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- Dayan & Abbott

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  - eg: tuning curves, receptive field, LNP
- Mechanistic (how?)
  - eg: compartmental models, Hodgkin-Huxley
- Interpretive/Explanatory (why?)
  - eg: efficient coding, optimal estimation/decision, wiring length, metabolic cost, etc

- Dayan & Abbott

Interaction with Experiments

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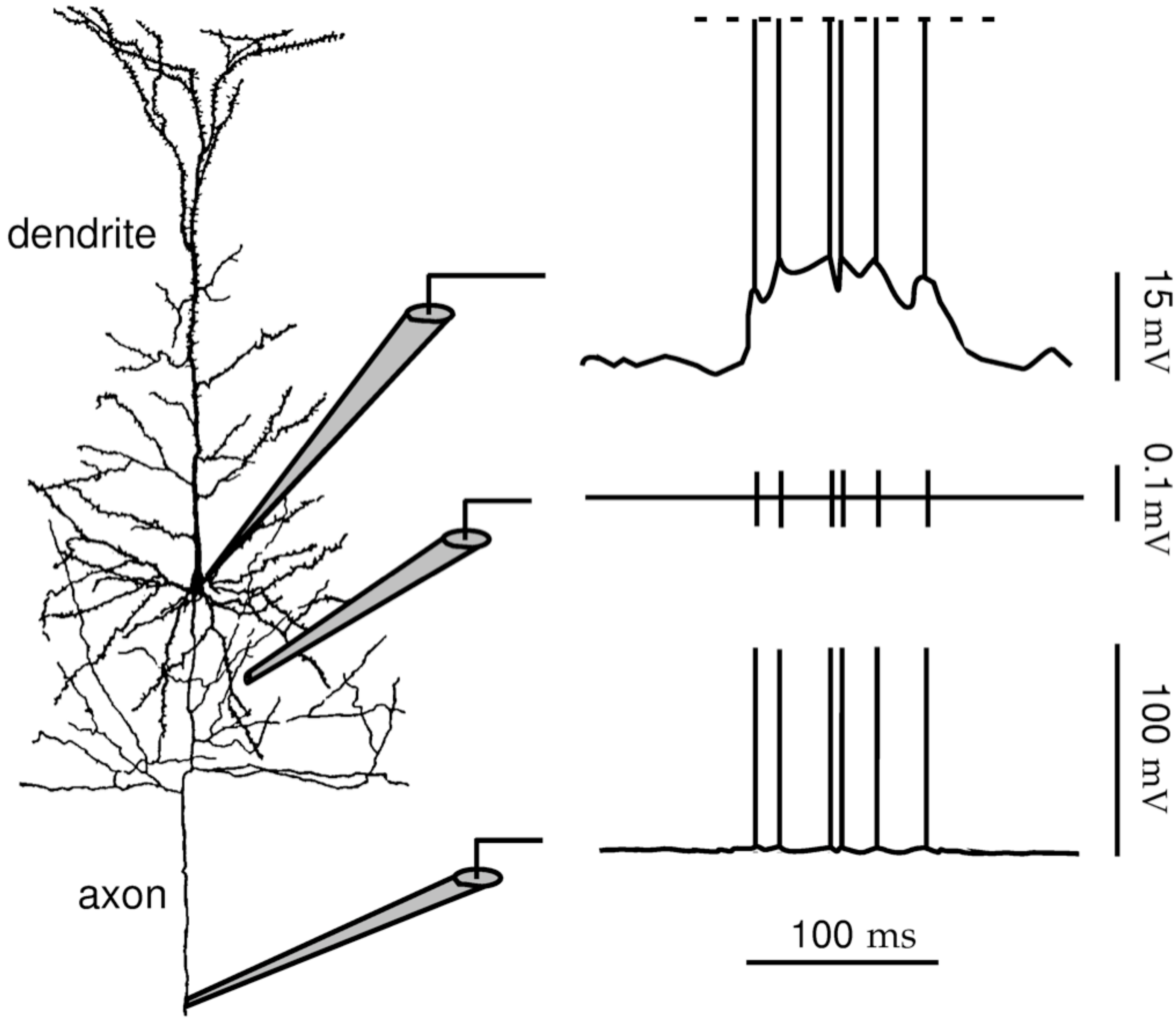
  - to refine model
  - to differentiate models
  - with optimized stimuli, to characterize cells

Descriptive Response Models (outline)

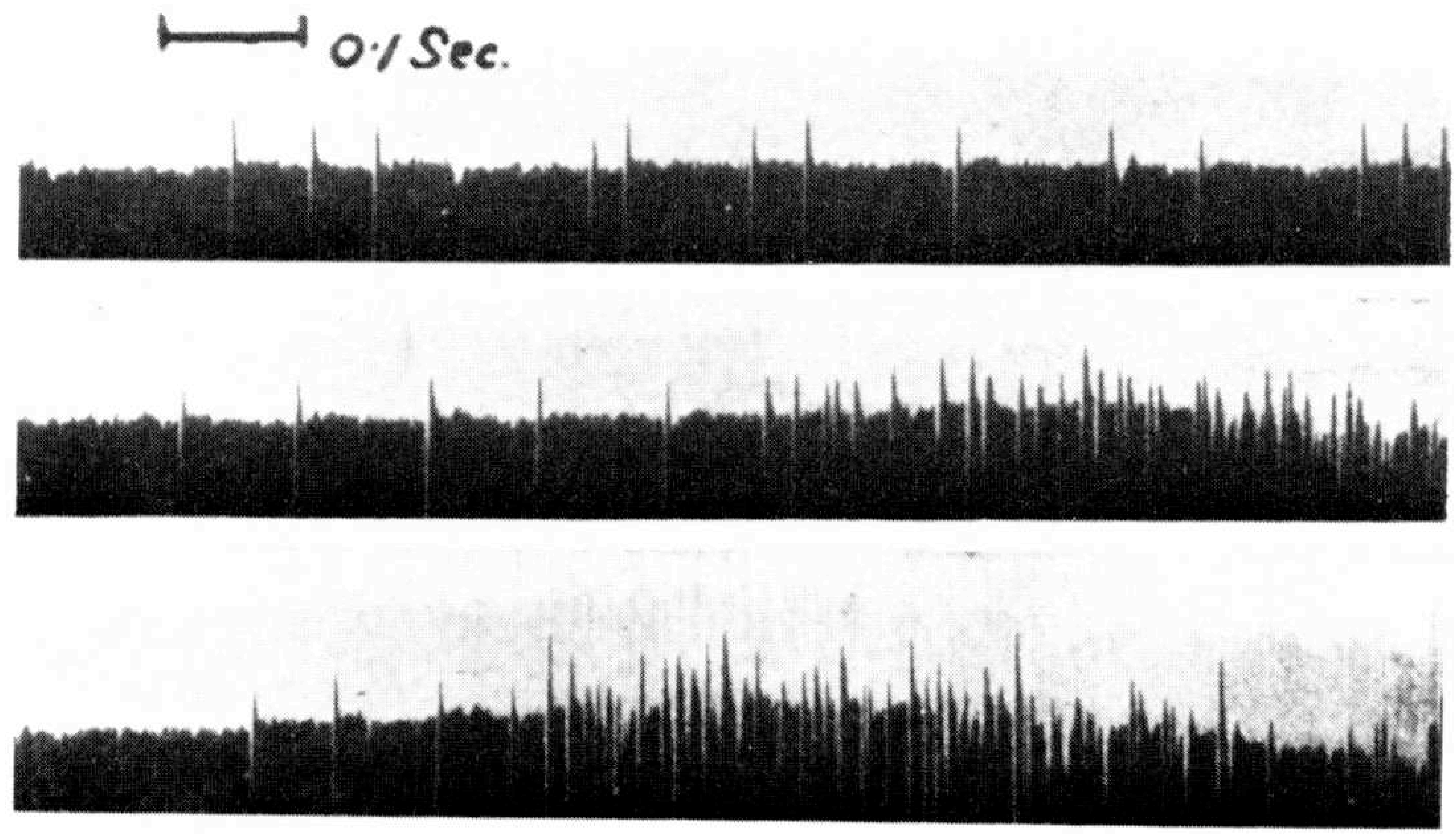
- Receptive fields and tuning curves
- Linear models
- Rate models
- Wiener/Volterra (polynomial) models
- LN models
- Poisson spiking
- Fitting/validating LNP models



- Dayan & Abbott

Rate coding

Some of Adrian's first recordings from very small numbers of individual nerve fibres. Each spiky deflection is a single nerve impulse. These records were taken from the sensory nerves of a cat's toe. The toe was flexed slowly, more quickly and very rapidly to produce these three traces. The frequency of firing depends on the strength of the stimulus – Adrian's law.



Receptive Fields

- Classical: A region of the retina (visual field) that must be stimulated directly in order to obtain a response in a neuron
  - Sherrington (1906), Hartline (1938), Kuffler (1953)

Receptive Fields

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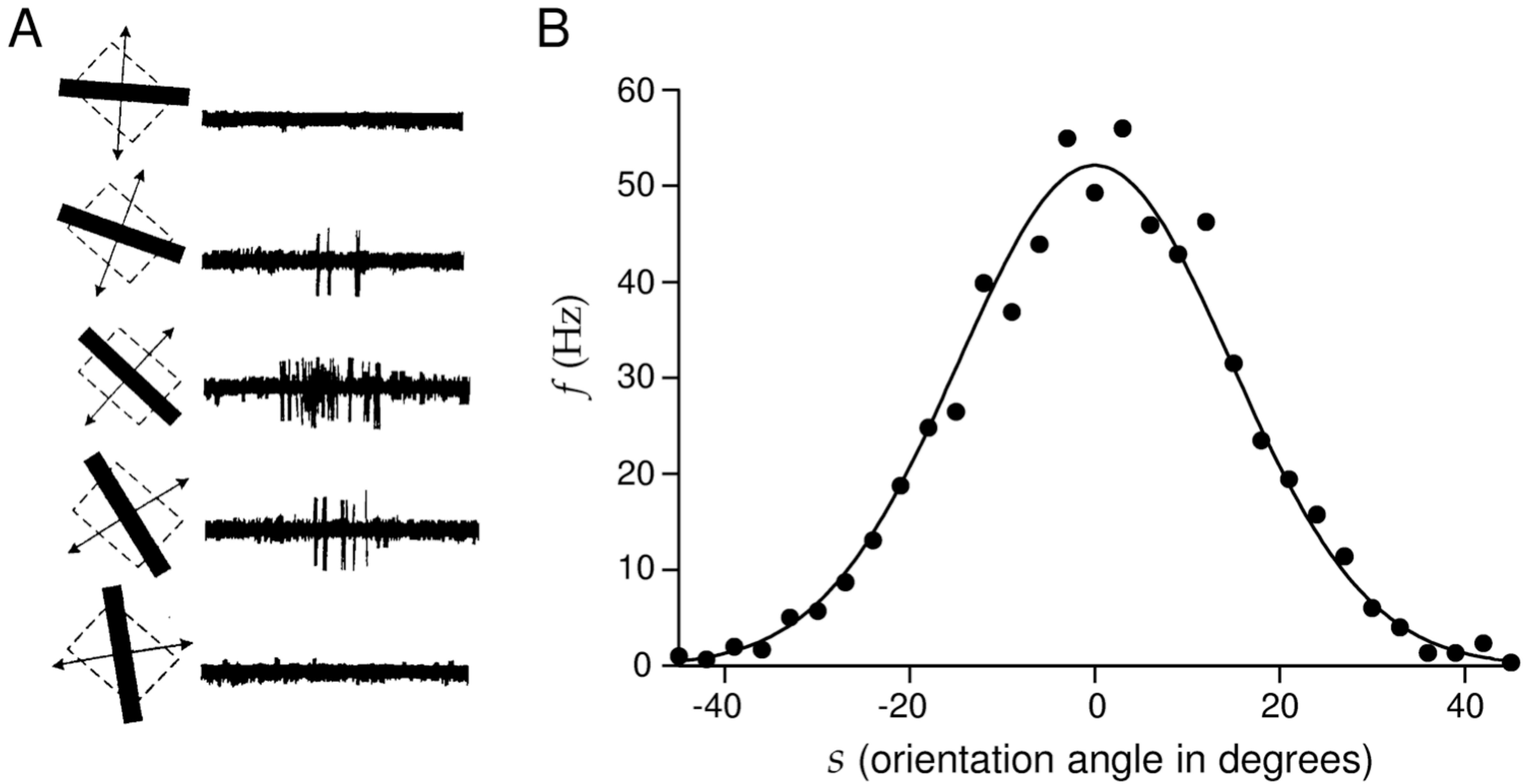
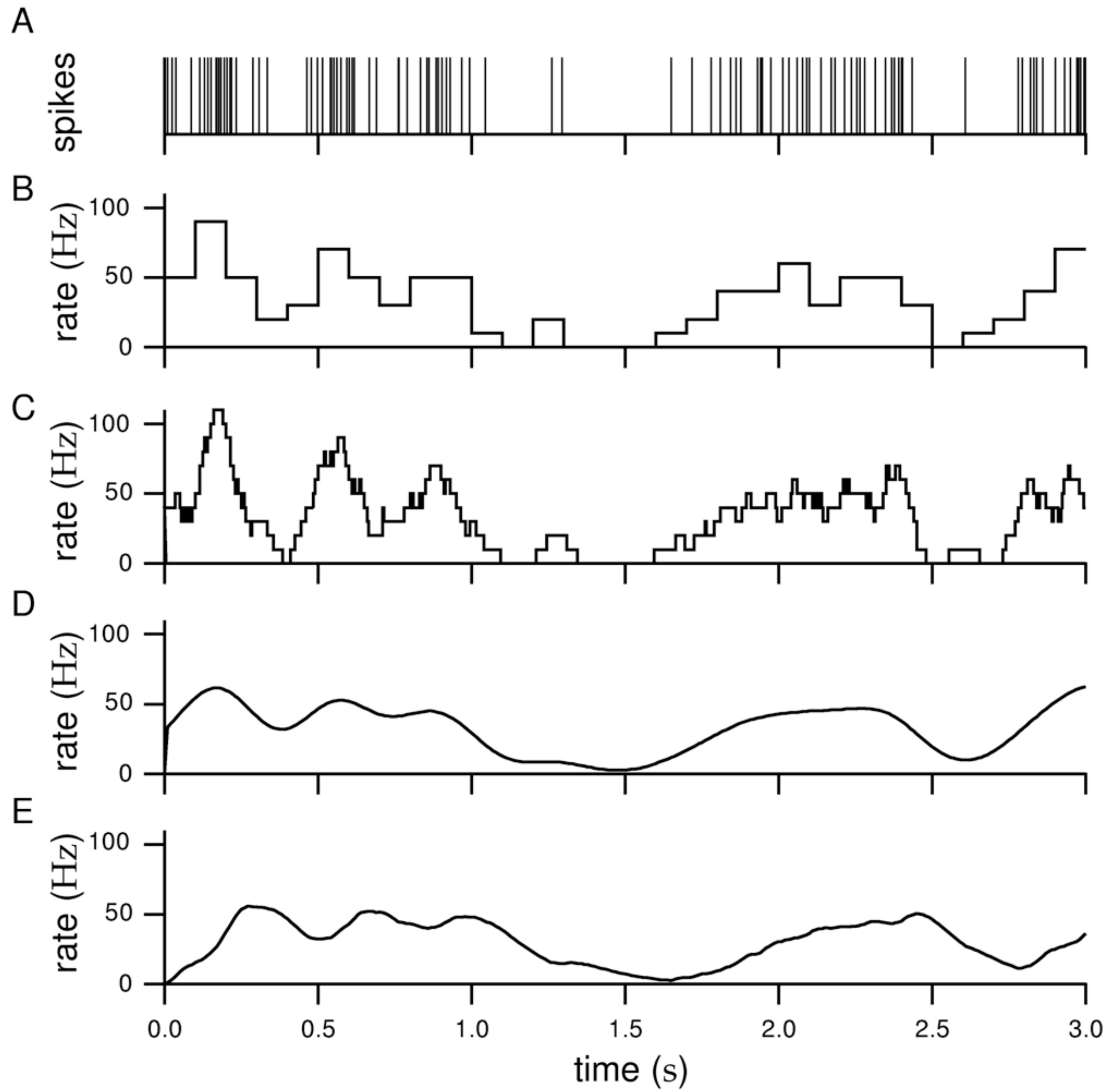
  - Sherrington (1906), Hartline (1938), Kuffler (1953)
- Modern generalization: Kernel that captures those attributes of the stimulus that generate/ modulate responses. Often assumed linear.



