A Spike Triggered Covariance Method for Characterizing Divisive Normalization Models

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Introduction

- Gain control is ubiquitous in the nervous system
- We seek an automated unbiased stimulus/analysis methodology for characterizing a neuron with gain control

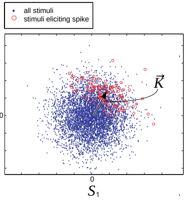
Analogous solution for linear receptive field [1,2,3]:

Assume a steady state model for spiking: $P(spike|\vec{S}) = g(\lfloor \vec{K}\vec{S} \rfloor)$

Need to recover:

- the linear kernel $\vec{K}$
- monotonic function g

Step 1: Spike-triggered average (STA) of stimuli can be used to recover linear kernel



Step 2: Projecting stimuli onto linear kernel allows recovery of monotonic function [2]

Characterizing Divisive Gain Control

Assume a divisive gain control model [e.g., 4] of the form:

$$P(spike|\vec{S}) = \frac{\lfloor \vec{K}\cdot\vec{S} \rfloor^2}{\sum_j w_j \langle \vec{K}_j \vec{S} \rangle^2 + \sigma^2}$$

Need to recover :

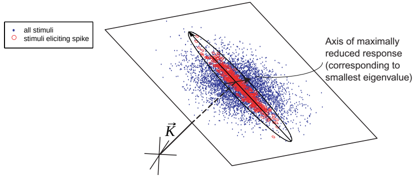
- numerator kernel $\vec{K}$
- divisive gain control kernels $\vec{K}_j$
- divisive weights w_j
- divisive constant σ

Direct Maximum Likelihood (ML) is impractical!

Proposed solution:

Step 1: Under simple assumptions (gain control signal symmetric about $\vec{K}$) STA produces an unbiased estimate of numerator kernel

Step 2: Eigenvector analysis of spike-triggered covariance (STC) reveals suppressive axes:



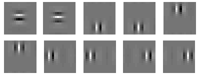
Step 3: ML can be used to recover divisive weights and constant:

$$\{\vec{w},\sigma\} = \arg\max_{\vec{w},\sigma} \prod_k P(spike|\vec{S}_k) \prod_j (1 - P(spike|\vec{S}_j))$$

Example: Model Simulation

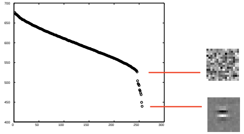
Model numerator kernel:

Model divisive kernels:

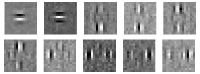


Step 1: STA estimated kernel:

Step 2: Smallest STC eigenvalues correspond to suppressive axes:



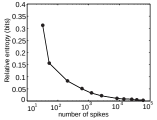
Suppressive kernels are mixed together, but span correct subspace:



Step 3: Divisive weights and constant determined by ML.

Relative entropy between true and estimated spike probabilities:

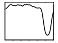
Accuracy depends on:
1. Number of stimulus samples
2. Stimulus dimensionality
3. Number of divisive kernels and their divisive strength



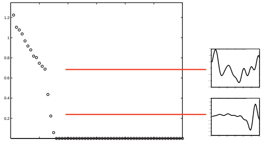
Example: Physiological Data

- Salamander ganglion cell data provided by D Chander and EJ Chichilnisky [5]
- Stimuli are full-field flickering white noise
- Stimuli are not spherically distributed [80,000 time samples, binary noise]. To avoid bias we discard low-variance axes and sphere remaining axes

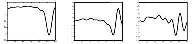
Step 1: STA estimated kernel:



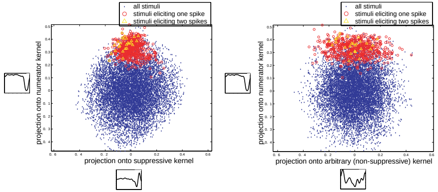
Step 2: Smallest STC eigenvalues correspond to suppressive axes:



All estimated suppressive kernels:



Suppressive versus non-suppressive axes:



Conclusions

- Spike-triggered covariance can be used to characterize divisive gain control
- Analysis on physiological data reveals meaningful suppressive axes
- Interesting issue: STA kernels vary with contrast [5]. We believe this is a bias due to the gain control signal. We are currently working on analysis techniques to characterize this bias

References

(1) J Victor, Proceedings of the National Academy of Sciences, 1979

(2) E J Chichilinsky, Network, 2001, in press

(3) D L Ringach, G Sapiro and R Shapley, Vision Research, 1997

(4) D J Heeger, Visual Neuroscience, 1992

(5) D Chander and E J Chichilinsky, Society for Neuroscience, 1999

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