1	0.2	0.25
STC (ms)	6.89	6.83	6.77	6.89	7.37

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

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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.