Characterizing neural responses to natural stimuli: most informative directions.

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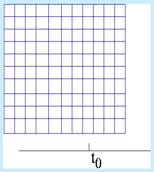
Dimensionality Reduction and Receptive Fields



Stimuli are drawn from a high-dimensional space

$$\vec{s} \rightarrow spike\ @\ t_0$$

Assumption: a neuron is looking for a small number k << dim($\vec{s}$) of certain features, receptive fields $\hat{e}_i$, i=1 to k.

$$\frac{P(spike\,|\,\vec{s})}{P(spike)} = f(s_1,\ldots,s_k) = \frac{P(\vec{s}\,|\,spike)}{P(\vec{s})}$$

Response is generated according to an arbitrarily nonlinear function within the relevant low-dimensional subspace.

Once the receptive fields are known, the input-output function can be mapped experimentally.

N. Brenner, W. Bialek, and R. de Ruyter van Steveninck, Neuron (2000)

How to find all of the receptive fields?

Current methods:

·k=1, reverse corelation

white noise: $\hat{e}_1 \propto \langle \vec{s}\,|\,spike \rangle$

correlated Gaussian noise $\hat{e}_1 \propto C^{-1}_{apriori} \langle \vec{s}\,|\,spike \rangle$

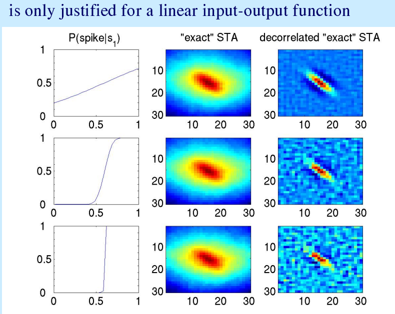
·k>1 spike-triggered covariance method
Diagonalize the difference between covariance matrices of all stimuli and those conditional on a spike:

$$\Delta\hat{C} = C_{spike} - C_{apriori}, \quad \Delta\hat{C}\hat{u}_i = \lambda_i \hat{u}_i$$

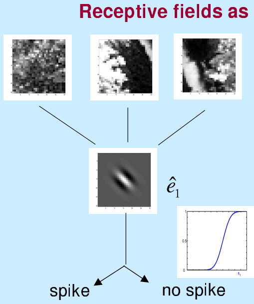
non-zero eigenvalues = # receptive fields & $\hat{e}_i \propto C^{-1}_{apriori}\hat{u}_i$

Underlying idea is to compare the probability distributions $P(\vec{s}\,|\,spike)$ and $P(\vec{s})$. The current methods are guaranteed to work only with Gaussian stimuli, because we use only first and second order statistics.

Analysis of responses to natural stimuli by reverse correlation is only justified for a linear input-output function



Receptive fields as maximally informative directions



initial stimuli - contrast($\vec{r}$),

$$\dim(\vec{s}) \sim 10^3$$

Consider a case of one relevant direction (receptive field)

$$\hat{e}_1\vec{s} = s_1, \quad \dim(s_1) = 1$$

nonlinear input-output function $f(s_1)$

If receptive field model is correct, then information is not lost by looking only at s_1

$$I(s_1;\{t_i\}) = I(\vec{s};\{t_i\})$$

regardless of stimuli statistics.

For any other direction $\vec{v}_{test}$, information is going to be less

$$I(\vec{s}\cdot\vec{v}_{test};\{t_i\}) \le I(\vec{s};\{t_i\})$$

Optimization scheme

· Pick a test direction $\vec{v}_{test}$, and maximize information $I(\vec{s}\cdot\vec{v}_{test};\{t_i\})$ with respect to $\vec{v}_{test}$

· Calculate the overall information per spike - $I_{spike} \equiv I(\vec{s};\{t_i\})$
[each stimuli has to be presented multiple times to build post-stimulus histograms

· If $I(\vec{s}\cdot\vec{v}_{test};\{t_i\}) = I_{spike}$ [up to differences from finite sampling effects], we are done.

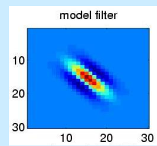
· Otherwise, increase the number of directions with respect to which information is optimized, i.e. maximize

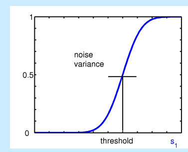
$$I(\vec{s}\cdot\vec{v}_1, \vec{s}\cdot\vec{v}_2;\{t_i\})$$

with respect to $\vec{v}_1$ and $\vec{v}_2$.

A model with one relevant direction (simple cell)

Spikes are generated according to projection on $\hat{e}_1$ and $P(spike\,|\,s_1)$.

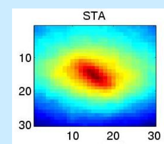




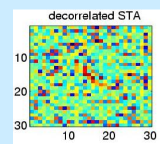
# of spikes ~50,000

reverse correlation analysis

Spatial correlations present in natural scenes broaden spike-triggered average



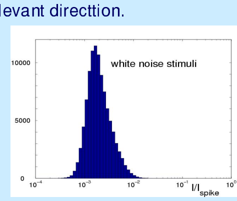
Decorrelating spike-triggered average according to the second-order statistics of natural scenes fails (smoothing can help somewhat).

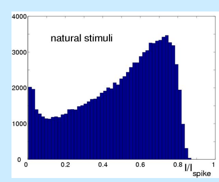


Maximizing $I(\vec{v}) \equiv I(\vec{s}\cdot\vec{v};\{t_i\})$

Before we start…

Histogram of information along 10^5 random vectors for a model cell with only one relevant directtion.

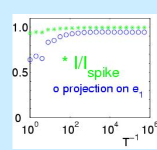


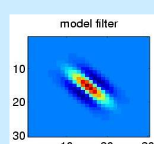


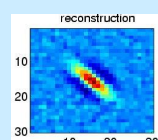
Due to correlations, information along a random vector is likely to be large.

It is important to check that the receptive field found by maximizing information gives a value which lies in the "gap".

Information I(v) is a continuous function, whose gradient can be calculated. Maximization is done using a combination of simulated annealing and gradient ascent.







Once the receptive field is known, the neuron's nonlinear input-output function can be mapped experimentally.

$P_{est}(spike\,|\,\vec{s}\cdot\vec{v}_{max})$ (crosses)

vs.

$P(spike\,|\,\vec{s}) = P(spike\,|\,s_1)$ (solid line)