Swipe Right to Spike

Analysis and modeling of spiking neurons

2019-01-08

#isiCNI2019

Slides and problem set:

https://github.com/rkp8000/imbizo_2019_spikes_tutorial

Outline

- Review of action potentials.
- Basic spike train analysis.
- Spiking neuron models.
- Short problem set time.
- Advanced spike train analysis.
- Other spike-based concepts.
- Full problem set time.

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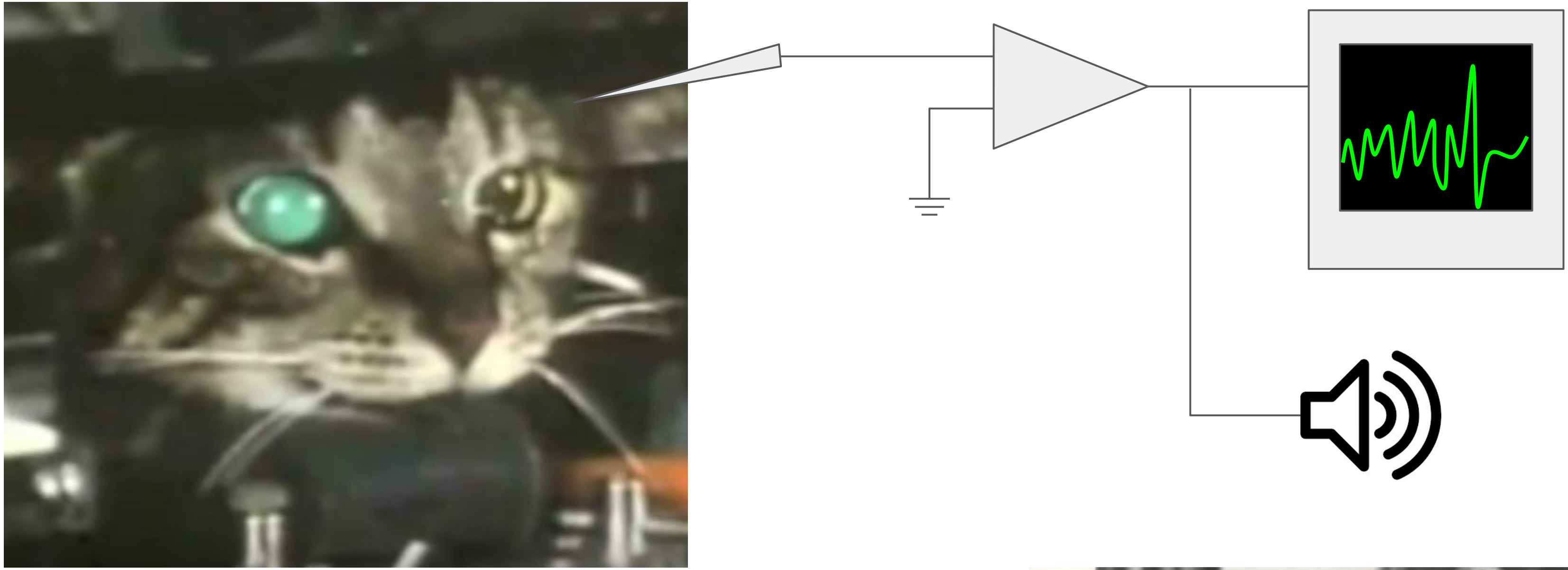
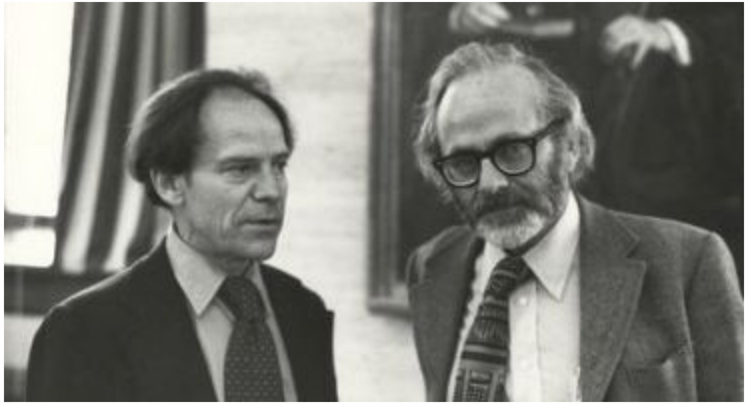
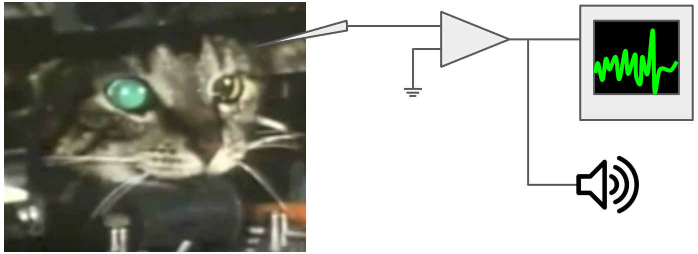




Hubel and Wiesel 1959



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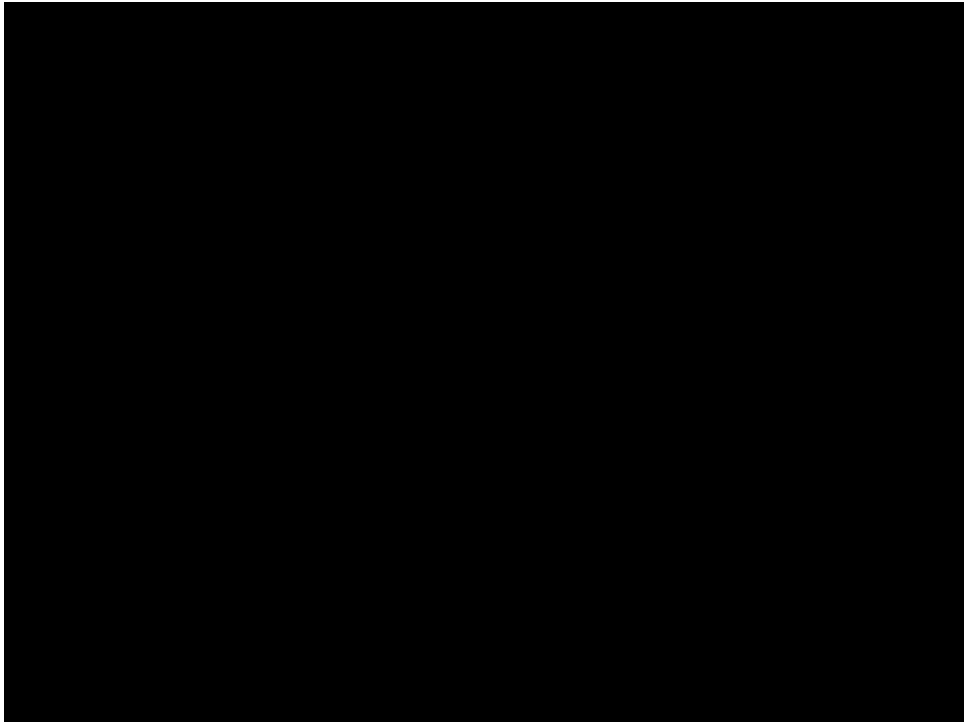
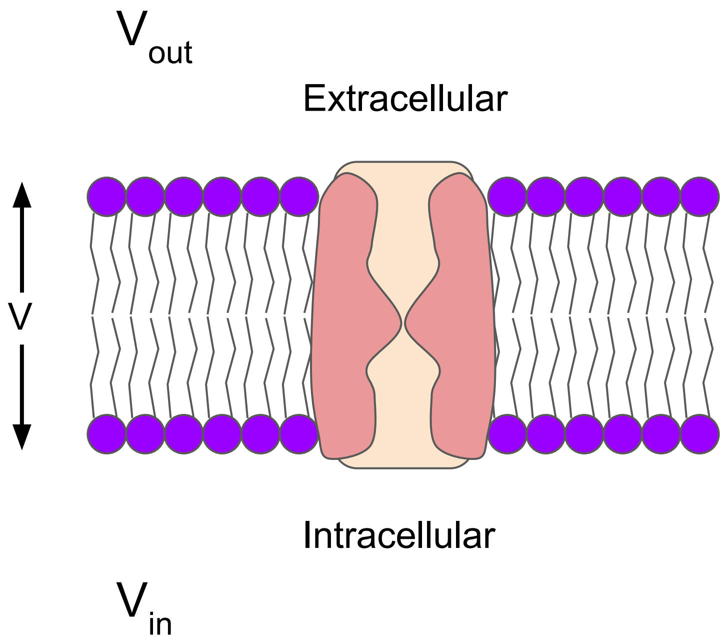


https://www.youtube.com/watch?v=8VdFf3egwfg

Spike generation and detection

Membrane potential = voltage diff across neuron membrane: $\mathbf{V_m = V_{in} - V_{out}}$