- Dayan & Abbott, after Hubel & Wiesel ‘62

Estimating firing rates



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Polynomial Model

(Volterra/Weiner Kernels)

$$r(\vec{x}) = k_0 + \vec{k}_1 \cdot \vec{x} + \vec{x}^T K_2 \vec{x} + \ldots$$

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const

□

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vector

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const vector matrix

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			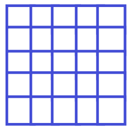	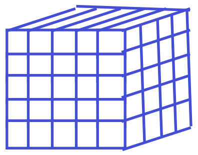
# pars:	1	n (20)	n^2 (400)	n^3 (8000)

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		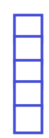	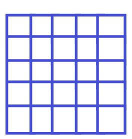	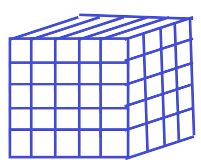
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- in practice, insufficient data to go beyond 2nd order

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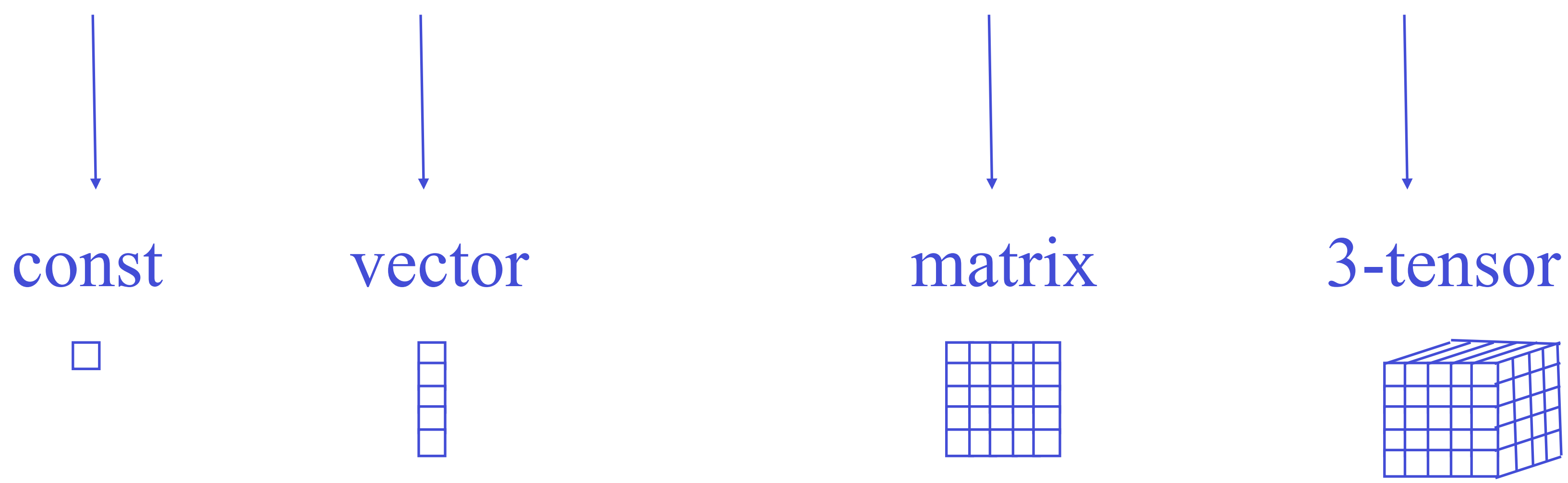

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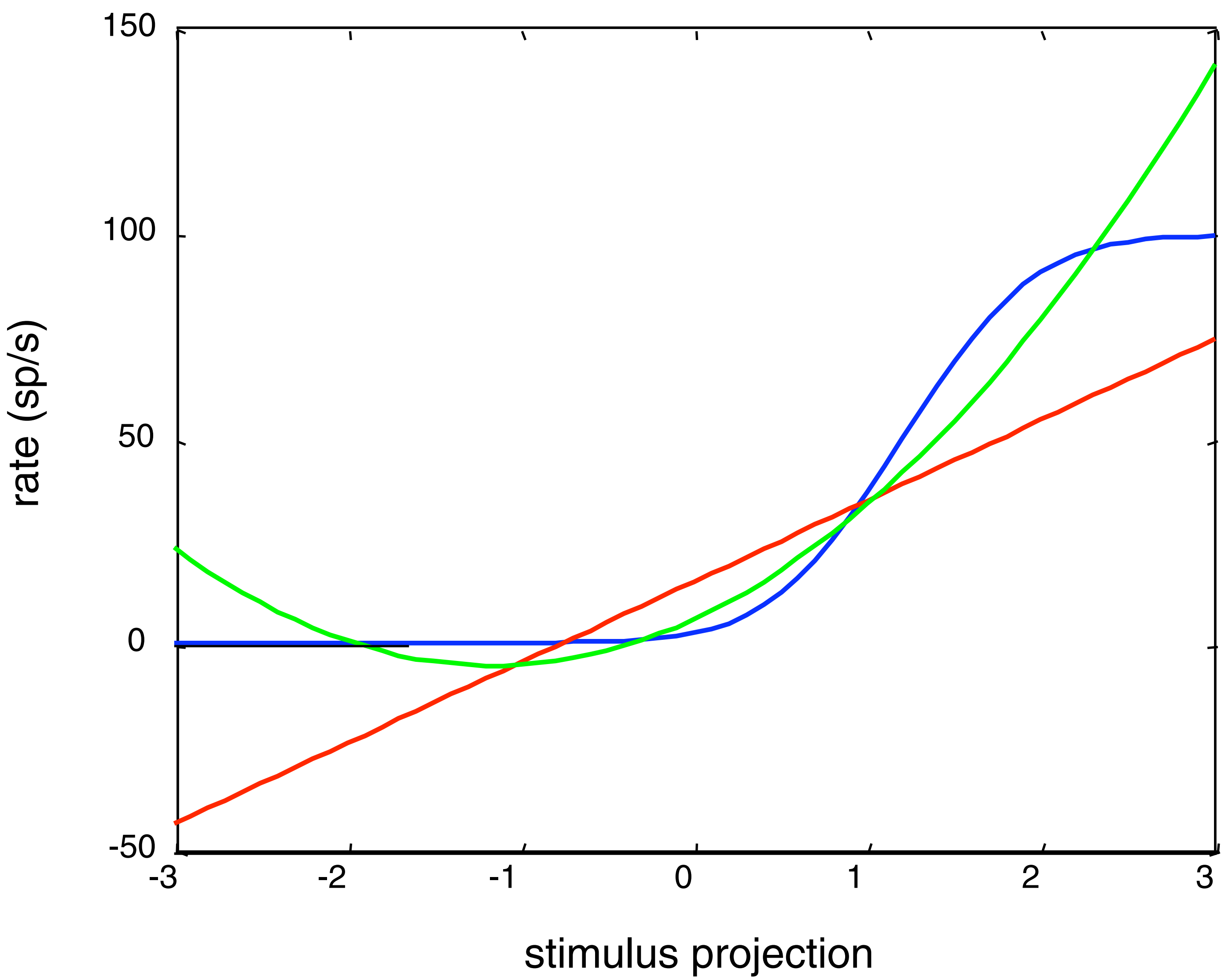

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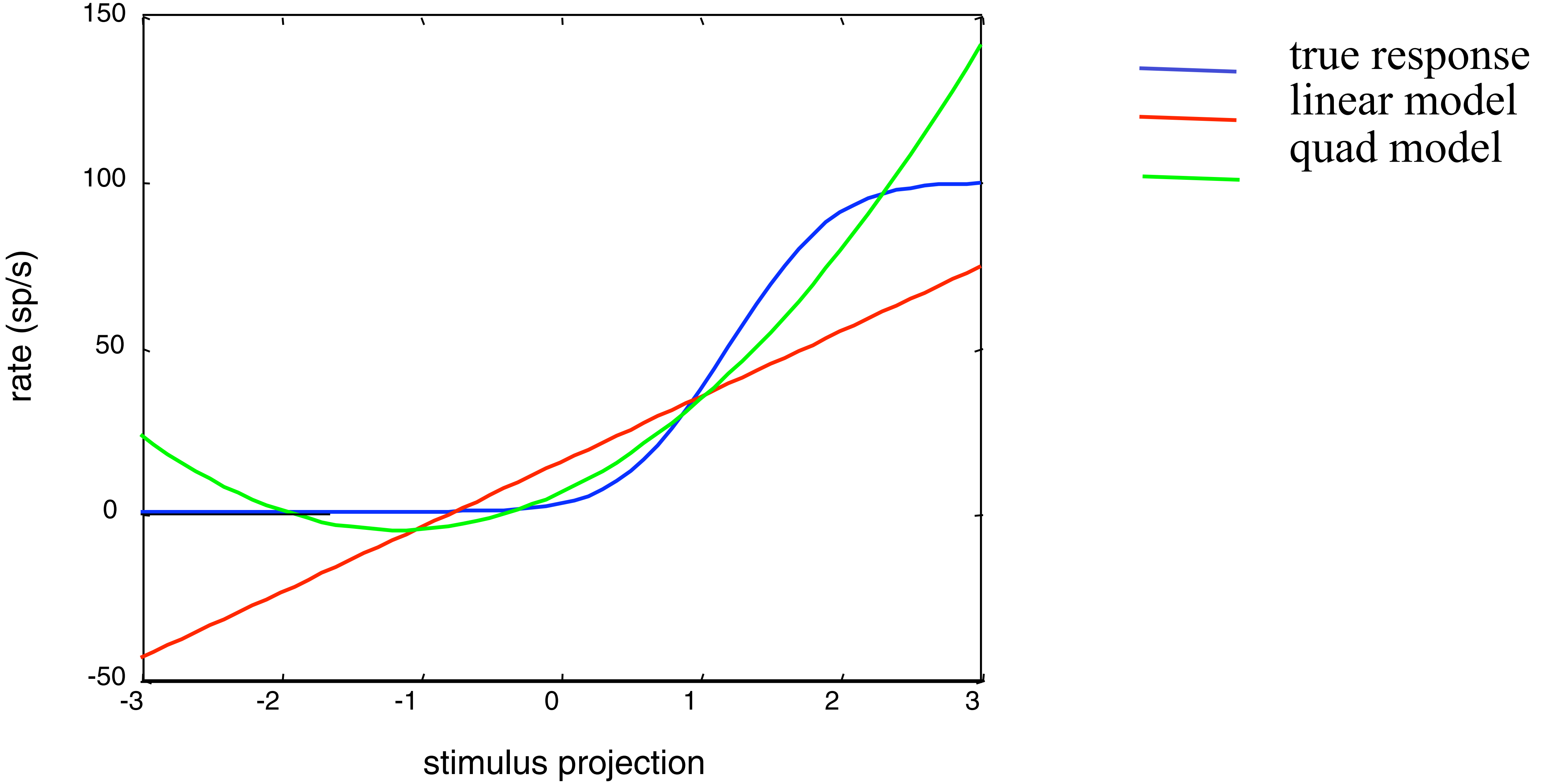
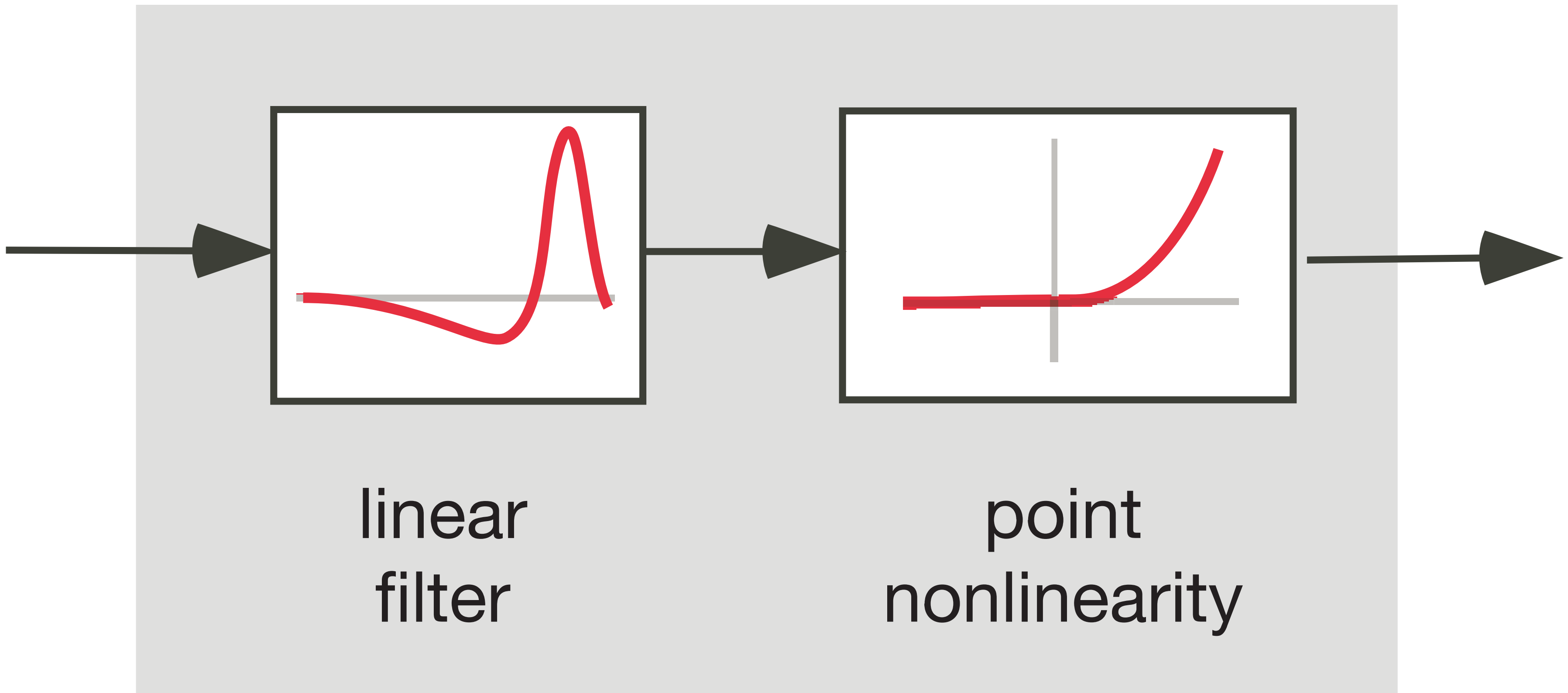
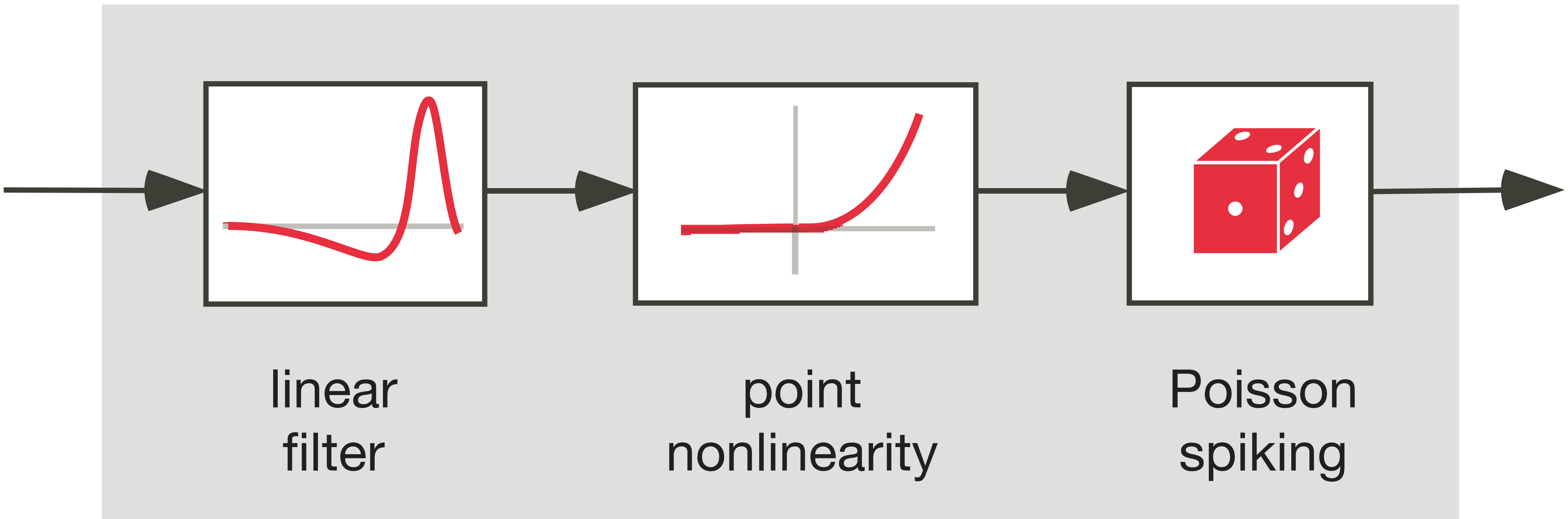


