Construction of direction selectivity in V1: from simple to complex cells

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Statistical tests of V1 connectivity

- The large number of feed-forward and recurrent inputs to neurons in primary visual cortex (V1) makes it difficult to untangle **what** is being computed, and **how** such computations are implemented biologically in simple and complex V1 neurons [1,2,3].
- While intracellular recordings can separate the contribution of excitatory and inhibitory inputs, it cannot tease apart the effects of multiple excitatory inputs, which is necessary to address complex cell properties.

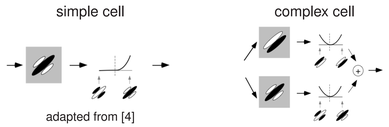
GOAL: Use extracellular data to identify the multiple inputs to V1 neurons & how they combine to generate direction selectivity (DS)

Background & Motivation

Random bar stimuli are a simple, relatively unbiased way to probe a cell wrt. motion perpendicular to its preferred orientation and determine its **spatiotemporal receptive field** (STRF).

Data provided by N. Rust & A. Movshon [1]
Extracellular recordings from macaque V1 cells during visual stimulation with patterns of optimally oriented bars, modulated by a binary m-sequence.

Models of simple and complex cells

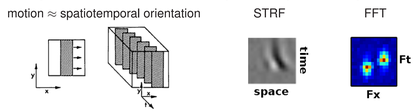


Simple Linear Nonlinear models and the energy model explain central features of orientation selective simple and complex cell responses in V1 [4].

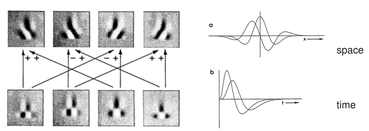
The energy model

Adelson & Bergen(1985) [7] suggested an abstract model for phase invariant **motion detectors** based on non-DS inputs. It explains DS simple and complex cell responses on a **conceptual level**.

2d representation of motion & spatiotemporal receptive fields



Constructing DS from spatiotemporally separable inputs



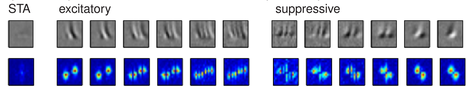
Questions left open by the energy model

- How can these combinations be biologically implemented?
- What do they tell us about more complicated response patterns?

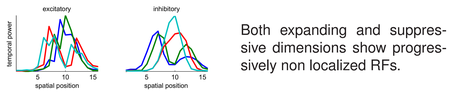
Nonlinear stimulus selectivity

We use **Spike Triggered Covariance (STC)** to identify the relevant subspace, i.e. the visual features that affect the firing rate of a cell [5].

Spatiotemporal STC features of an example complex cell:

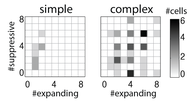


Problem: STC only identifies a set of dimensions that span the space containing the preferred features – **not the features themselves!**



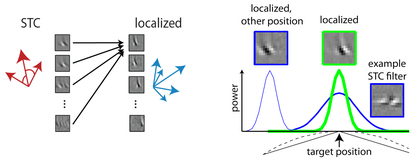
Both expanding and suppressive dimensions show progressively non localized RFs.

Most simple and complex cells show multiple expanding AND suppressive STC directions
Rust et al (2005)



Identifying biologically plausible filters

We assume inputs to V1 cells to be spatially confined → At each spatial position, we identify the n most localized features from STC space.

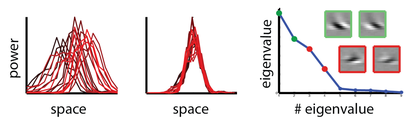


This results in an overcomplete set of localized filters:

RESULT 1: Localized features ...

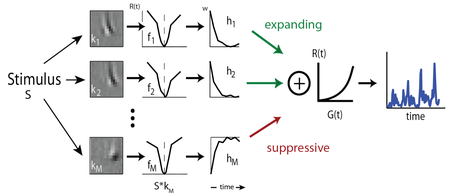
- form homogeneous filterbanks with **simple-cell-like spatiotemporal shape** (envelope, tilt & spatial frequency).
- are well described by a set of single quadrature pairs of filters that is spatially translated (for excitation and suppression).
- represent true inputs properties much more accurately than STC.

e.g. they recover the true inputs of a **simulated** complex cell



Complex cell stimulus selectivity can be characterized by pools of spatially shifted inputs with nearly identical properties.

Characterizing V1 computation



$$\text{firing rate} = F\Big(\sum_i h_i * f[S(t) * k_i]\Big)$$

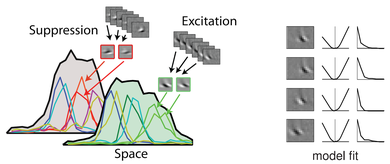
The Generalized Nonlinear Modeling framework (GNM) ...

- Represents an extension of the Generalized Linear Model (GLM, see e.g. [8]) using linear combinations of **nonlinear stimulus transformations** called 'modules' [3].
- Estimates shape of nonlinearities (f_i) and temporal dependencies (h_i) from **extracellular** data using **multilinear methods** [3,8,9].
- The internal receptive fields k_i cannot be estimated in the same efficient way. They can, however, be refined using local search based on the full model likelihood.
- We use regression with a sparsity prior [11] to select the relevant features from the highly overcomplete set of localized filters.
- Correlations between the non orthogonal features call for regularization.

RESULT 2: Computation underlying DS is consistent with the energy model

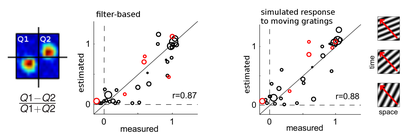
- Most complex cell RFs show roughly bowlshaped nonlinearities.
- The specific nonlinear combination of multiple localized features approximately extracts local motion energy [7].