Typical resting $V_m = V_{rest} \sim -70$ mV

Spike generation and detection

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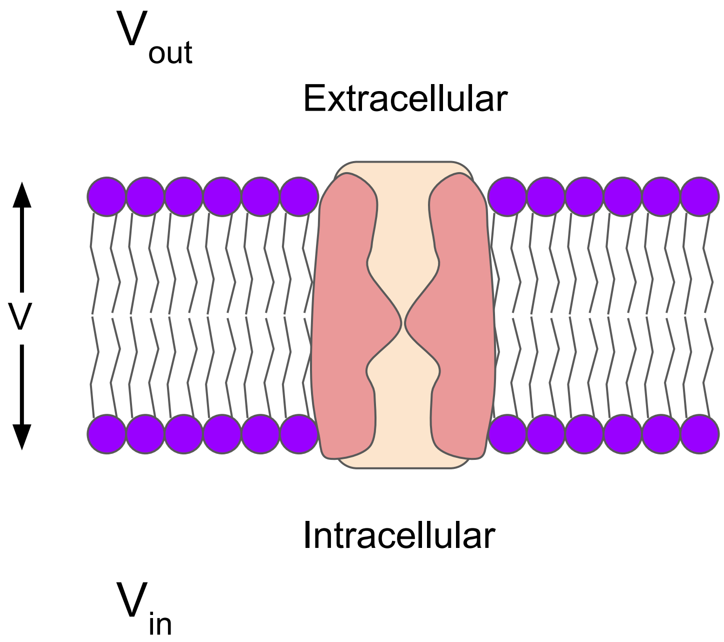

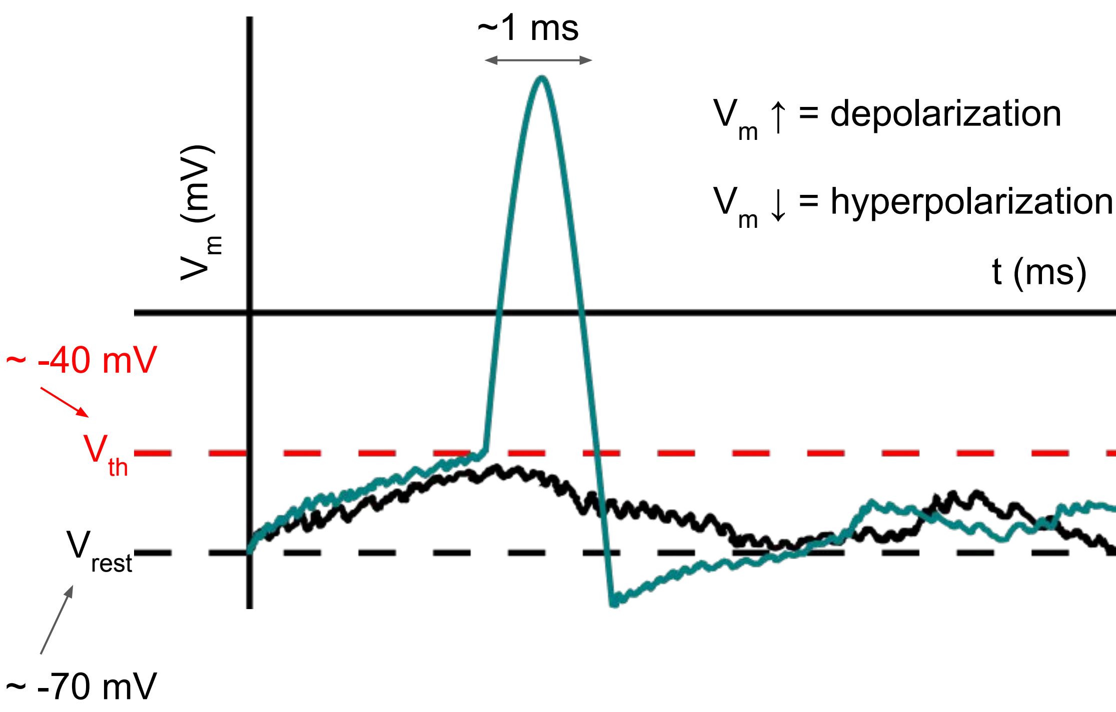

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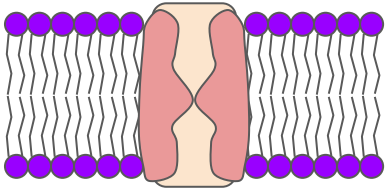

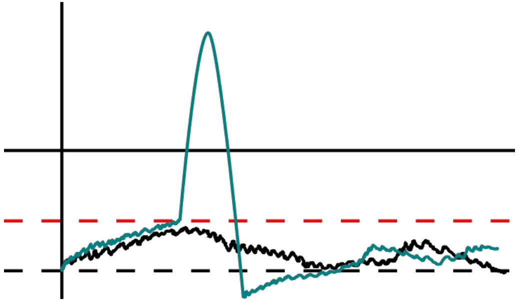

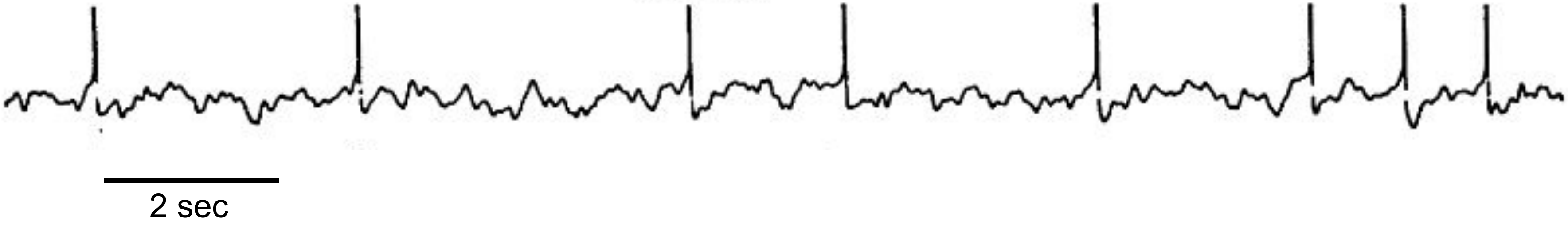

Bryant and Segundo, 1976.

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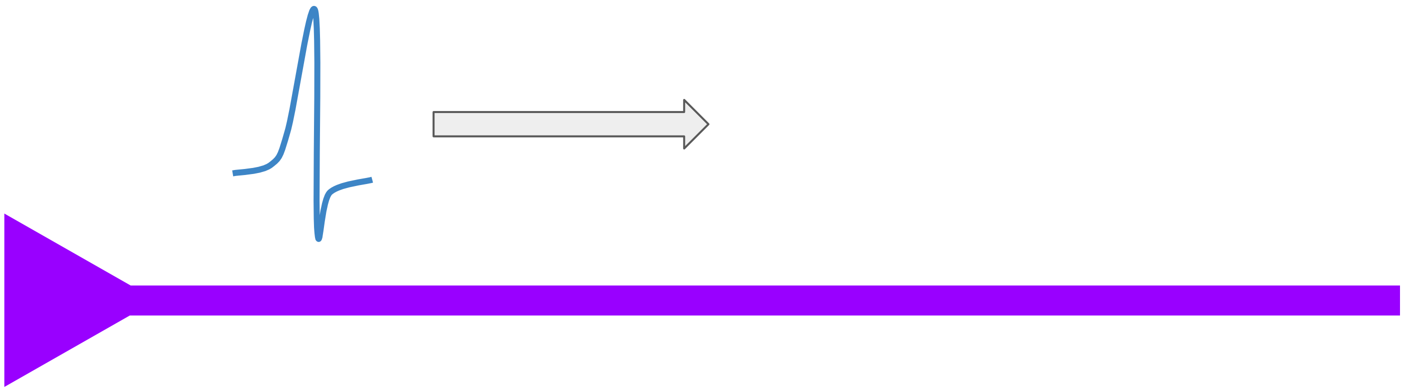

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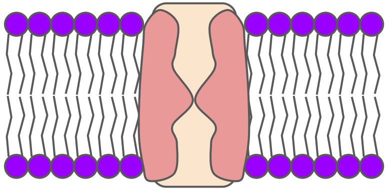

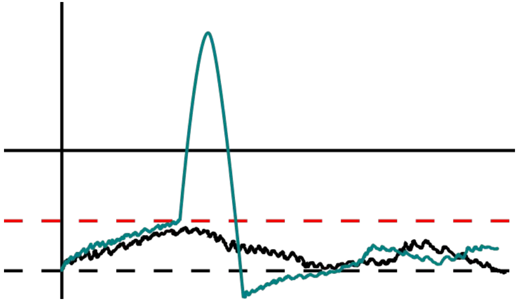

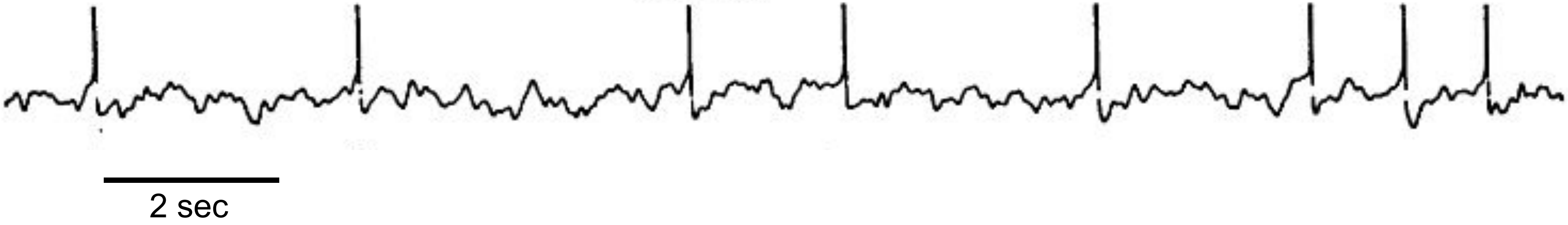

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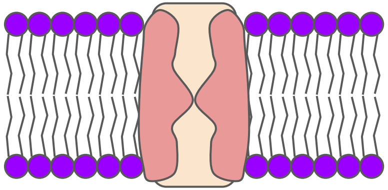