LN cascade model



- Threshold-like nonlinearity => linear classifier
- Classic model for Artificial Neural Networks
  - McCullough & Pitts (1943), Rosenblatt (1957), etc
- No spikes (output is firing rate)

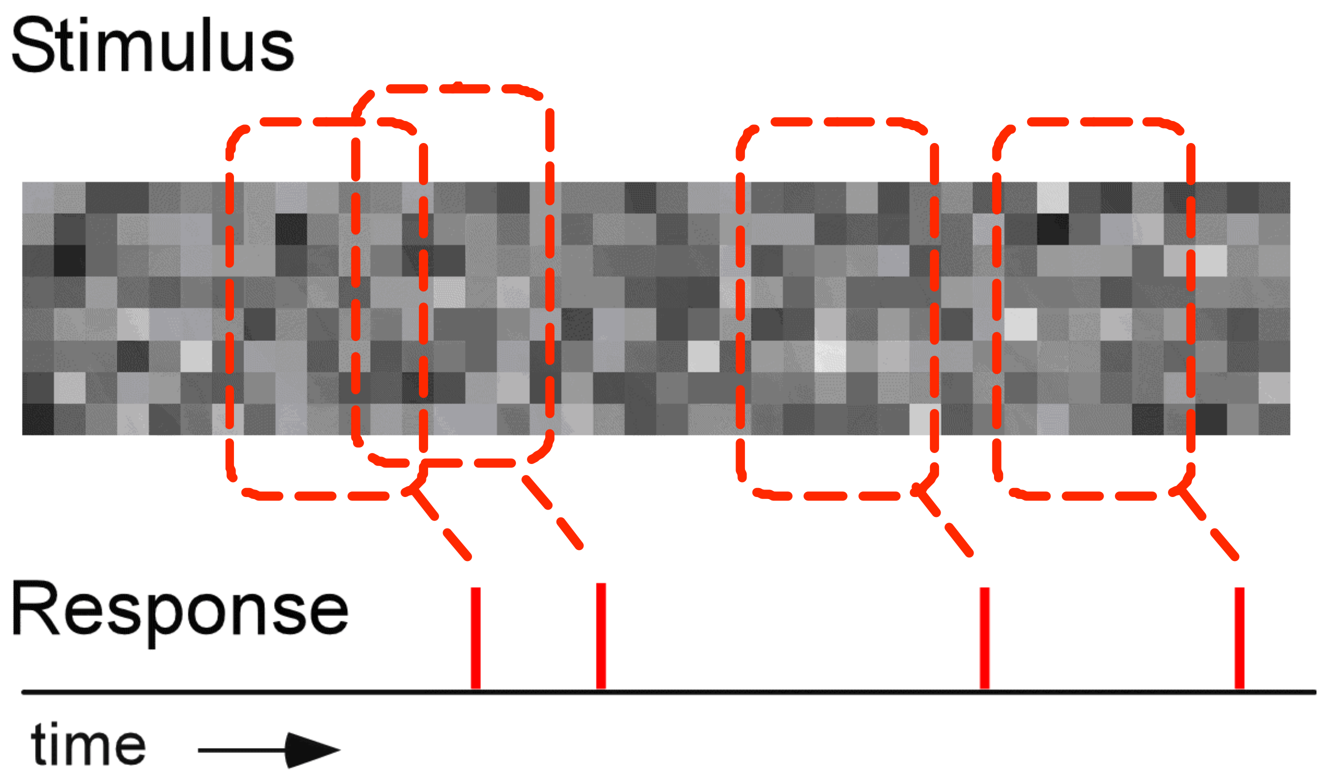
LNP cascade model



- Simplest successful descriptive spiking model
- Easily fit to (extracellular) data
- Descriptive, and interpretable (although *not* mechanistic)

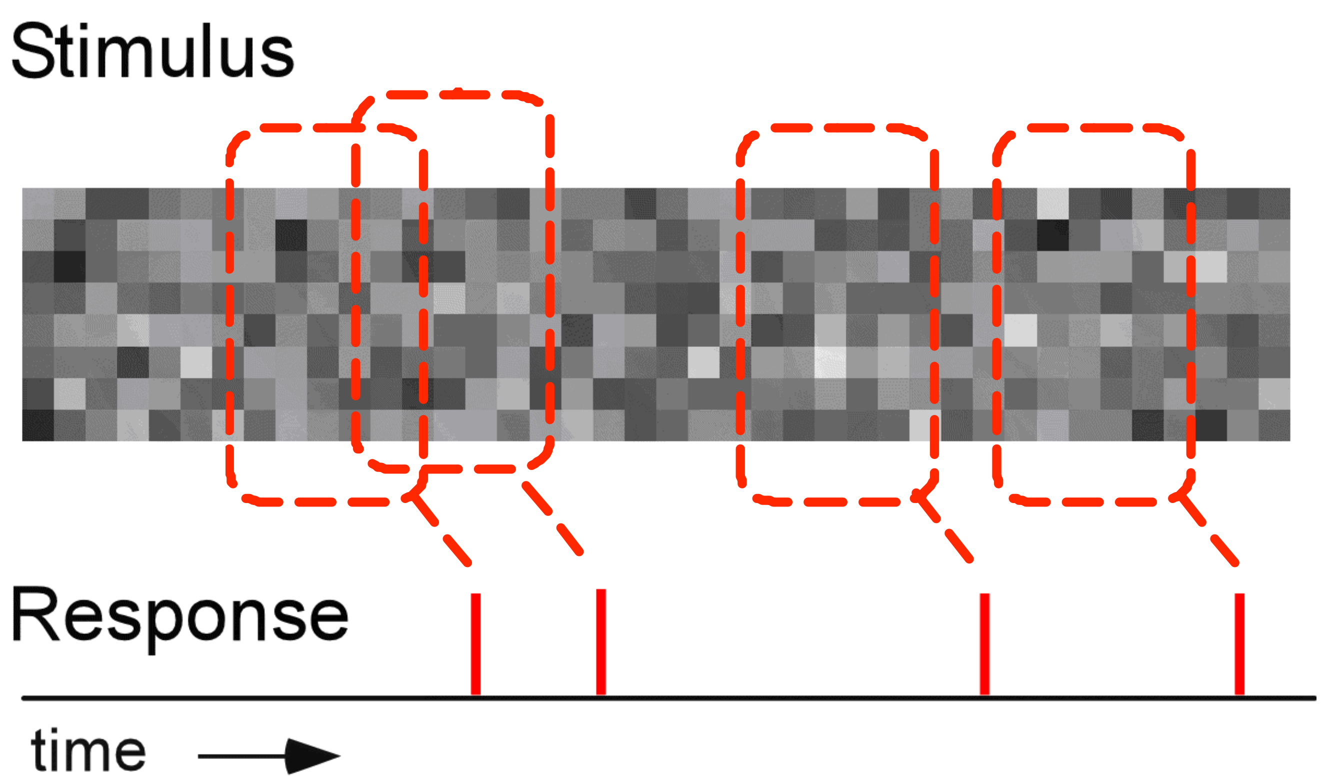
Geometric view of Poisson models

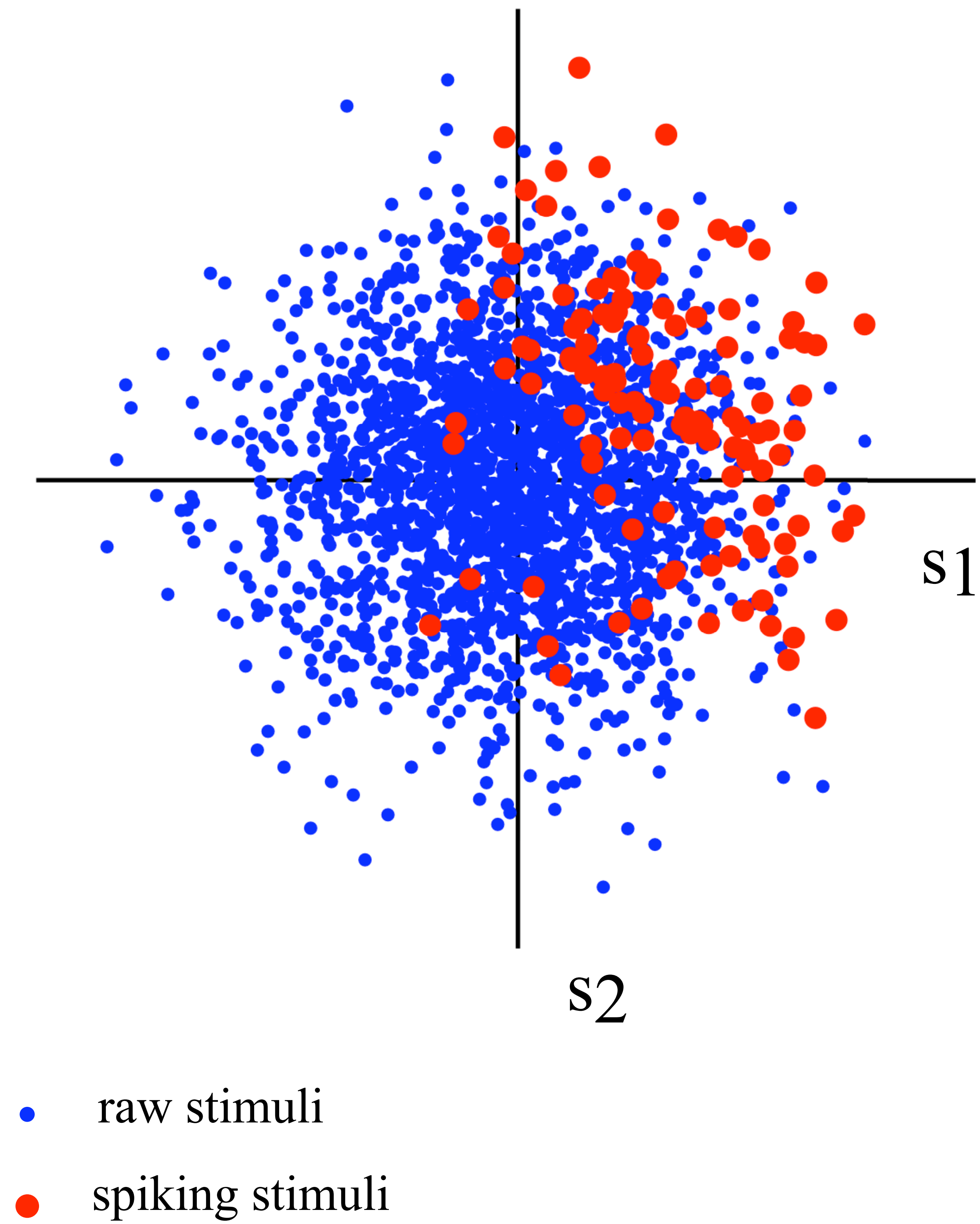
1D stimulus over time
(e.g., flickering bars)



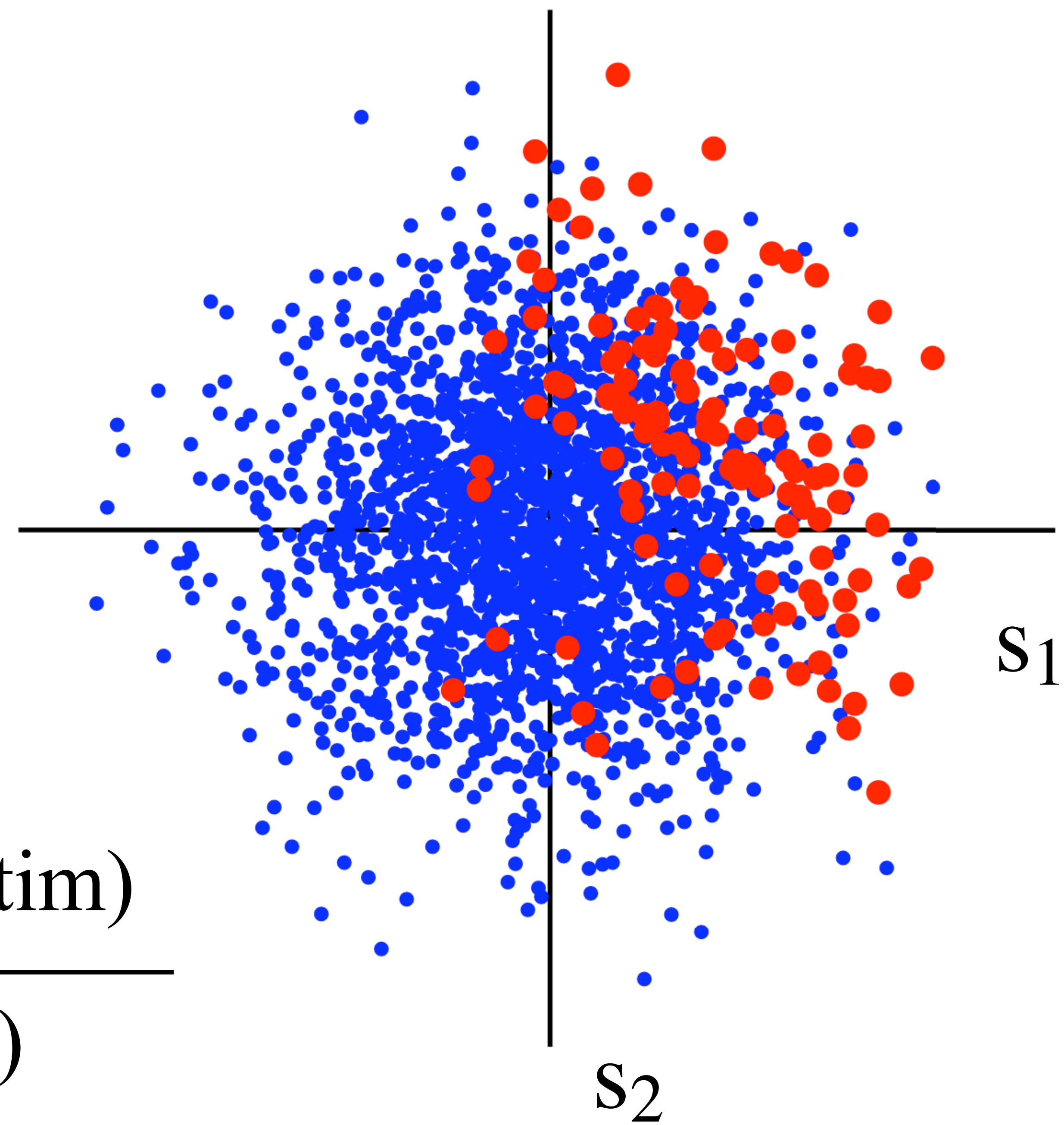
- 8 x 6 stimulus block
  = 48-dimensional vector