Our model suggests how "the energy model" might be implemented with populations of localized filters and how their properties can be inferred



Beyond the energy model, this allows to:

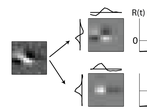
- Estimate **DS of different model components** (e.g. 2-D Fourier transform of the receptive fields [5]) and their impact on simulated responses of the full model to gratings.
- Predict **further cell properties** depending on the nonlinear interaction of multiple features (e.g. Modulation Index).



RESULT 3: Construction of DS in simple cells

A "Very" simple cell: excitation only

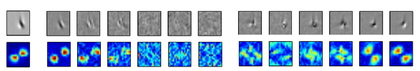
Note: Most thalamic inputs are NOT direction selective – How can DS be plausibly constructed?



DS in simple cells can be reproduced in a model with two non-DS excitatory inputs that are rectified and summed without requiring multiplication or more abstract mathematical operations.

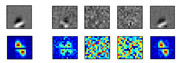
B Typical simple cell: excitation AND suppression

Most simple cells show more than one excitatory filter and often have DS suppression as well.



Can we reproduce this pattern of opposing excitatory and suppressive directions using only non-DS inputs?

- Suppressive DS with opposing STA/excitation **cannot** be constructed from non-DS inputs.

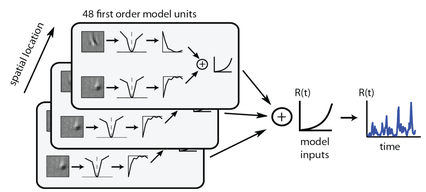


- HOWEVER: Model with non-DS excitatory & DS suppressive inputs reproduces observed excitatory & suppressive DS.

RESULT 4: Complex cells ≈ 2^{nd} order cells (C)

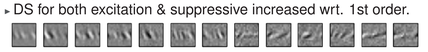
We were unable to produce DS complex cells (phase-invariance+DS) using a biologically plausible first-order model (like those above).

- We constructed 2nd order complex cells from a population of **purely excitatory** DS simple ON and OFF cells from the same study.



2nd order model reproduces properties of complex cell filters:

- Opposing, spatially widespread excitation & suppression.
- DS for both excitation & suppressive increased wrt. 1st order.

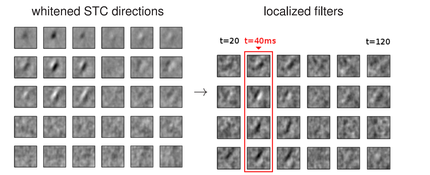


DS suppression in complex cells can arise from properties of first order cells and does not require direct DS inhibition, consistent with intracellular recordings [6]).

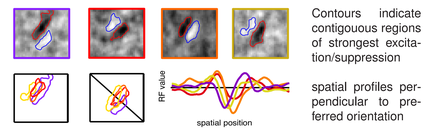
Extension to natural movie sequences

Same ideas apply to more complex stimuli, allowing to examine processing of complex cells under more naturalistic conditions.

Data: Silicon polytrode recordings of multiple cat V1 neurons to 2D spatiotemporal pink noise & natural movies [10].



Localized filters show similar orientation preference at different spatial phases. This provides a possible mechanism to achieve phase independent orientation sensitivity.



Contours indicate contigouous regions of strongest excitation/suppression

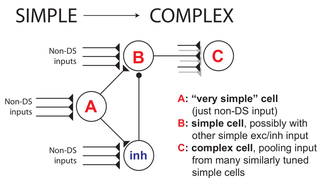
spatial profiles perpendicular to preferred orientation

Summary

We can use extracellular data to infer:

- Relevant **stimulus dimensions** & characteristic **input properties**.
- **Computation:** How these features are combined.

This provides statistical evidence for the following **circuit diagram:**



A: "very simple" cell
(just non-DS input)
B: simple cell, possibly with other simple exc/inh input
C: complex cell, pooling input from many similarly tuned simple cells

References

[1] Rust NC, Schwartz O, Movshon AJ, Simoncelli, EP (2005) Spatiotemporal Elements of Macaque V1 Receptive Fields. Neuron, 46: 945-956.
[2] Touryan J, Lau B, Dan Y (2002) Isolation of relevant visual features from random stimuli for cortical complex cells. The Journal of Neuroscience, 22: 10811-10818.
[3] Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (submitted) Temporal precision in the visual pathway through the interplay of excitation and inhibition. http://www.cfs.umd.edu/biology/ntlab/GNM/
[4] Carandini M, et.al. Do we know what the early visual system does? The Journal of Neuroscience(2005) 25(46):10577-10597.
[5] Schwartz O, Pillow JW, Rust NC, Simoncelli EP (2006) Spike-triggered neural characterization. Journal of Vision, 6: 484-507.
[6] Priebe N, & Ferster D (2005) Direction selectivity of excitation and inhibition in simple cells of the cat primary visual cortex. Neuron, 45: 133-145.
[7] Adelson E, & Bergen J (1985) Spatiotemporal energy models for the perception of motion. Journal of the Optical Society of America, 2: 284-299.
[8] Paninski L (2004) Maximum likelihood estimation of cascade point-process neural encoding models. Network: Comput Neural Syst 15: 243-62.
[9] Ahrens MB, Paninski L, Sahani M (2008) Inferring input nonlinearities in neural encoding models. Network: Comput Neural Syst, 19: 35-67.
[10] Blanche TJ, Spacek MA, Hetke JF, Swindale NV (2005) Polytrodes: high density silicon electrode arrays for large scale multiunit recording. J. Neurophys. 93 (5): 2987-3000.
[11] Gerwinn S, Macke J, Seeger M, S (2008): Bayesian inference for spiking neuron models with a sparsity prior. In: NIPS Proceedings 2007: 529-536.

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