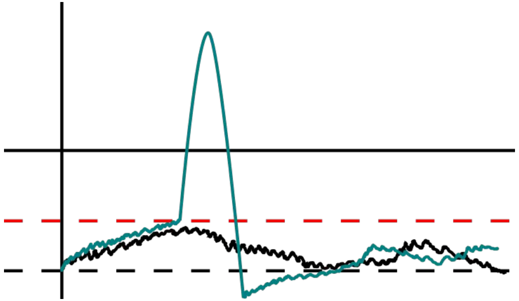

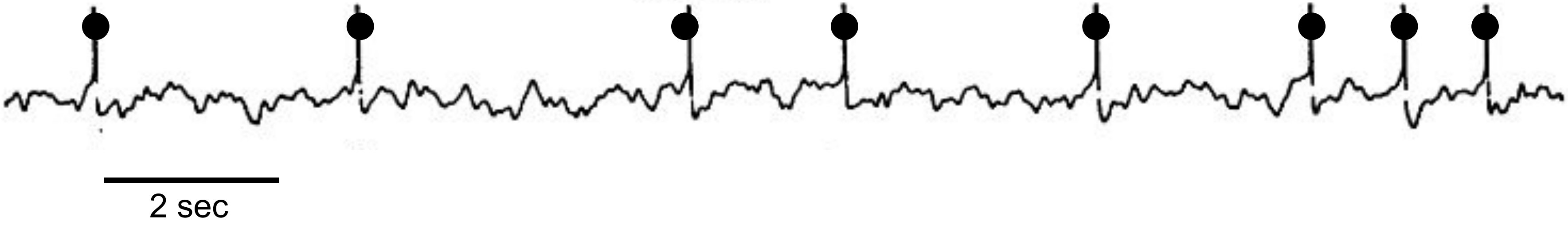

Bryant and Segundo, 1976.

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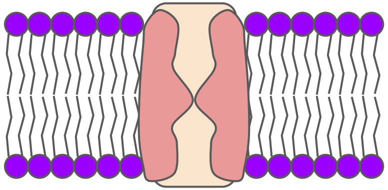

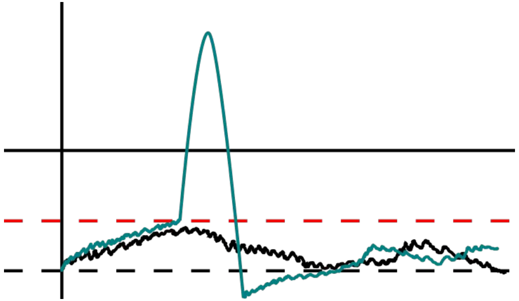

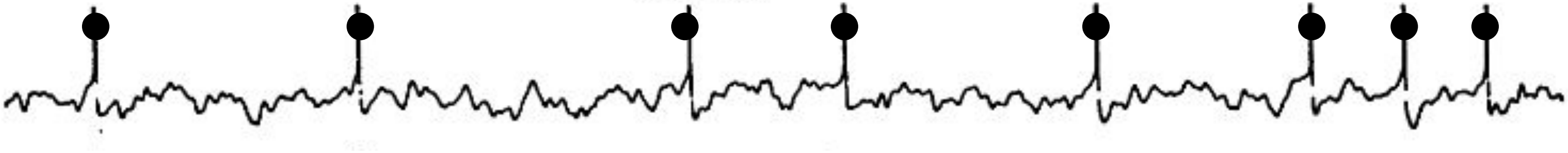

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Bryant and Segundo, 1976.

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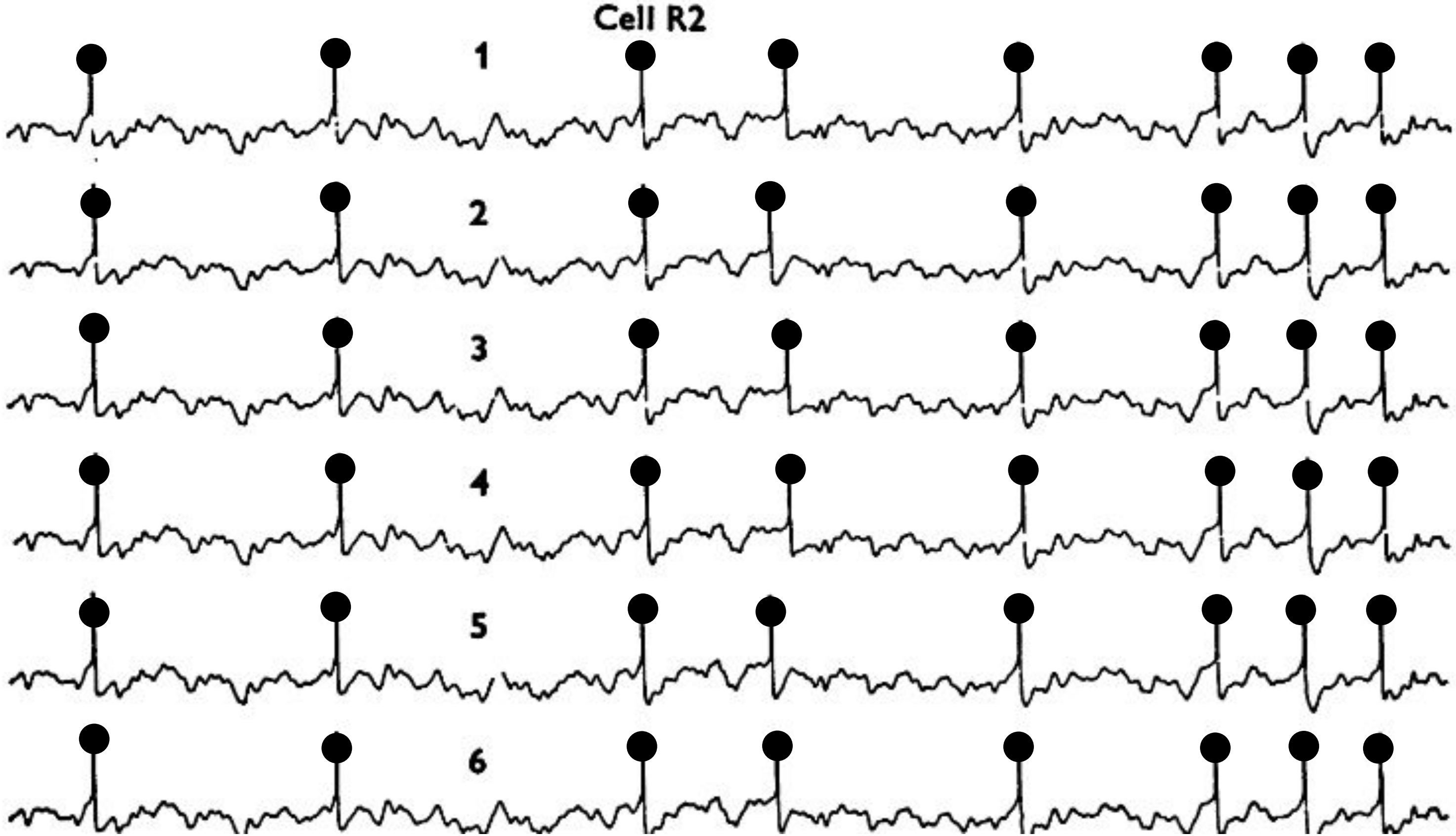
Spiking basics: raster plots and PSTHs

How repeatable are spike trains?

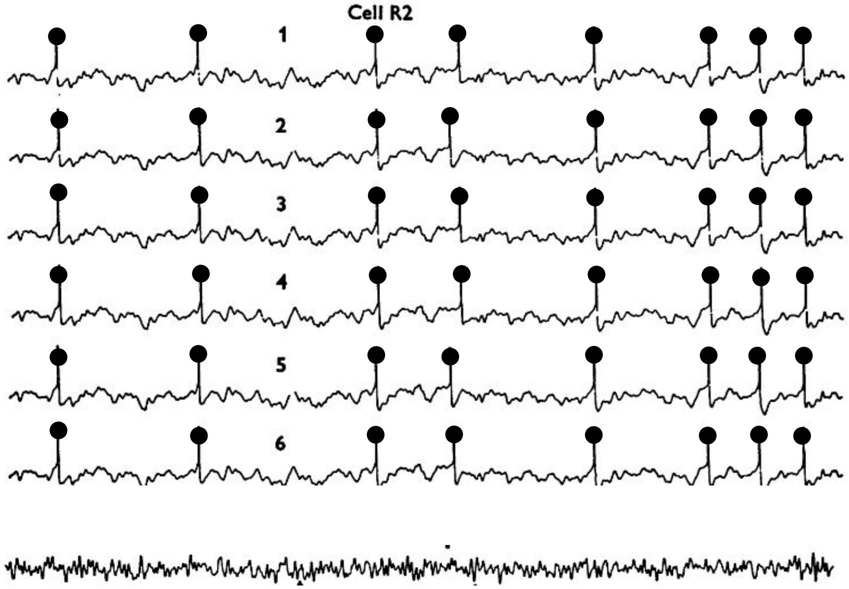
Spiking basics: raster plots and PSTHs

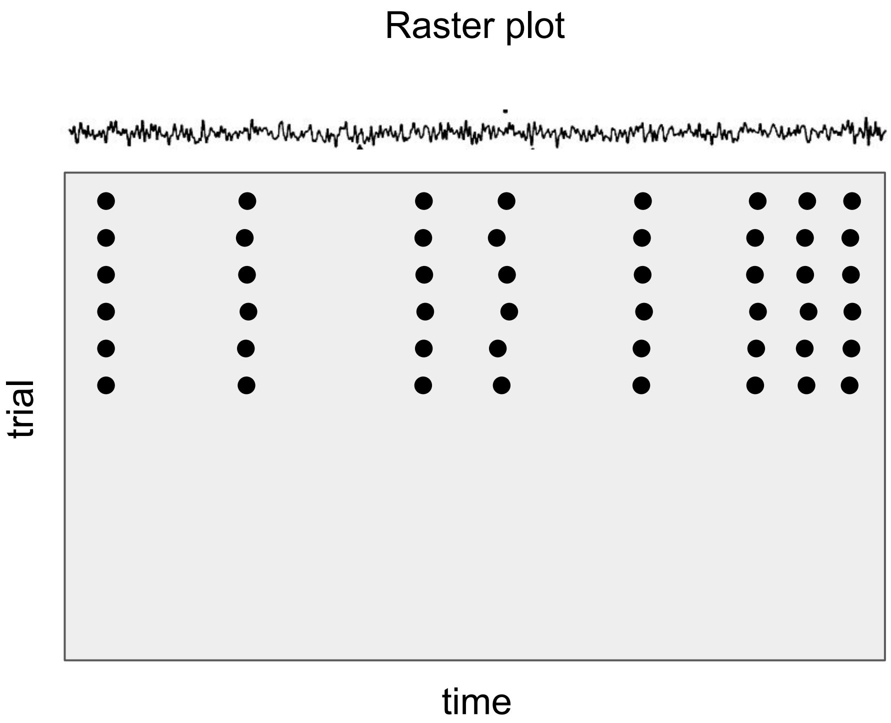


2 sec

Bryant and Segundo, 1976.