Geometric picture





Neural response is captured by relationship between the distribution of red points (spiking stim) and blue points (raw stim)



Expressed in terms of Bayes' rule:

$$P(\text{spike}|\text{stim}) = \frac{P(\text{spike, stim})}{P(\text{stim})}$$

Cannot be estimated directly

ML estimation of LNP

[on board]

ML estimation of LNP

If $f_\theta(\vec{k} \cdot \vec{x})$ is convex (in argument and theta),
and $log\, f_\theta(\vec{k} \cdot \vec{x})$ is concave,
the likelihood of the LNP model is convex
(for all observed data, $\{n(t), \vec{x}(t)\}$)

[Paninski, '04]

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Examples: $e^{(\vec{k} \cdot \vec{x}(t))}$

$$(\vec{k} \cdot \vec{x}(t))^\alpha, \quad 1 < \alpha < 2$$

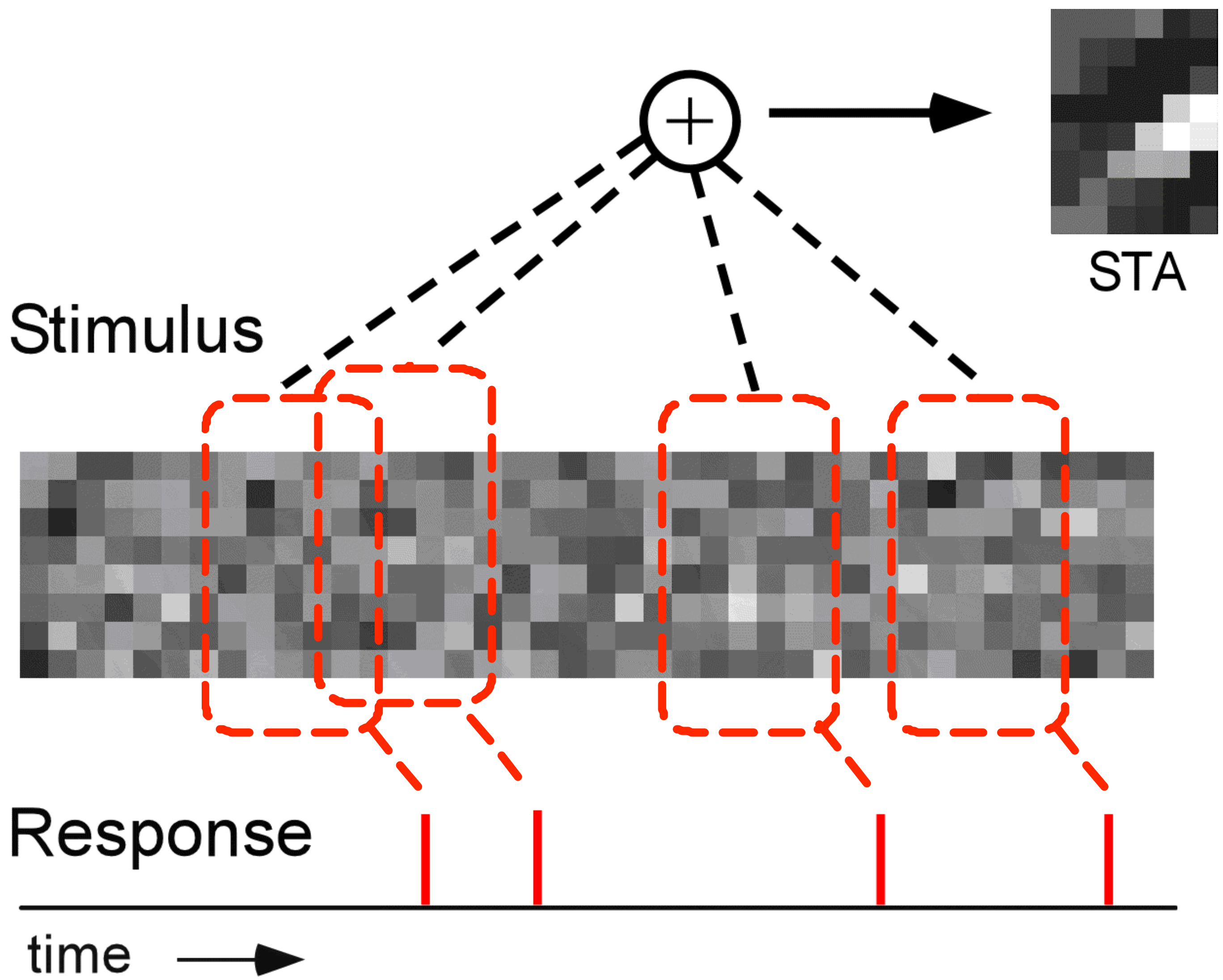
[Paninski, '04]

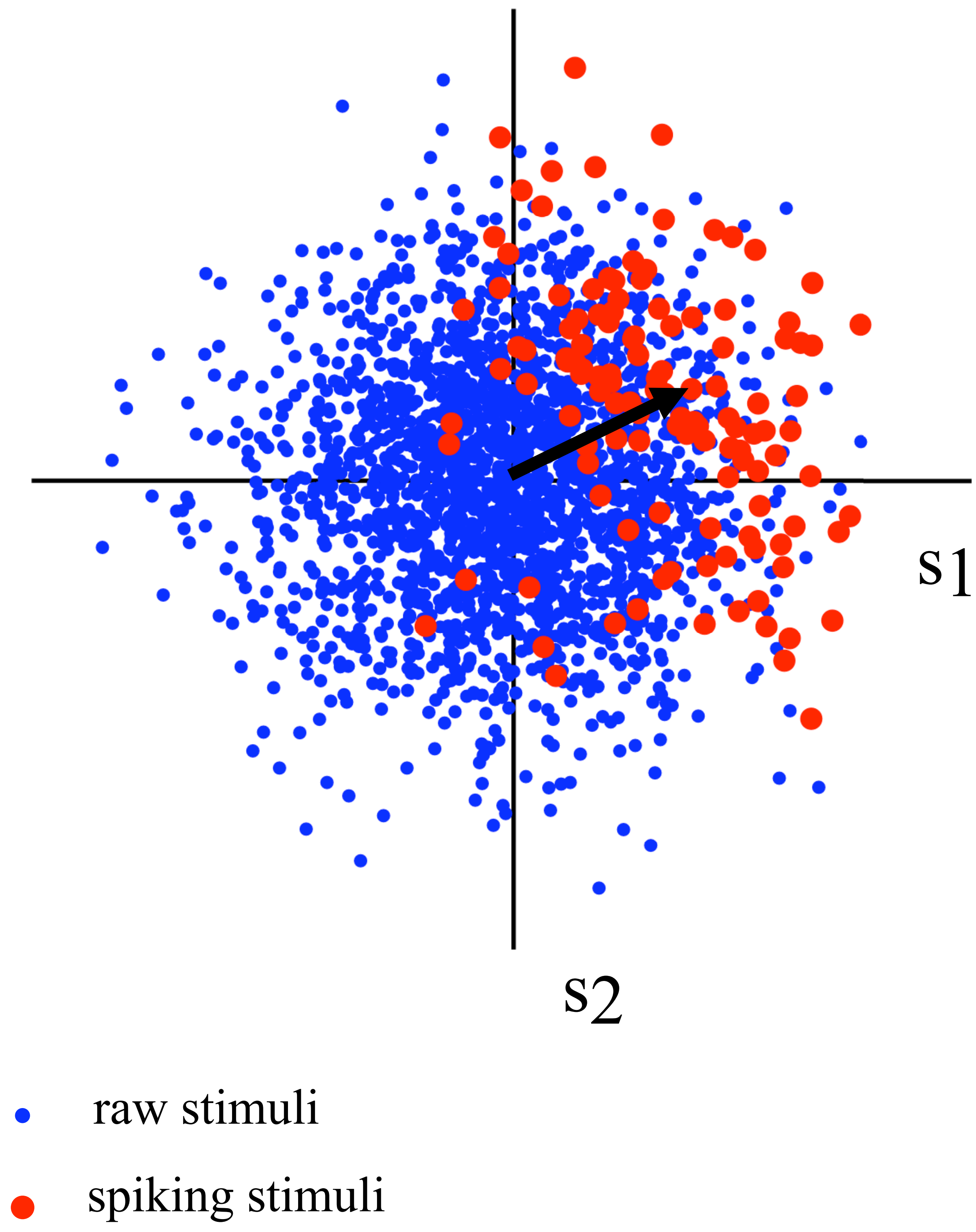
Simple LNP fitting

- Assuming:
  - stochastic stimuli, spherically distributed
  - spike counts in small time bins (0,1)
  - neural response is such that mean of spike-triggered ensemble is shifted
- Reverse correlation gives an unbiased estimate of k [on board]
- For exponential f, this is same as ML

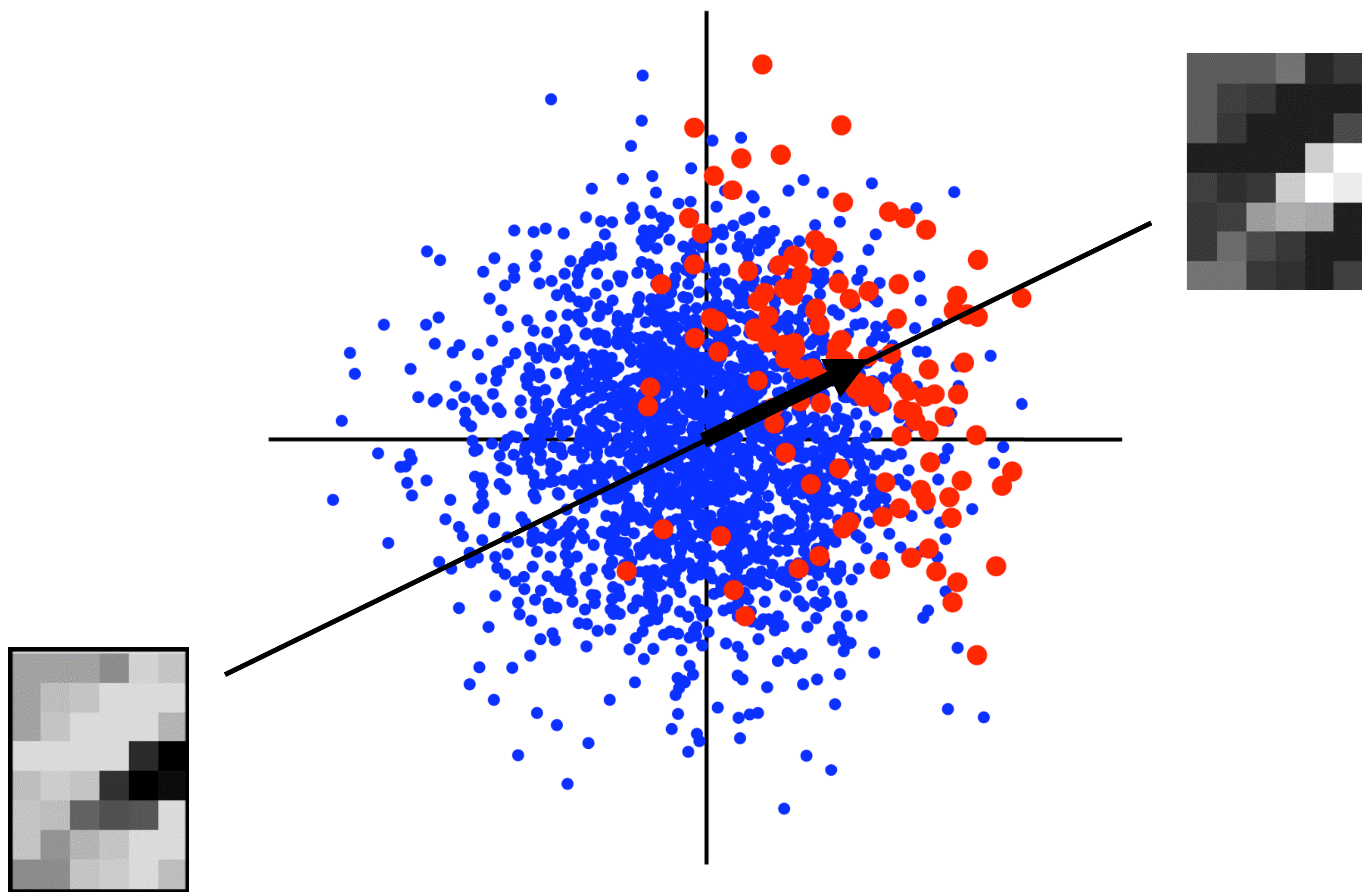
- Bussgang 52; de Boer & Kuyper 68

Computing the STA

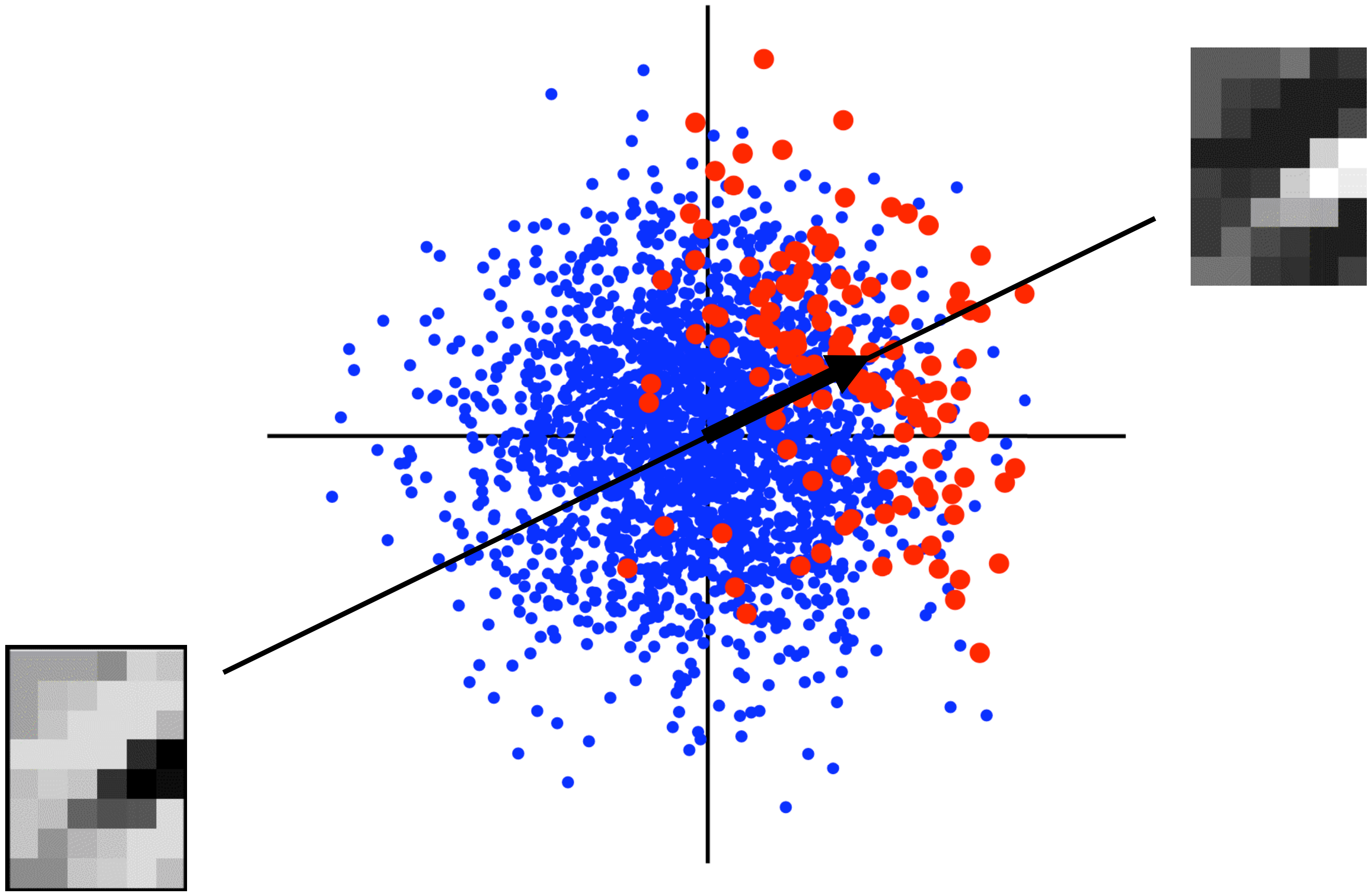




STA corresponds to a “direction” in stimulus space



Projecting onto the STA



$$P\left(\text{spike}(t) \mid \vec{k}\cdot\vec{s}(t)\right) = P\left(\text{spike}(t)\ \&\ \vec{k}\cdot\vec{s}(t)\right)/P\left(\vec{s}(t)\right)$$