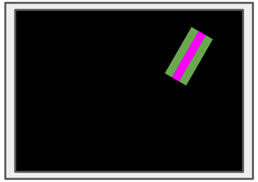
Spiking basics: raster plots and PSTHs

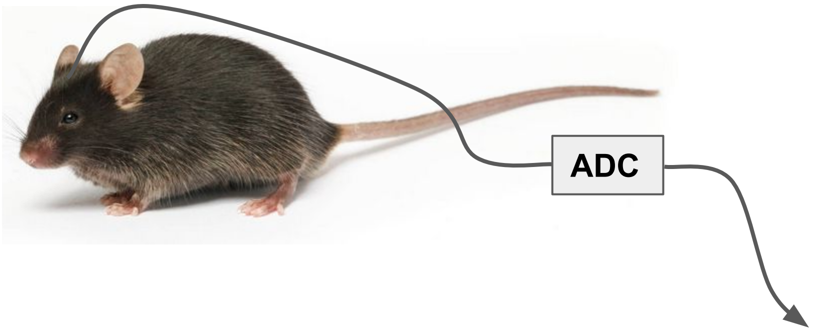


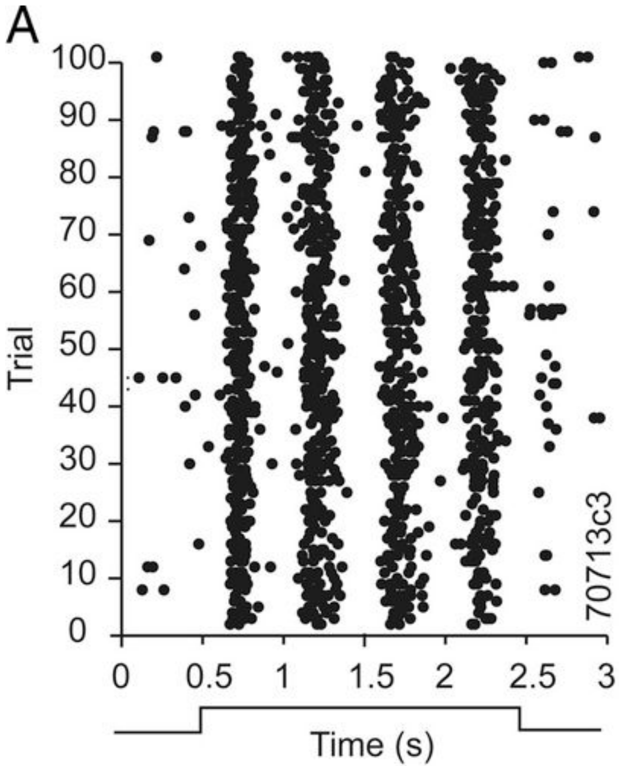


Bryant and Segundo, 1976.

Spiking basics: raster plots and PSTHs





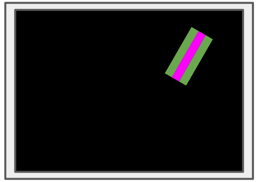


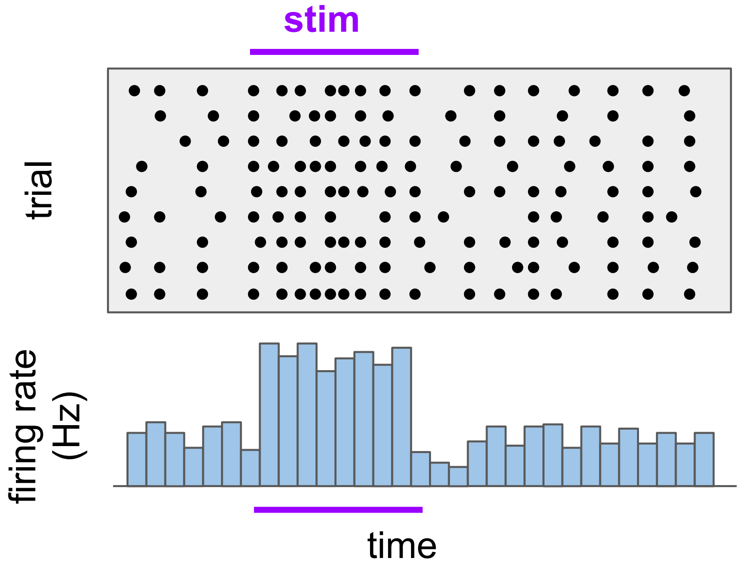
[Gao, Deangelis, Burkhalter 2010]

Spiking basics: raster plots and PSTHs

How do you summarize a raster plot?

Spiking basics: raster plots and PSTHs



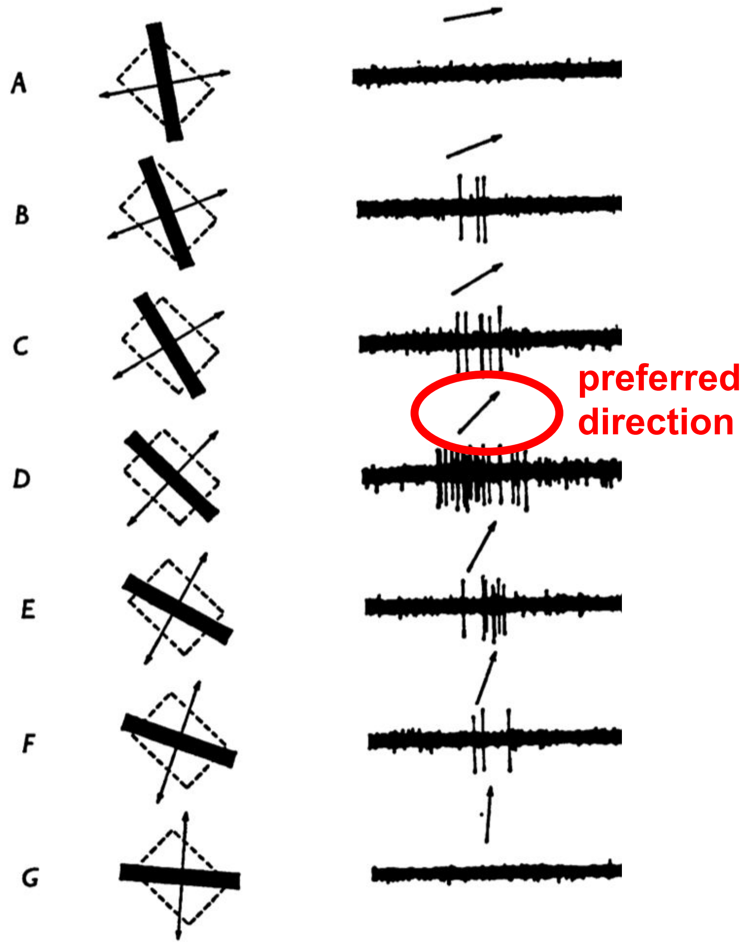


peristimulus time histogram

Spiking basics: tuning curves

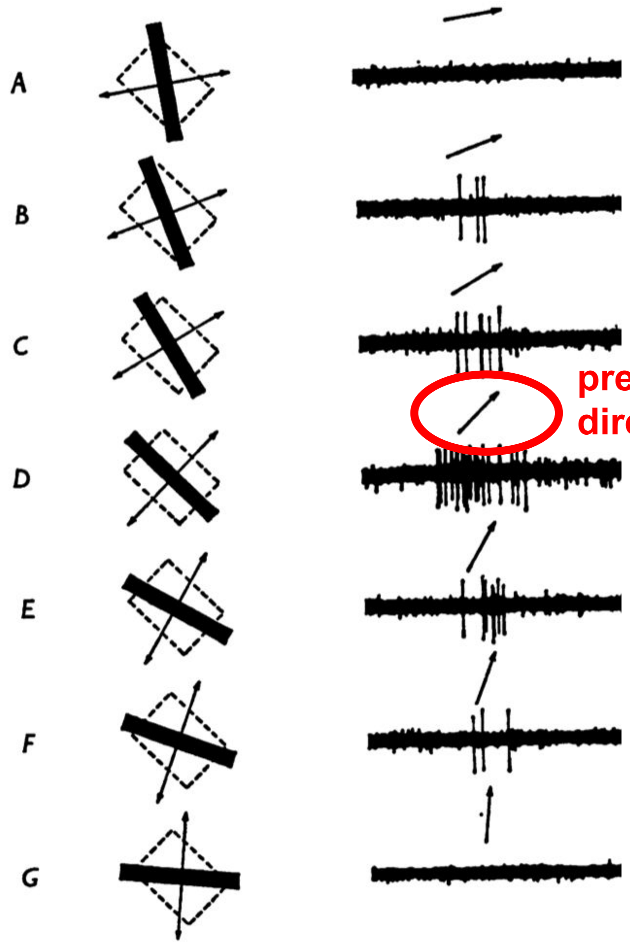
How do spike responses depend on stimulus?

Spiking basics: tuning curves



Hubel and Wiesel, 1968

Spiking basics: tuning curves



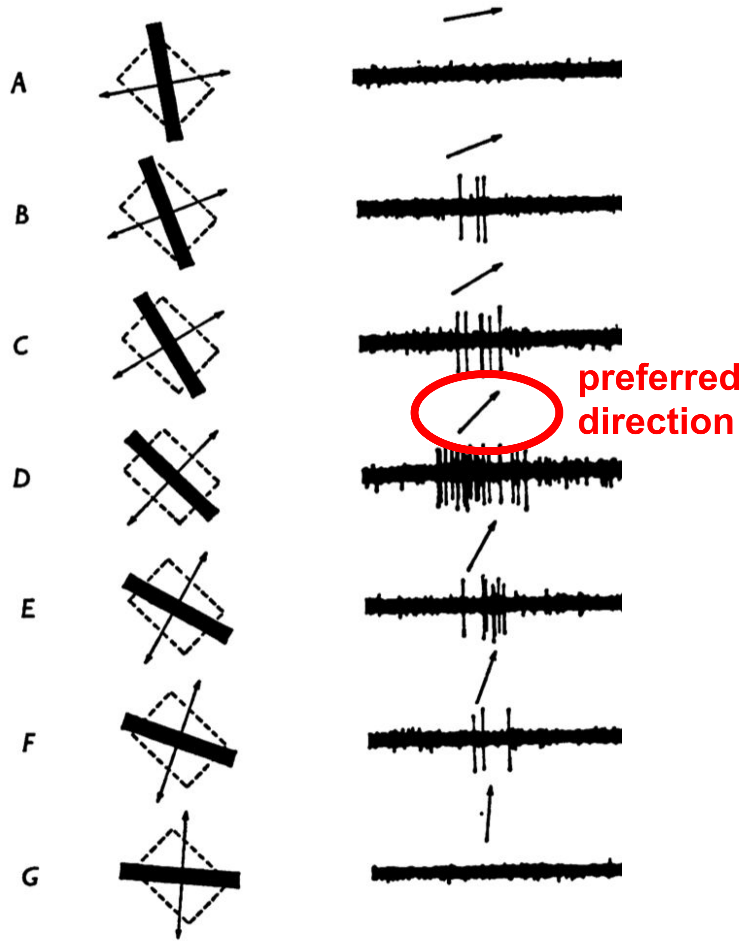
preferred direction

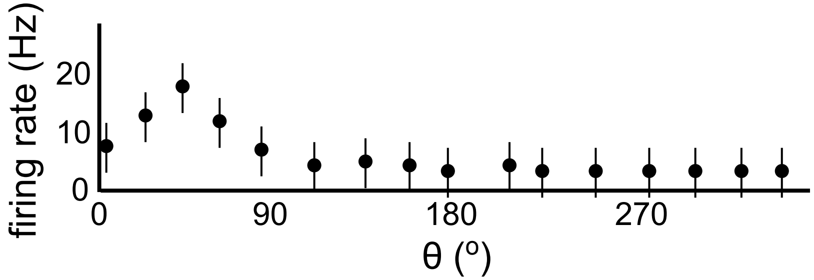
Trial	1	2	3	...
	0	0	0	...
	2	1	3	...
	6	8	5	...
	20	23	18	...
	10	7	8	...
		⋮		

spike counts

Hubel and Wiesel, 1968

Spiking basics: tuning curves





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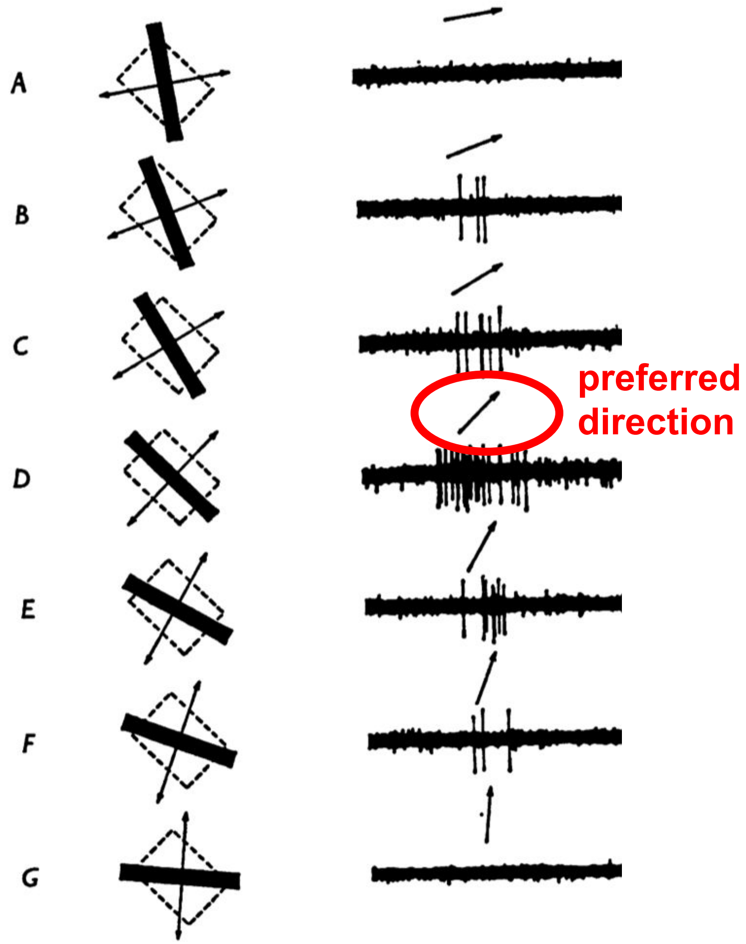

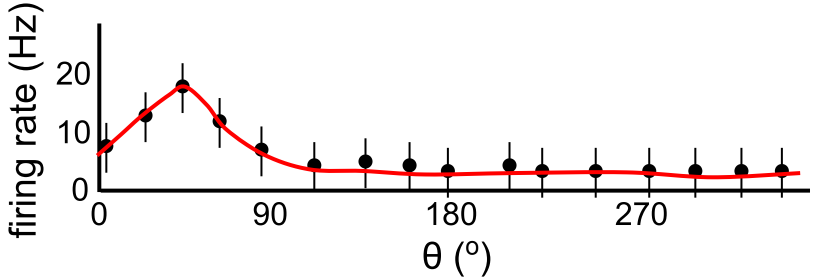

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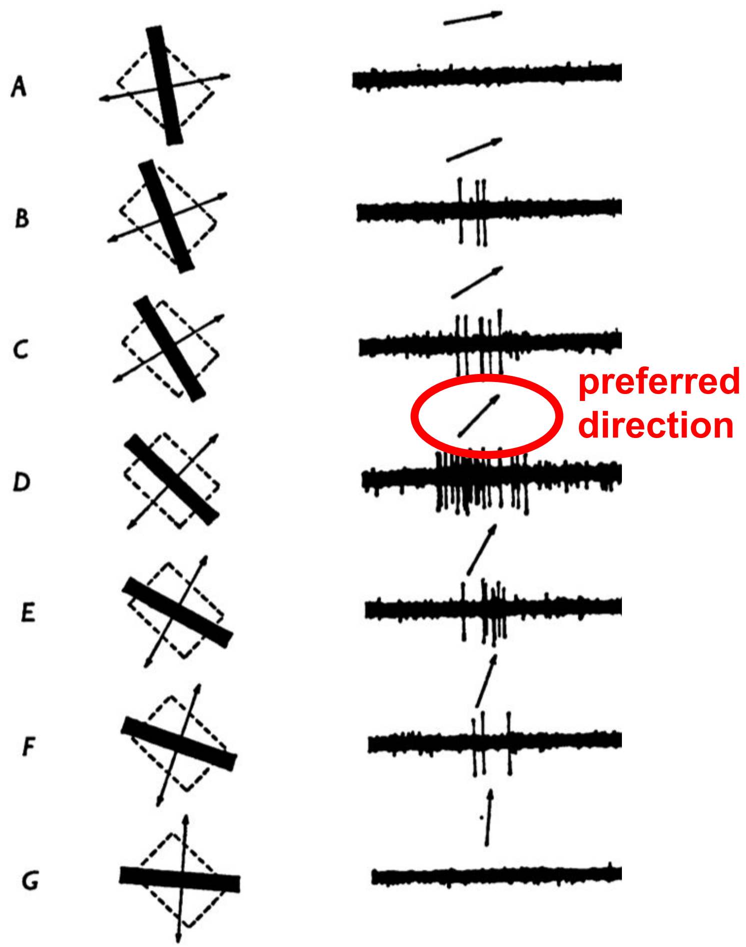
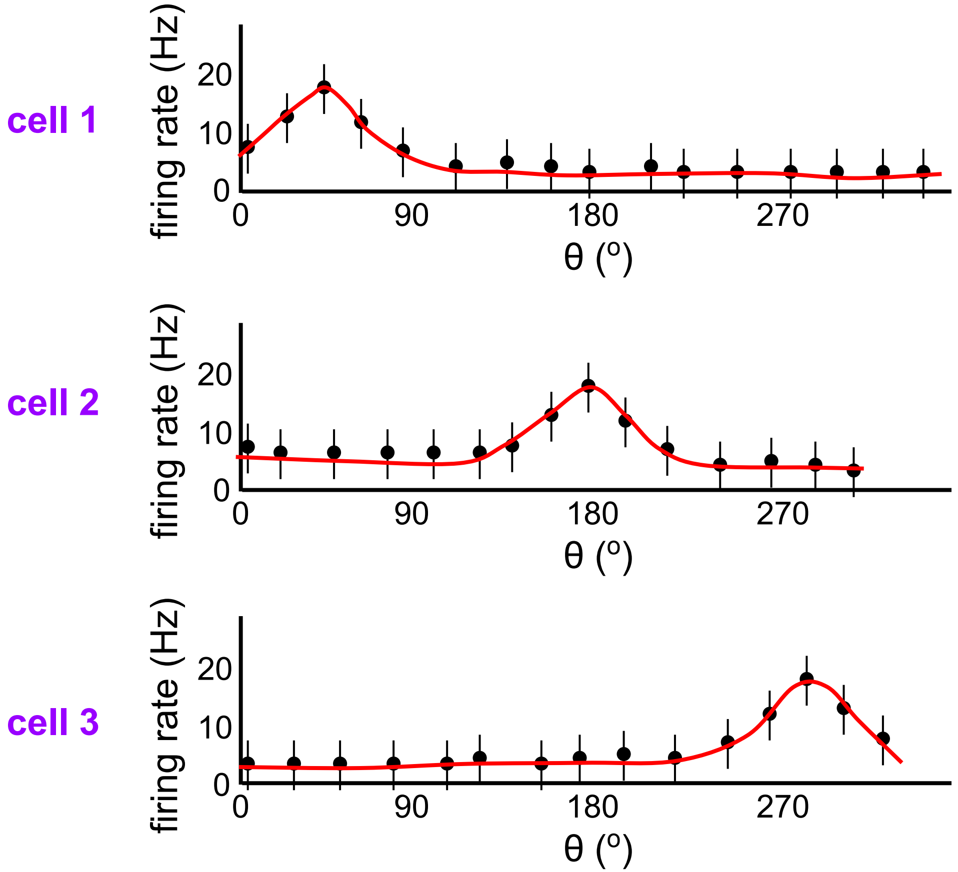