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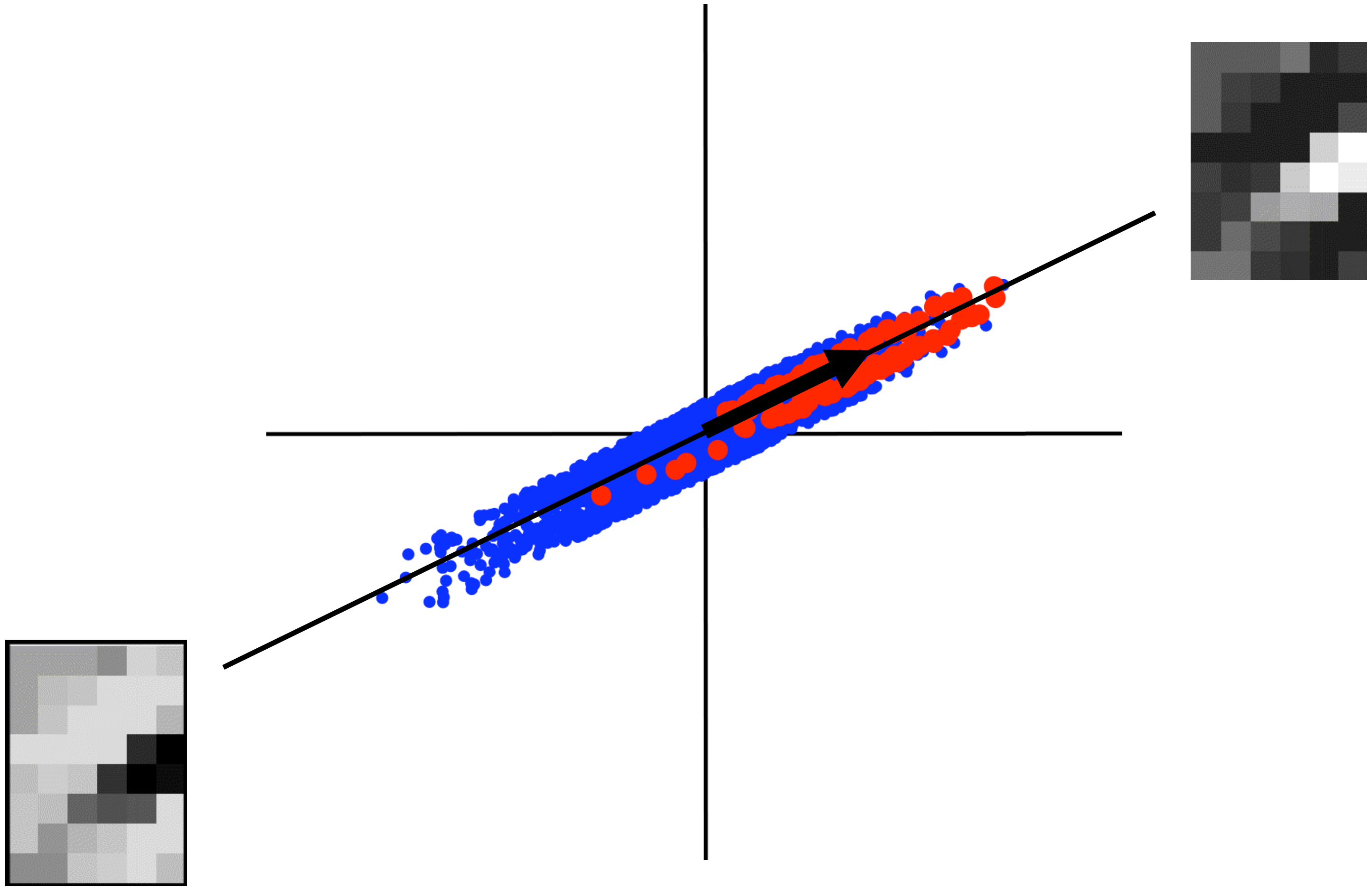

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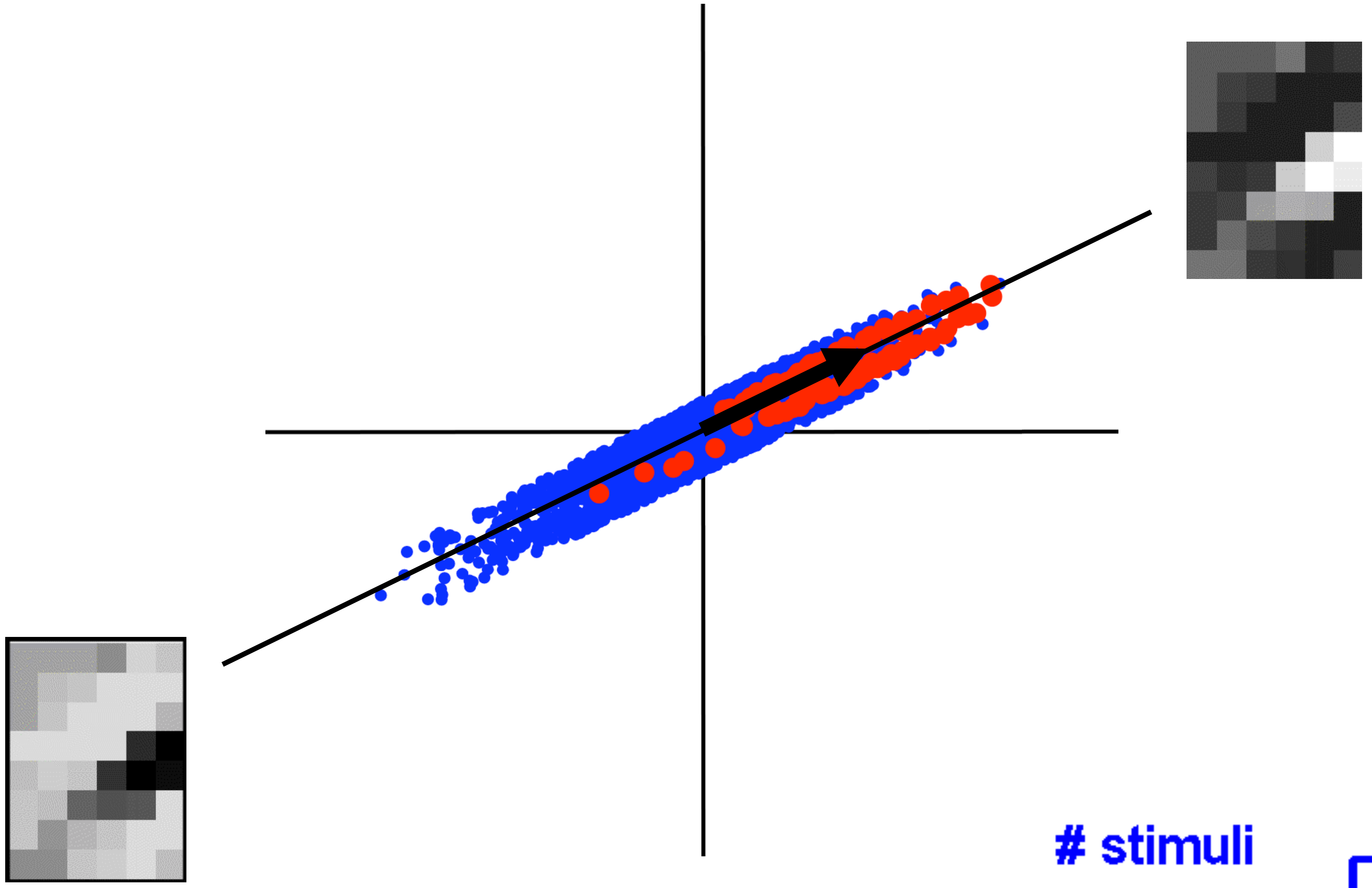

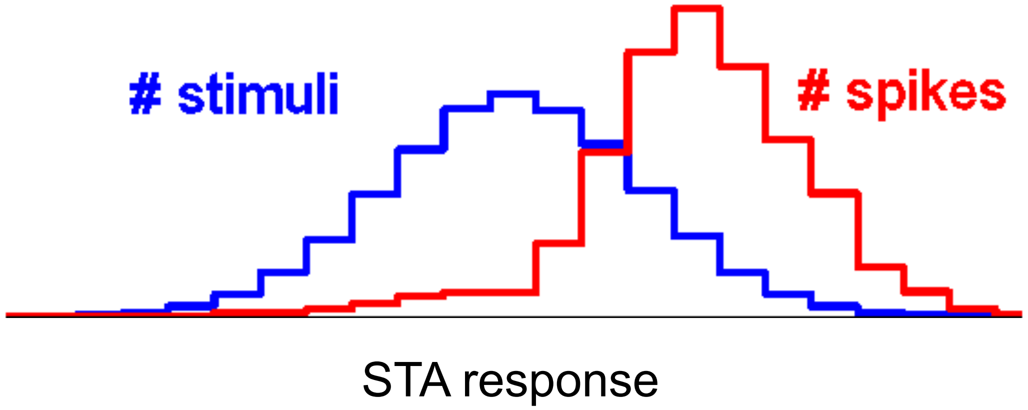

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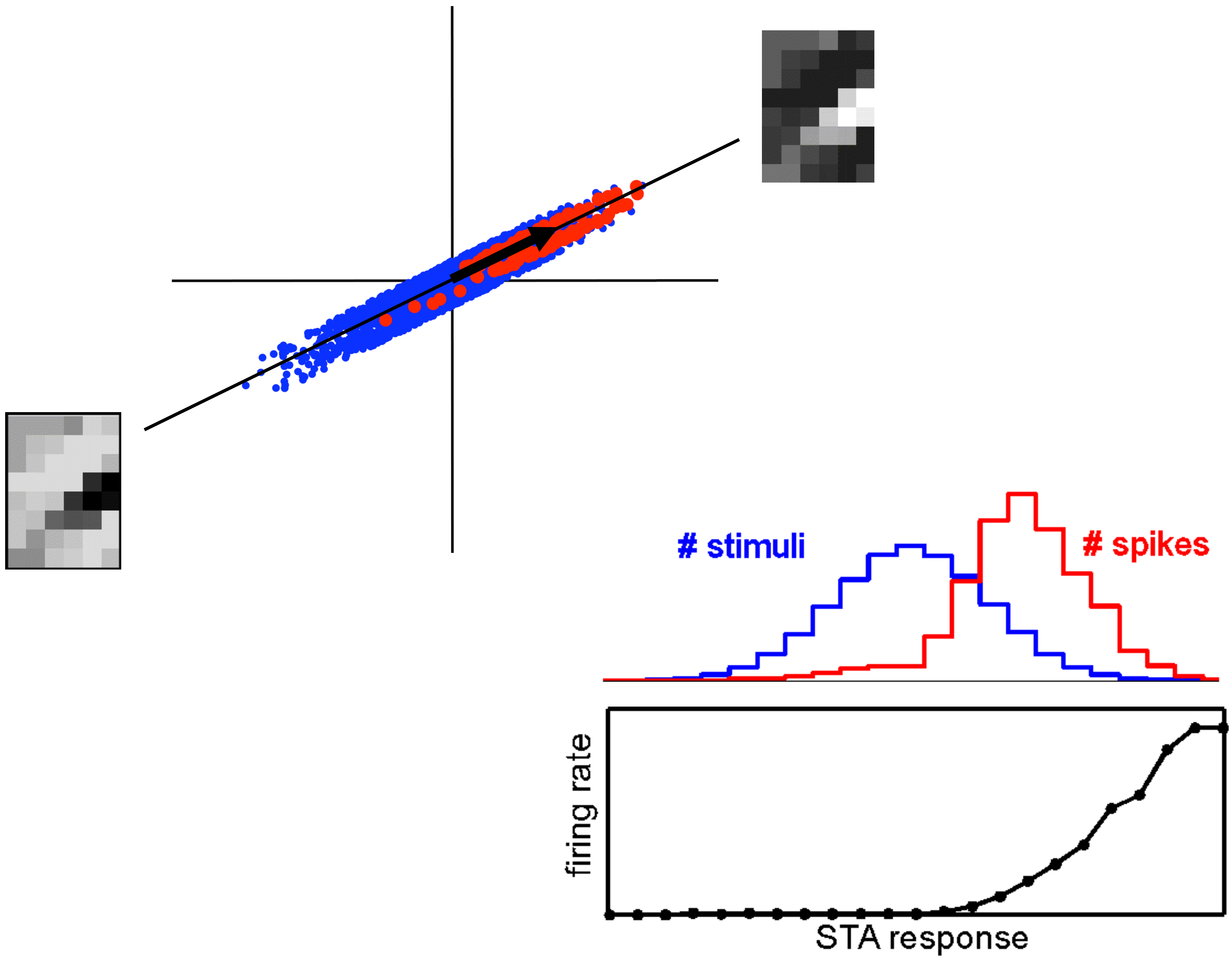
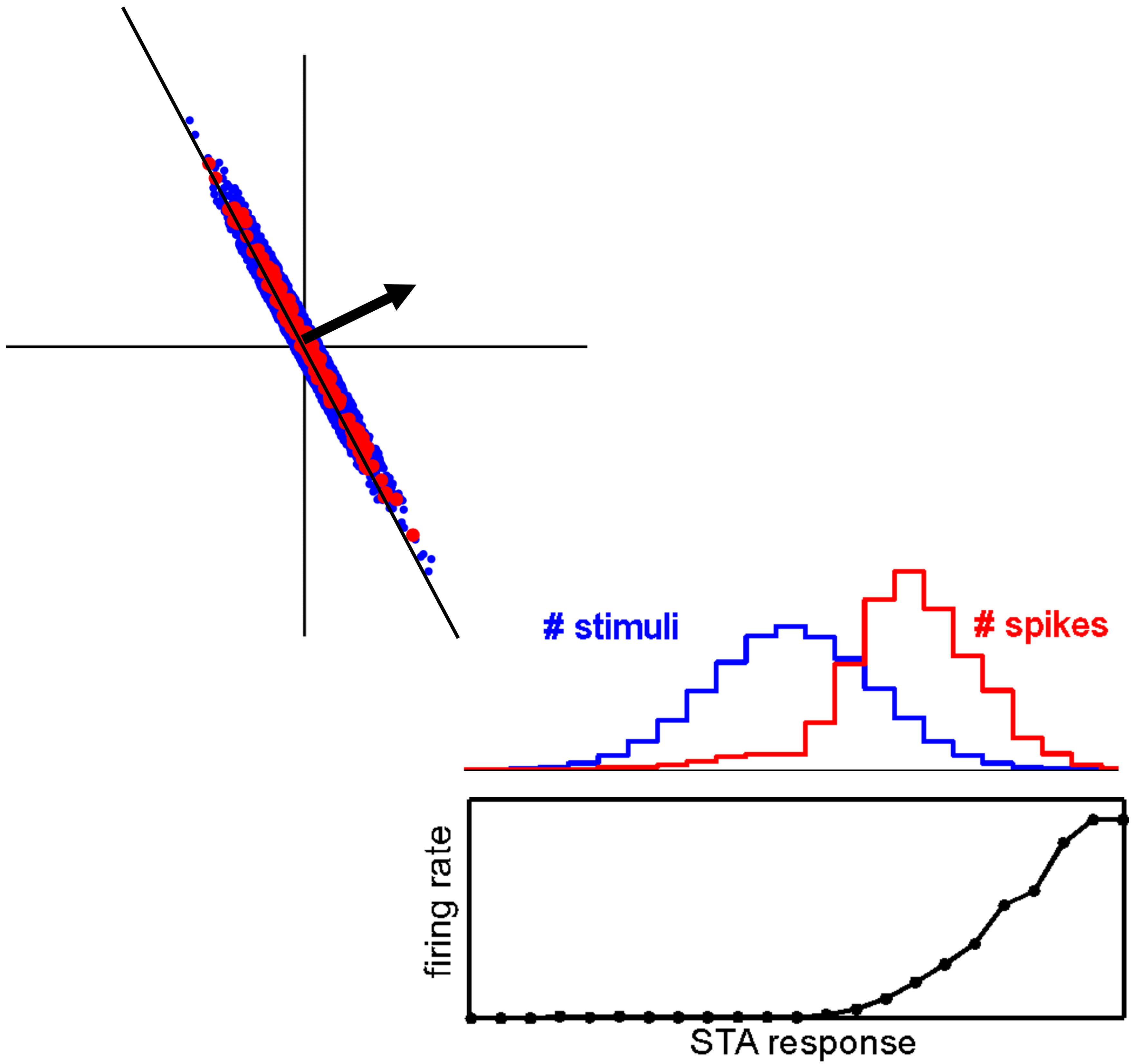


Projecting onto an axis orthogonal to the STA



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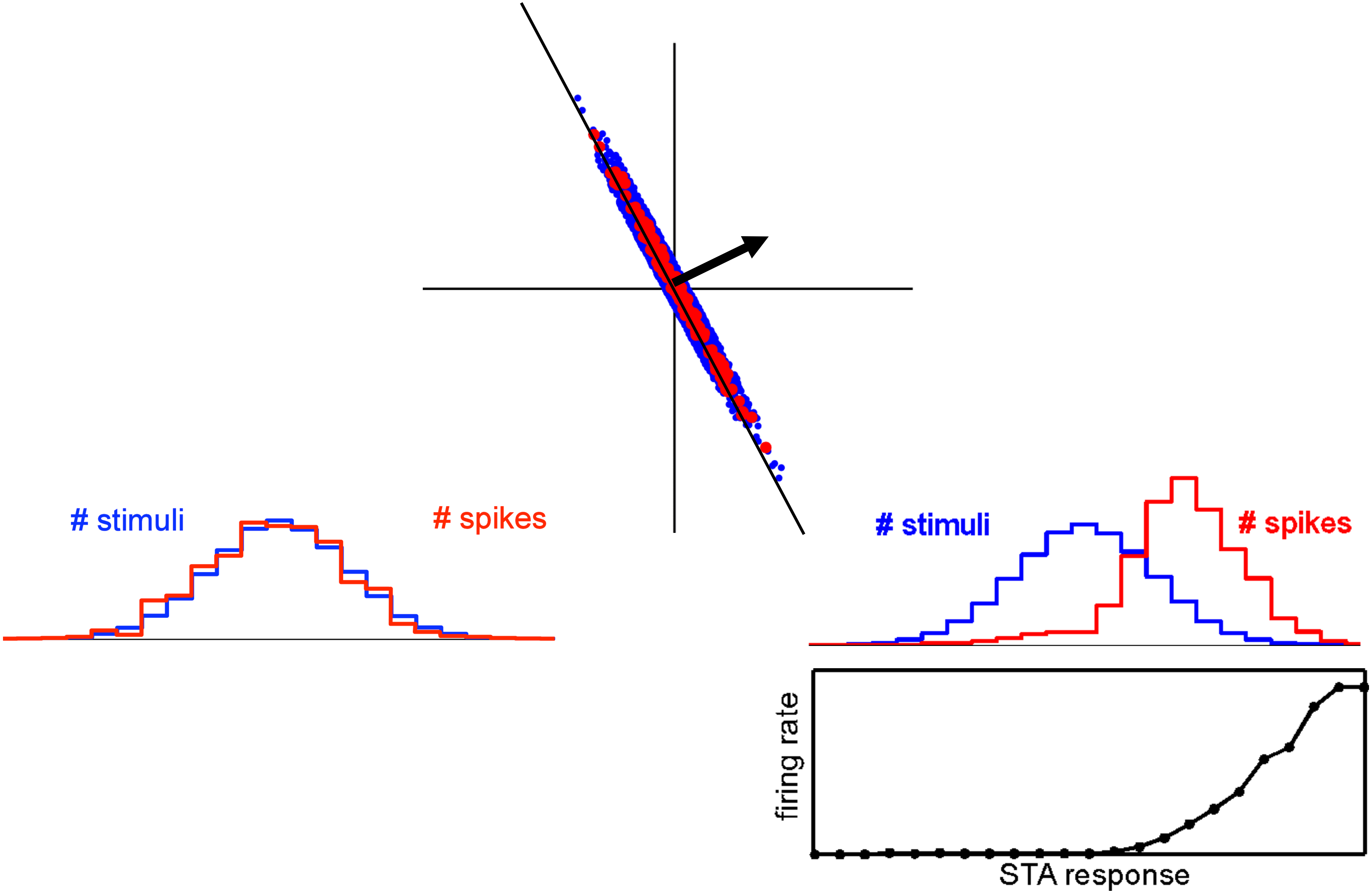

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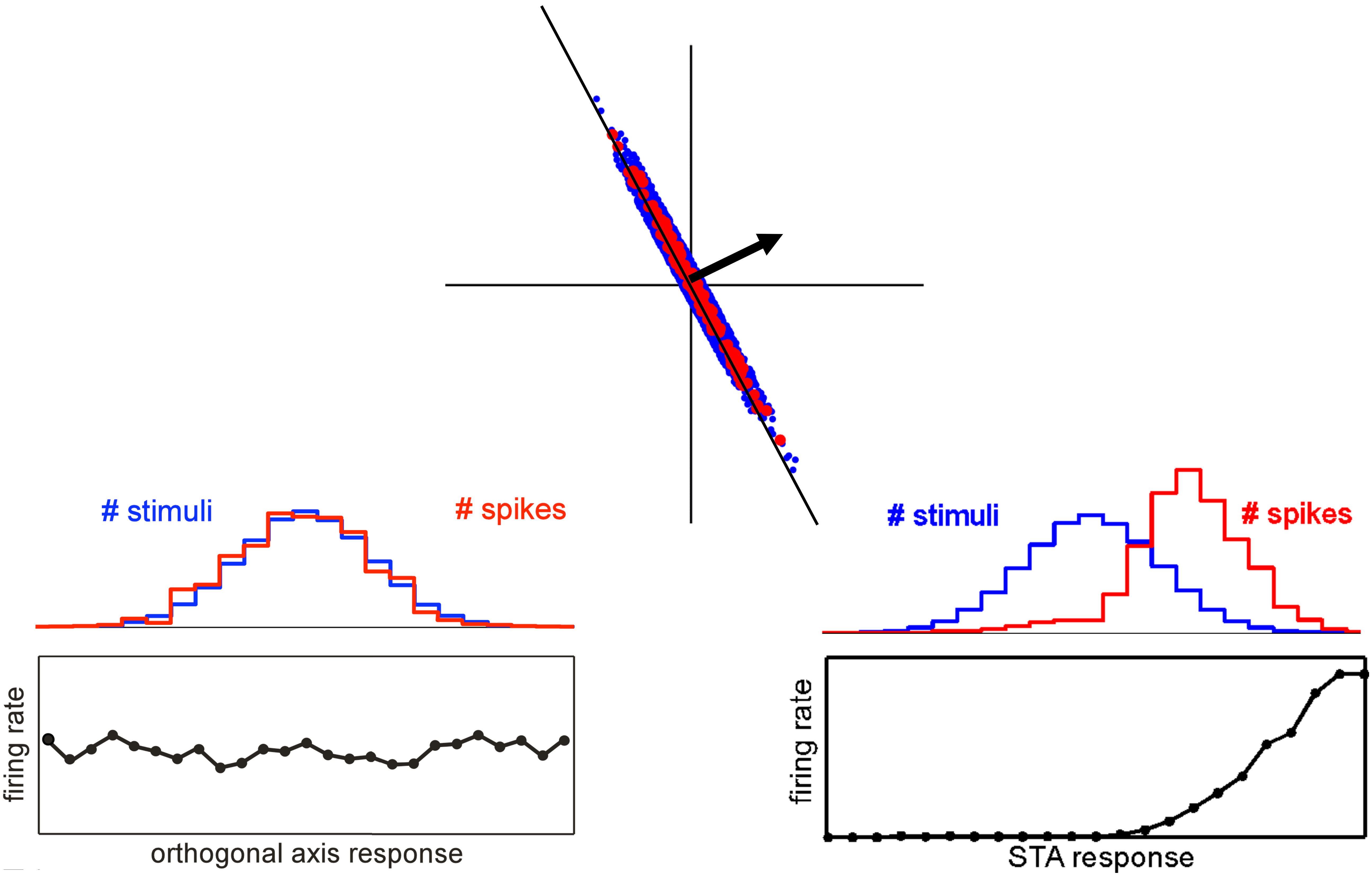


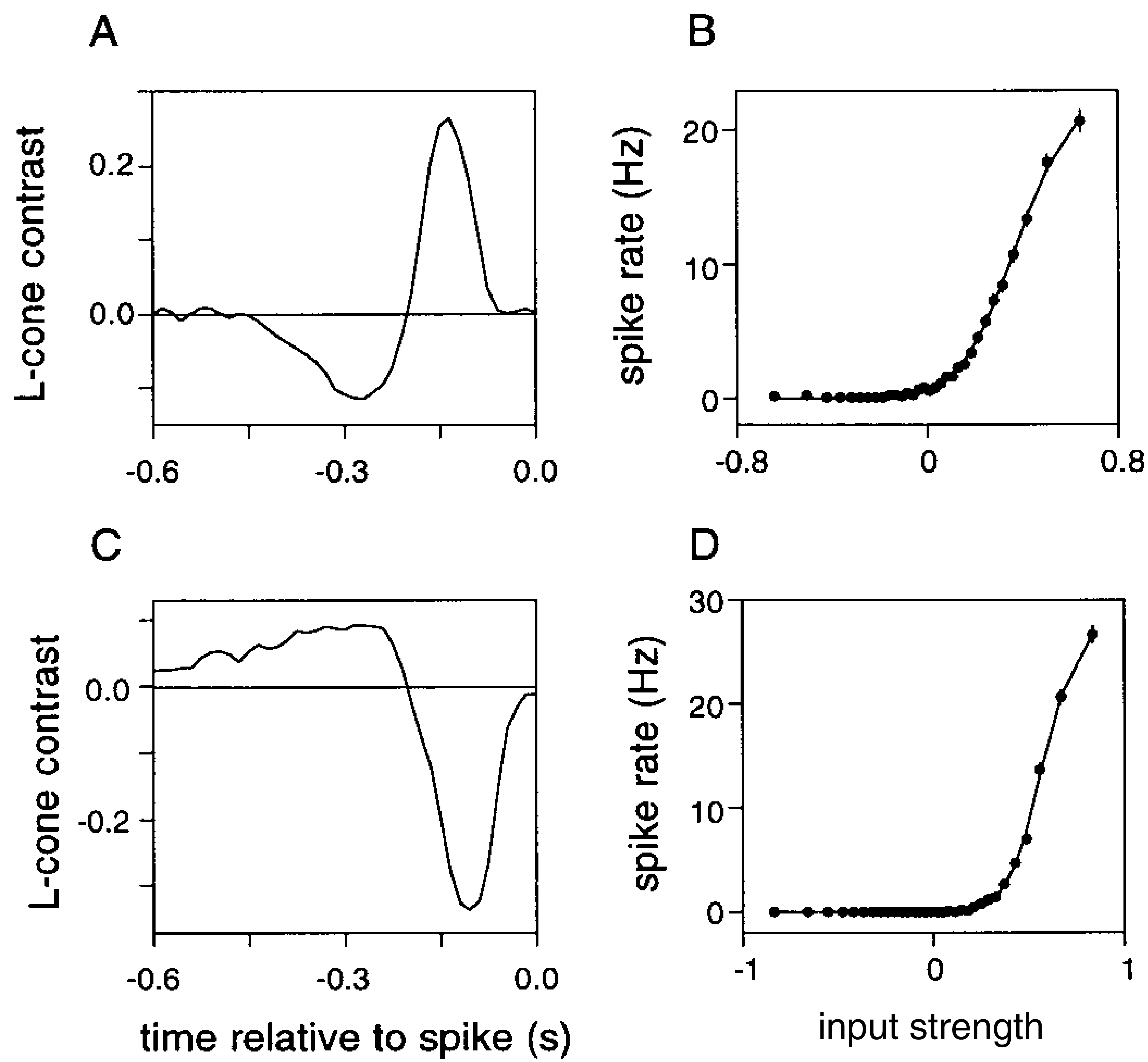
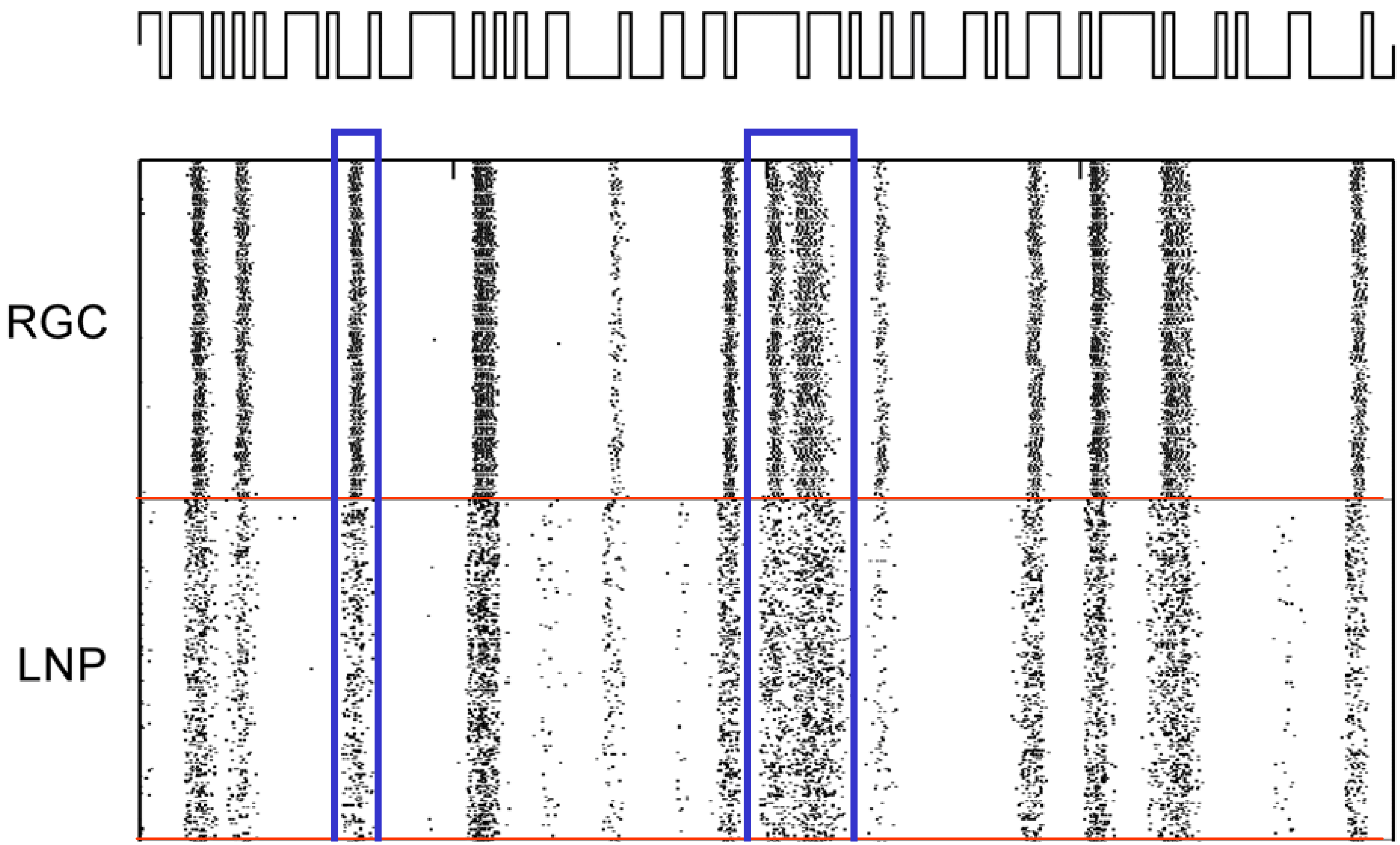
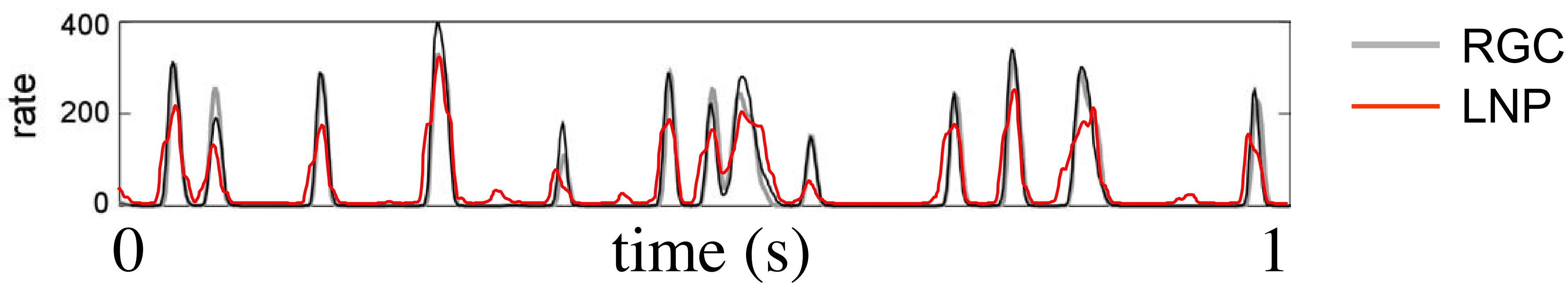