Hubel and Wiesel, 1968

Spiking basics: the inter-spike interval distribution

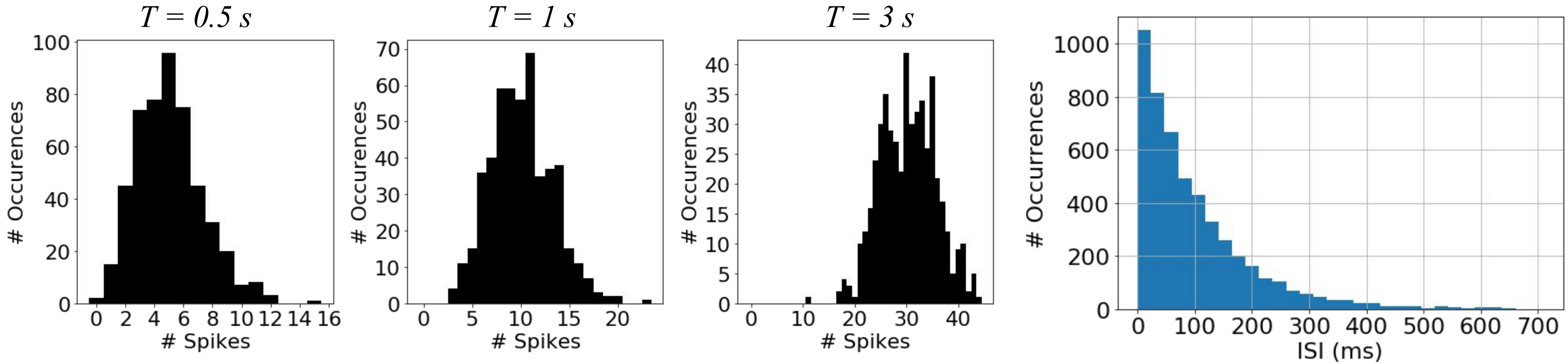
Unless all inputs fixed, spike times generally quite variable: ***what distribution underlies this variability?***

“Most random” spiking = ***Poisson-distributed*** spike counts (all spikes conditionally independent given rate).

$$\text{Poisson}(k|\lambda) = \frac{\lambda^k e^{-\lambda}}{k!}$$

$$p(k_{spks}|r, T) = \text{Poisson}(k_{spks}|\lambda = rT) \longrightarrow P(ISI) = r\exp(-rISI)$$

r = 10 Hz:



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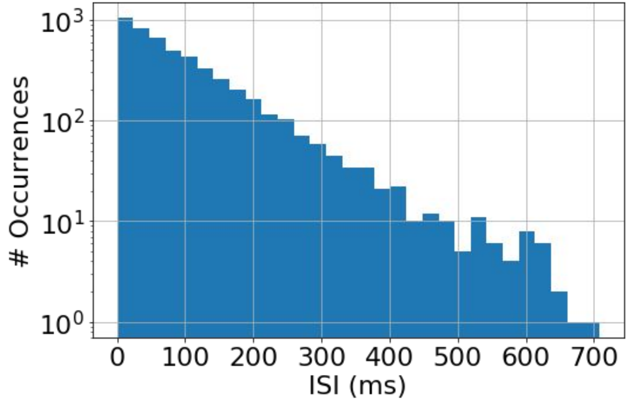
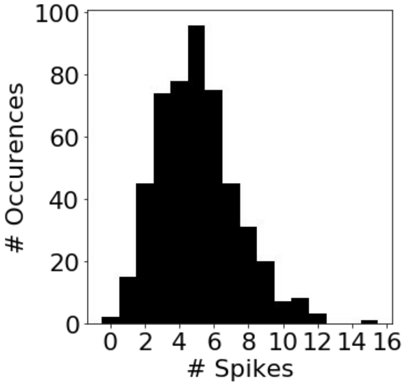
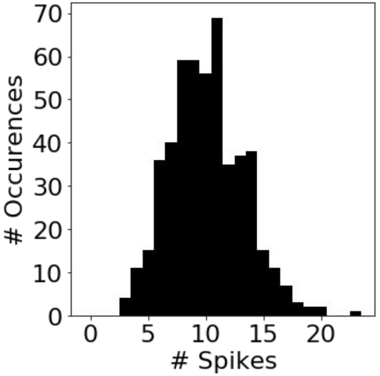


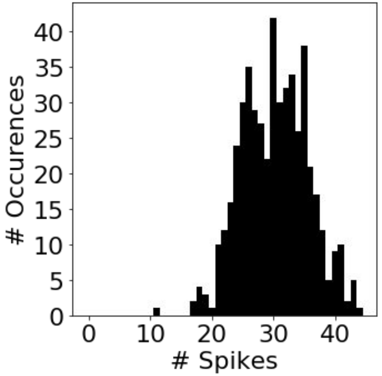
T = 0.5 s

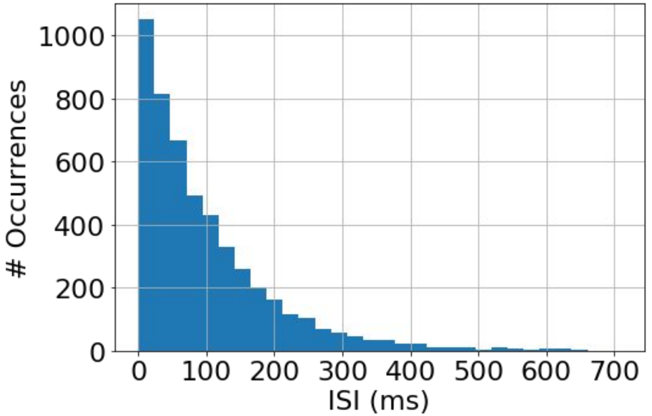


T = 1 s



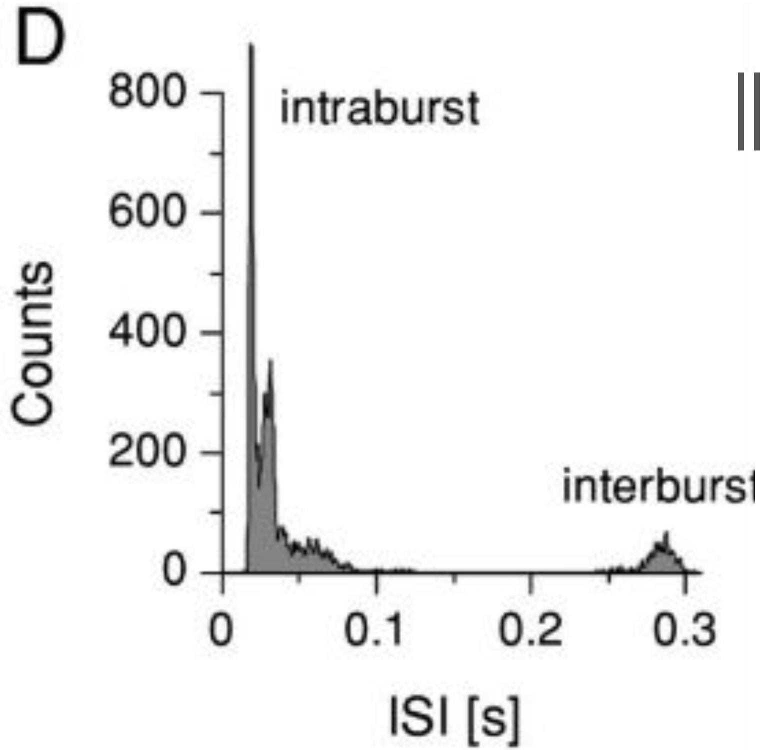
T = 3 s





Spiking basics: the inter-spike interval distribution

Q: What type of firing pattern yields the ISI distribution below?
A: Burst firing.