Figure 3. Characterization of light response in one ON cell (*A*, *B*) and one OFF cell (*C*, *D*) simultaneously recorded in salamander retina. *A*, *C*,

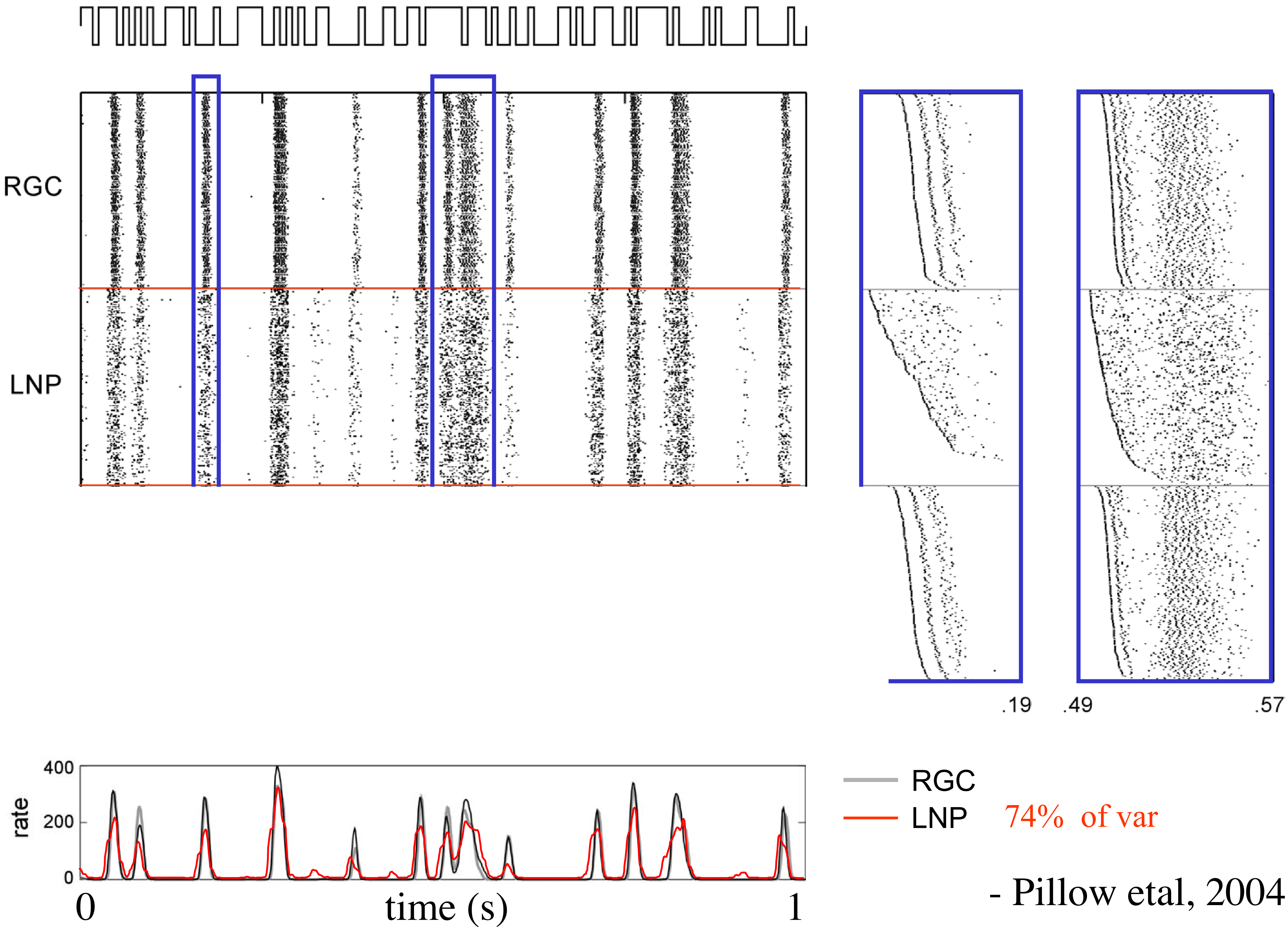
\- Chander & Chichilnisky 01





74% of var

- Pillow etal, 2004



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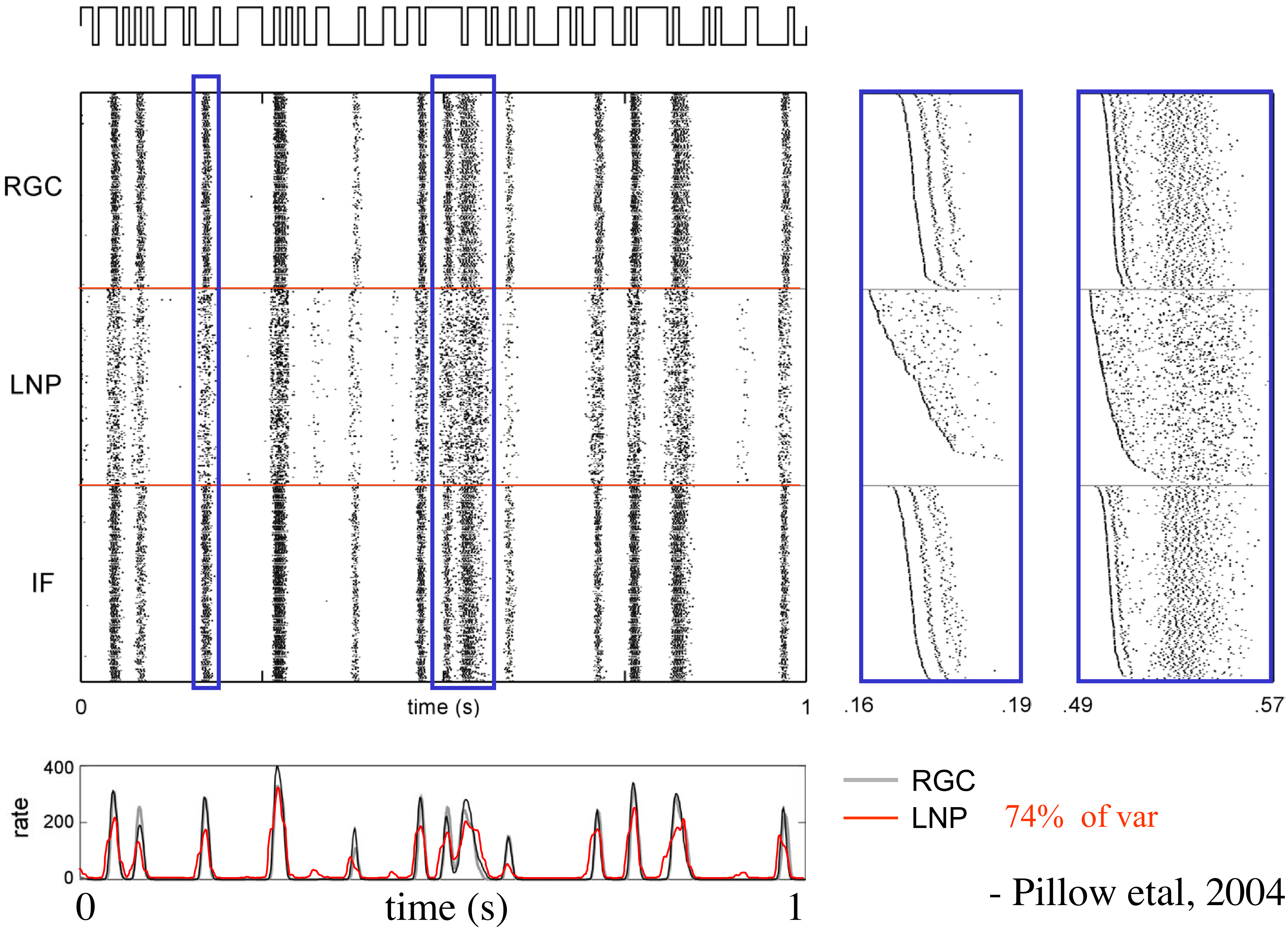

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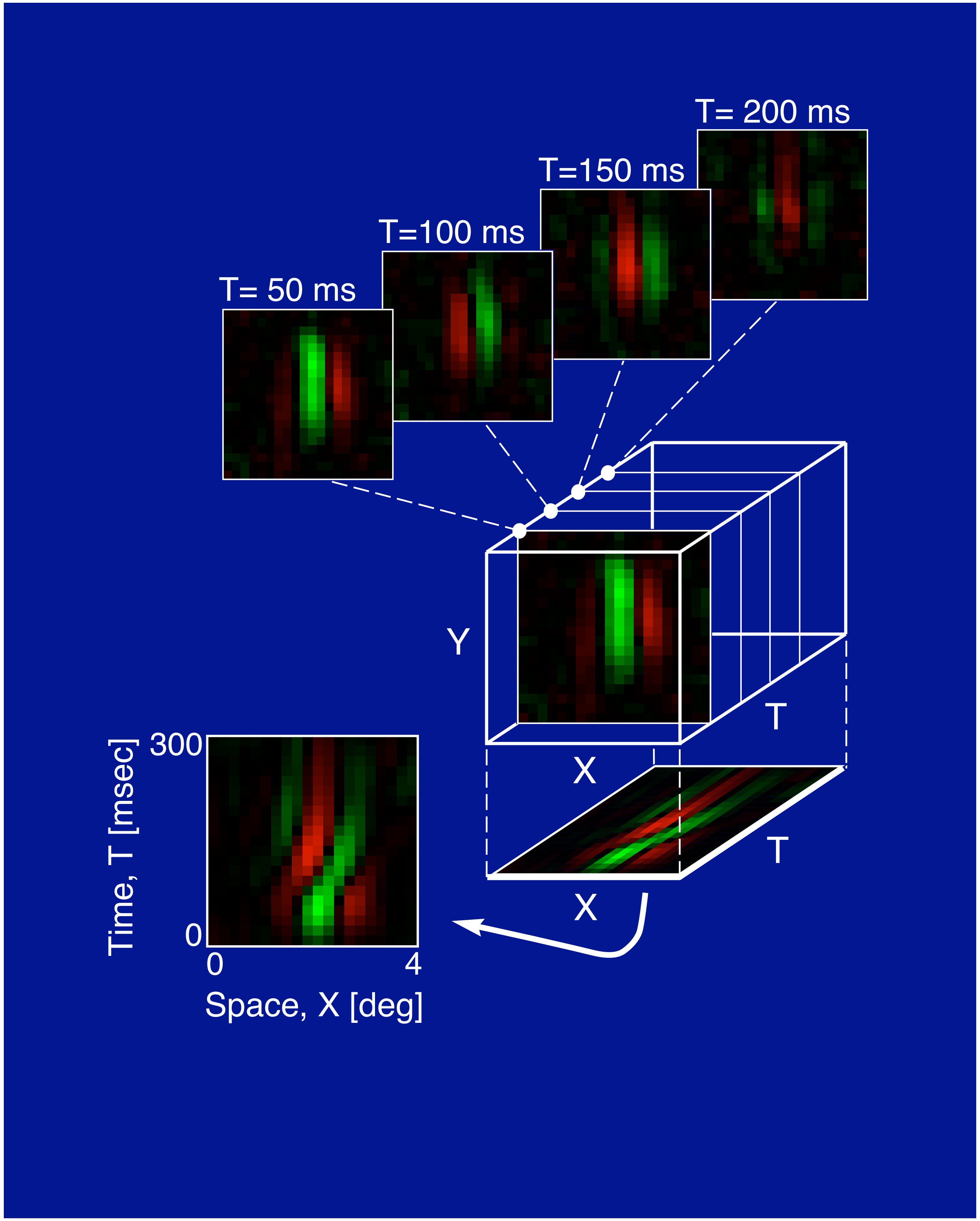
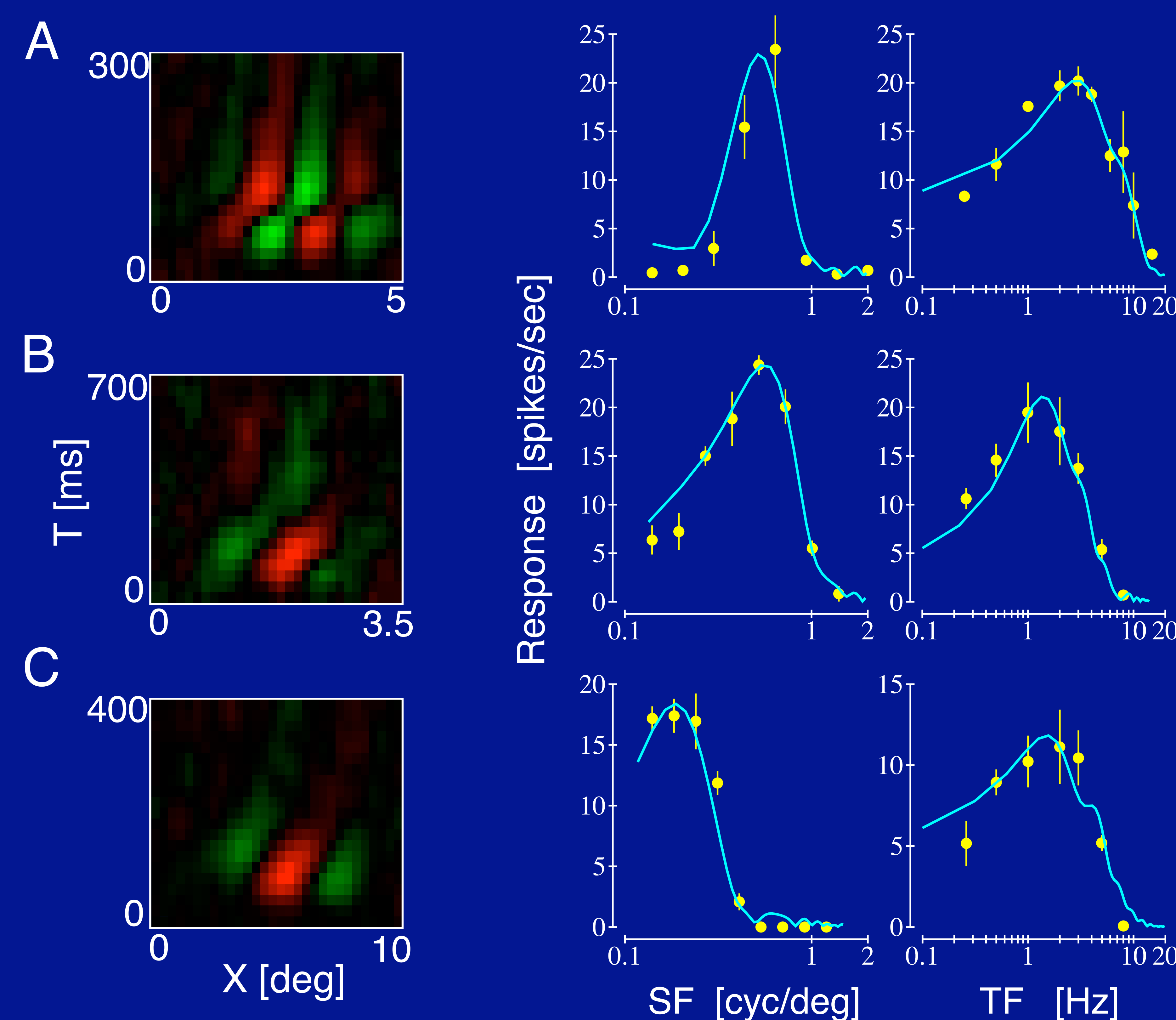
V1 simple cell



- Ozhawa, etal



A
B
C
300
0
5
700
3.5
400
10
T [ms]
X [deg]
Response [spikes/sec]
SF [cyc/deg]
TF [Hz]
0.1
1
2
10
20
25
15
5

LNP summary

- LNP is the defacto standard descriptive model, and is implicit in much of the experimental literature
- Accounts for basic RF properties
- Accounts for basic spiking properties (rate code)
- Easily fit to data
- Easily interpreted
- BUT, non-mechanistic, and exhibits striking failures (esp. beyond early sensory/motor) ...

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- Symmetric nonlinearities and/or multi-dimensional front-end (e.g., V1 complex cells)

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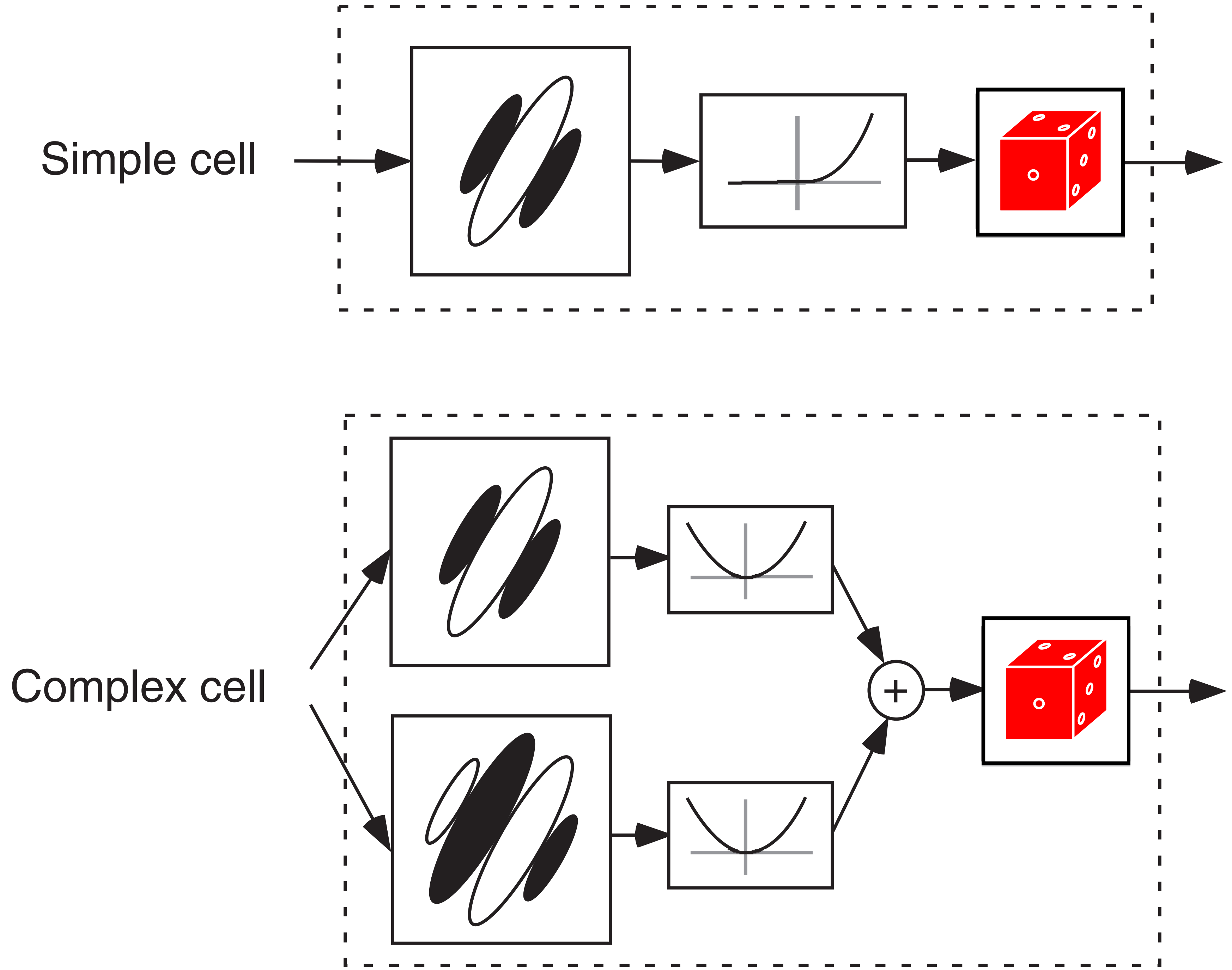
  ➡ Subspace LNP

Classic V1 models



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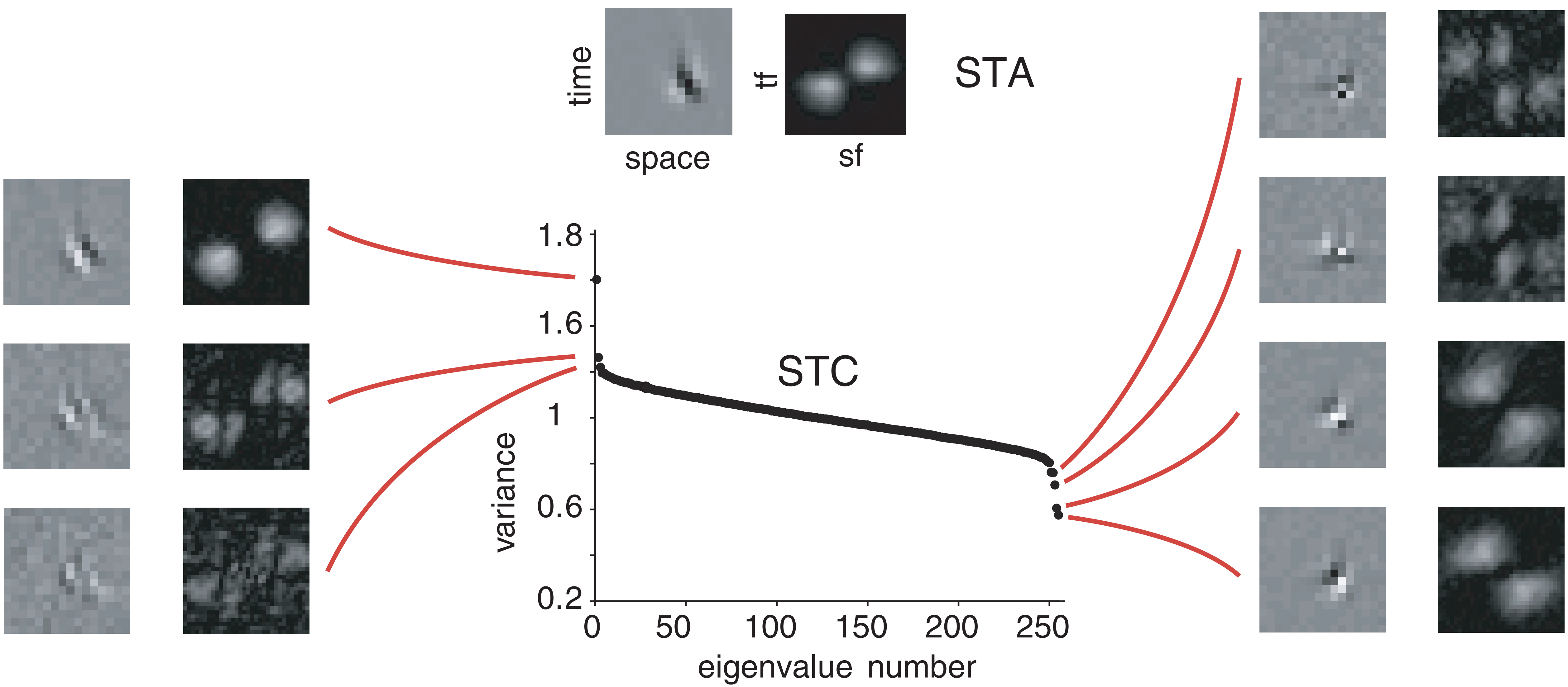

[Rust, Schwartz, Movshon, Simoncelli, ‘05]

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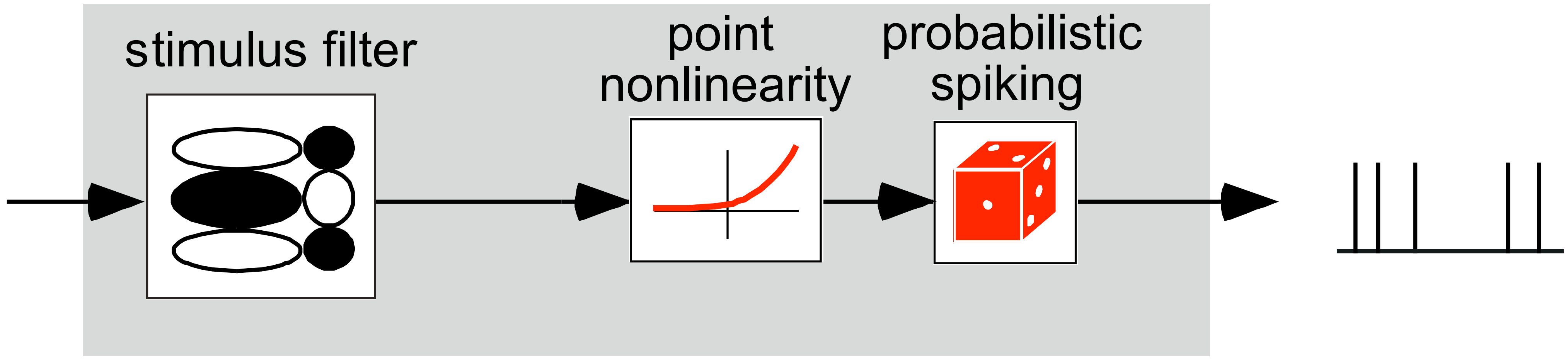
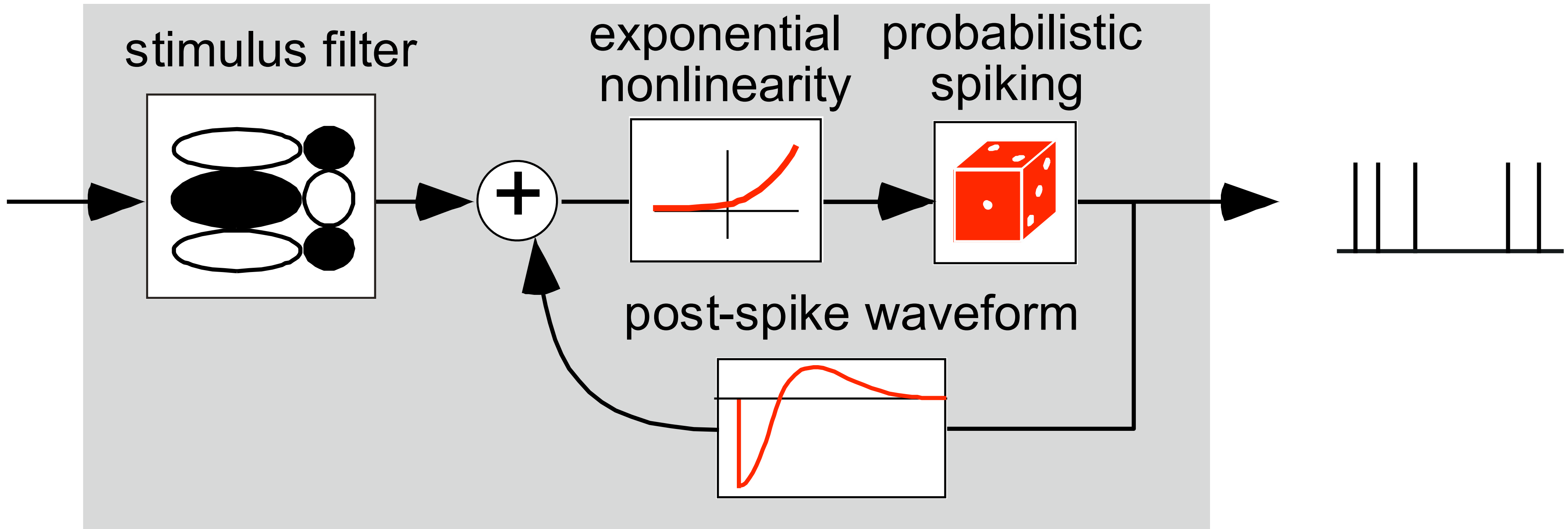
Linear-Nonlinear-Poisson (LNP)



Recursive LNP



[Truccolo et al '05;
Pillow et al '05]

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  ➡ Subspace LNP [movshon lecture?]
- Responses depend on spike history, other cells
  ➡ Recursive models (GLM) [paninski lecture]
- White noise doesn't drive mid- to late-stage neurons well

LNP limitations

- Symmetric nonlinearities and/or multi-dimensional front-end (e.g., V1 complex cells)
  ➡ Subspace LNP [movshon lecture?]
- Responses depend on spike history, other cells
  ➡ Recursive models (GLM) [paninski lecture]
- White noise doesn't drive mid- to late-stage neurons well
  ➡ Specialized "afferent" stimuli [movshon lecture]

Credits

- Spike-triggered covariance: Odelia Schwartz, Jonathan Pillow, Liam Paninski, Nicole Rust
- Stochastic integrate-and-fire & rLNP models: Jonathan Pillow, Liam Paninski
- V1/MT physiology/modeling: Nicole Rust, Tony Movshon (NYU)
- Retinal physiology/modeling: Jonathon Shlens, Valerie Uzzell, Divya Chander, EJ Chichilnisky (Salk Institute)