Szűcs et al. 2003

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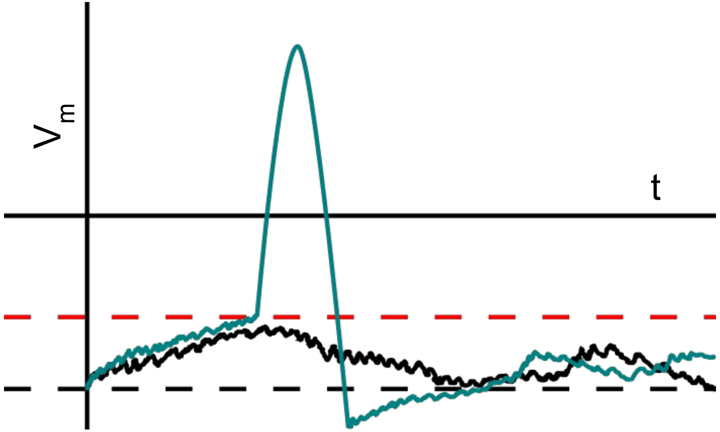
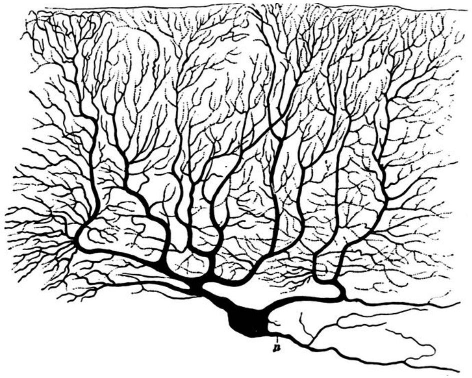
Spiking neuron models

Hodgkin-Huxley model

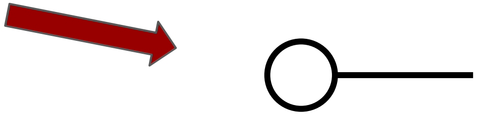
$$\begin{cases} \dfrac{dV_m}{dt} = \dfrac{I}{C_m} - \dfrac{\bar{g}_K n^4}{C_m}(V_m - V_K) - \dfrac{\bar{g}_{Na} m^3 h}{C_m}(V_m - V_{Na}) - \dfrac{\bar{g}_l}{C_m}(V_m - V_l) \\ \dfrac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n \\ \dfrac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m \\ \dfrac{dh}{dt} = \alpha_h(V_m)(1-h) - \beta_h(V_m)h \end{cases}$$



Realistic neuron morphology!



Can we simplify?



Spiking neuron models: the leaky integrate-and-fire (LIF) neuron

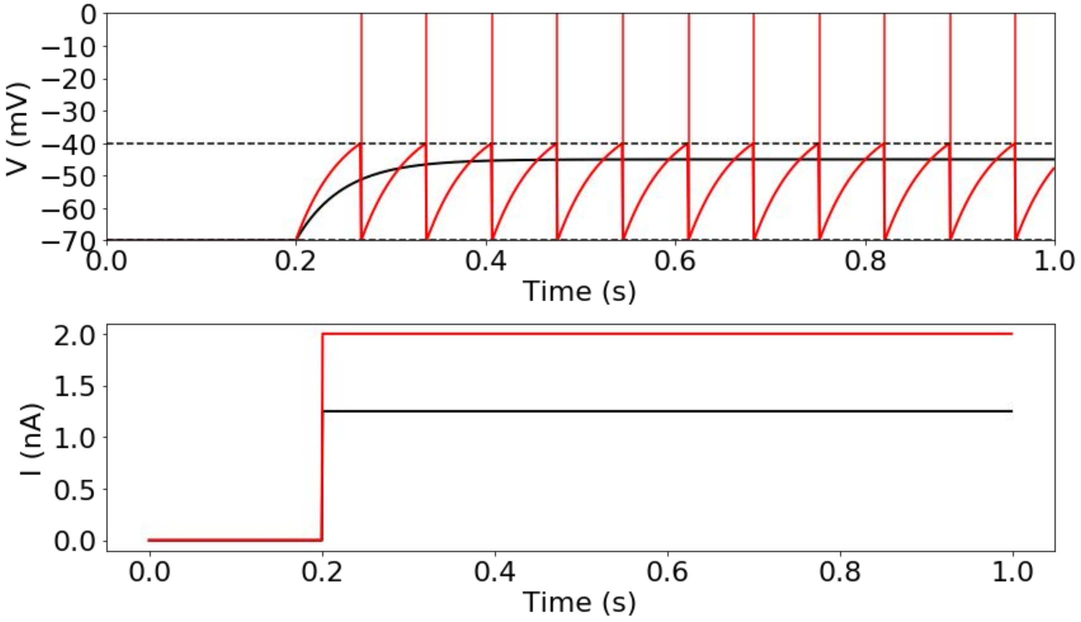
$$\tau \frac{dV}{dt} = -(V(t) - V_{leak}) + RI(t)$$

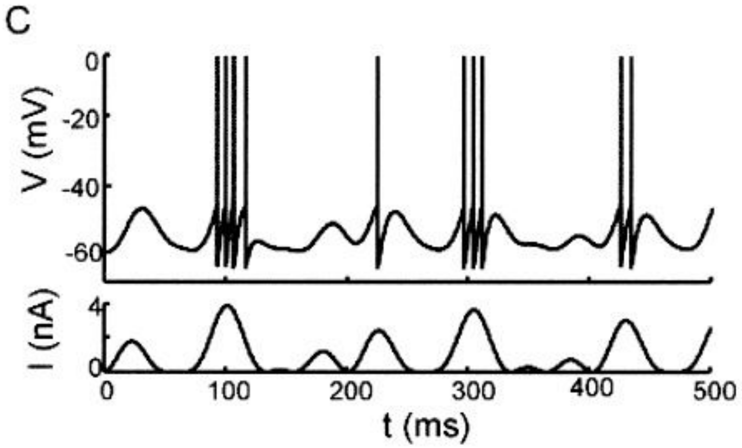
discretize →

$$\tau \frac{V_t - V_{t-1}}{\Delta t} = -(V_{t-1} - V_{leak}) + RI_t$$

$$V_t = V_{t-1} + \frac{\Delta t}{\tau}[-(V_{t-1} - V_{leak}) + RI_t]$$

If $V > V_{th}$ then $V \rightarrow V_{reset}$





Abbott 1999

Spiking neuron models: modeling synapses (starting point for spiking networks)

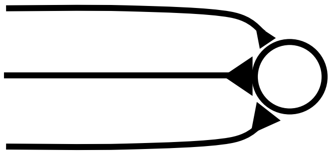
Presynaptic spikes as sum of delta functions

$$y(t) = \delta(t - t^0_{spk}) + \delta(t - t^1_{spk}) + \ldots \delta(t - t^n_{spk})$$

Current-based synapses

single presynaptic

$$\tau \frac{dV}{dt} = -(V(t) - V_{leak}) + RI(t) + \underline{wy(t)}$$



multiple presynaptic

$$\tau \frac{dV_i}{dt} = -(V_i(t) - V_{leak}) + RI_i(t) + \underline{\textstyle\sum_j w_{ij} y_j(t)}$$

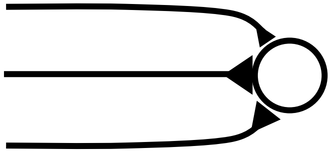
Conductance-based synapses

single presynaptic

$$\tau \frac{dV}{dt} = -(V(t) - V_{leak}) + RI(t) + \underline{RI_{syn}(t)}$$

$$I_{syn}(t) = g_{syn}(t)(E_{syn} - V(t))$$

$$g_{syn}(t) = w \sum_{t^k_{spk}} \alpha(t - t^k_{spk})$$



multiple presynaptic? (problem 6)

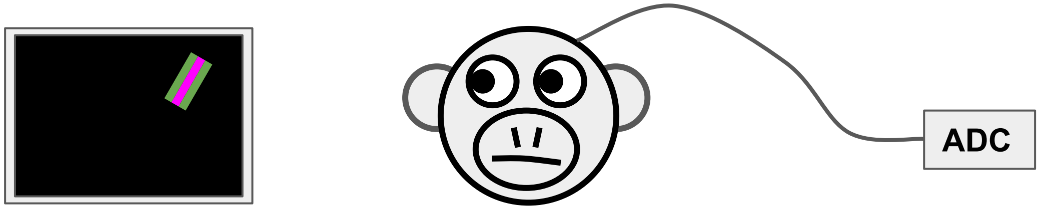
Problem set part 1

https://github.com/rkp8000/imbizo_2019_spikes_tutorial

problems_1.ipynb

(Scientific Python tutorial)
(https://github.com/rkp8000/imbizo_2019_python_tutorial)

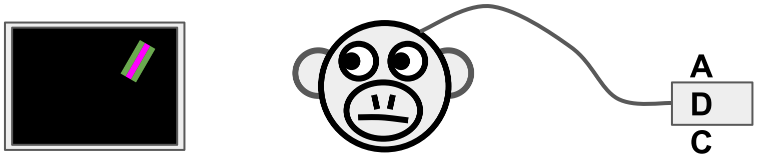
General neural response models

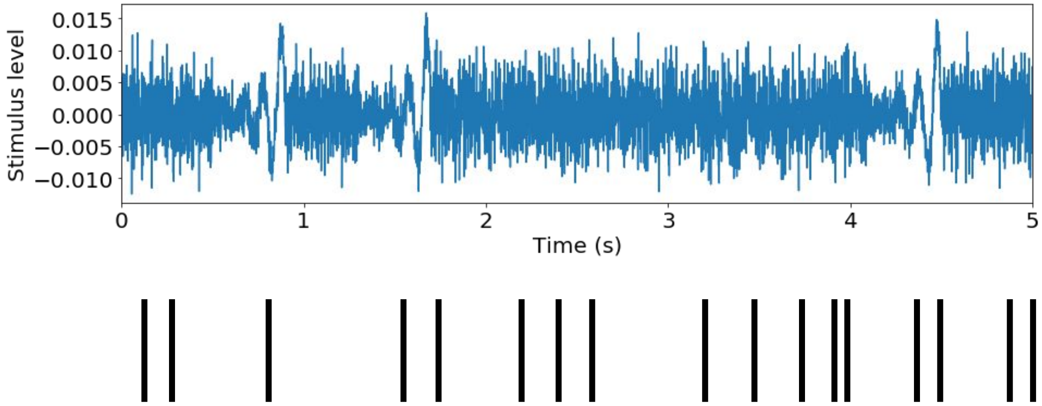


What if we don’t want to model current directly?

General neural response models

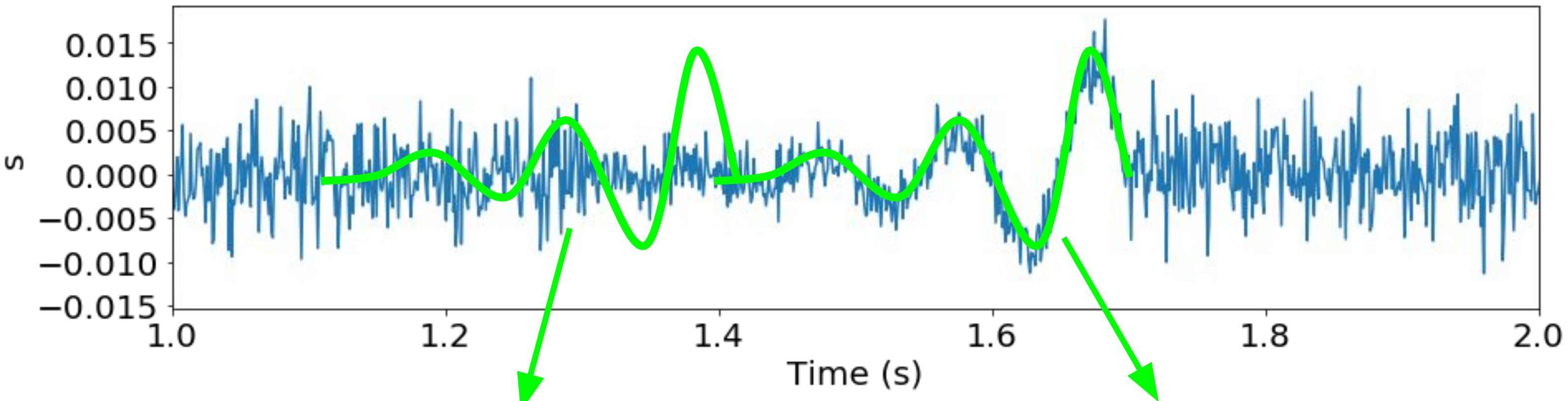
Approach:
Assume neuron cares about specific stimulus features.





Interlude: Linear filtering

Given a time-series (or image, movie, etc), how do we look for specific "features"?



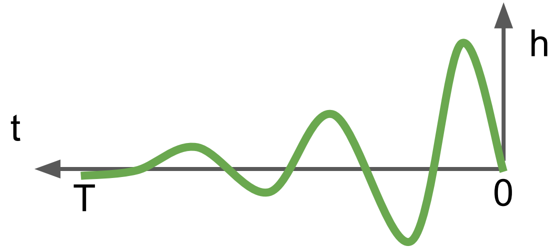
$\int_0^T h(\tau)s(t-\tau)d\tau$ ~ 0

$\int_0^T h(\tau)s(t-\tau)d\tau$ >> 0

Answer:

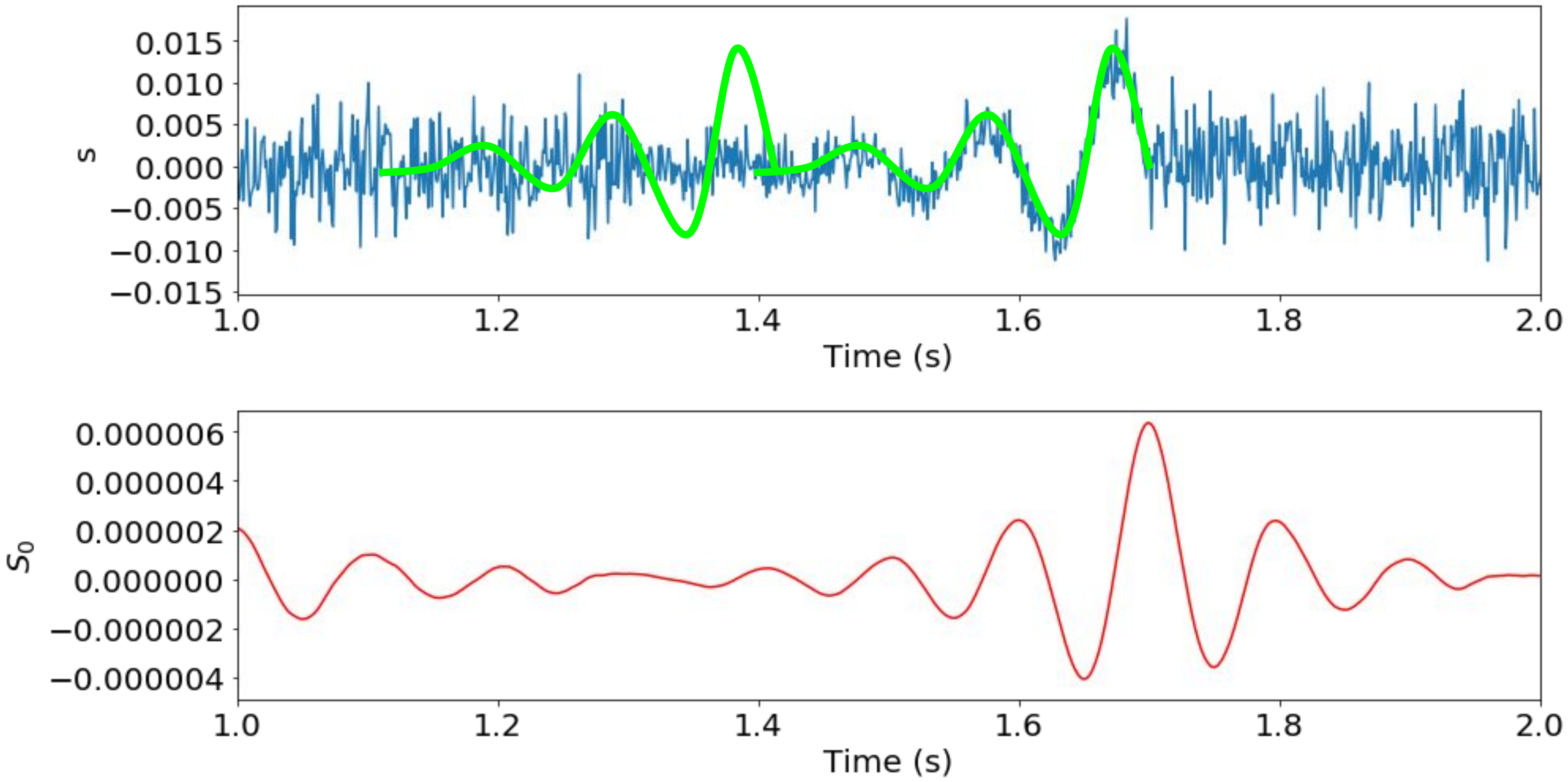
1. Create "filter" with same shape as target feature.

2. Slide filter along time-series and take inner product with windowed time-series.

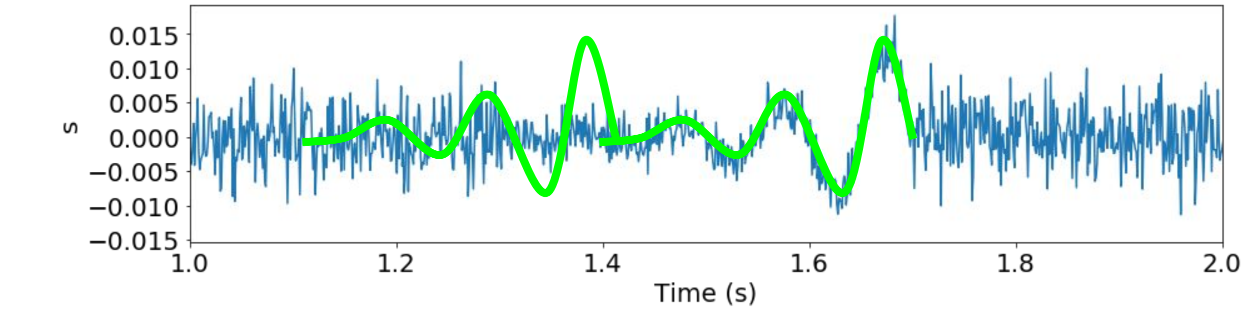


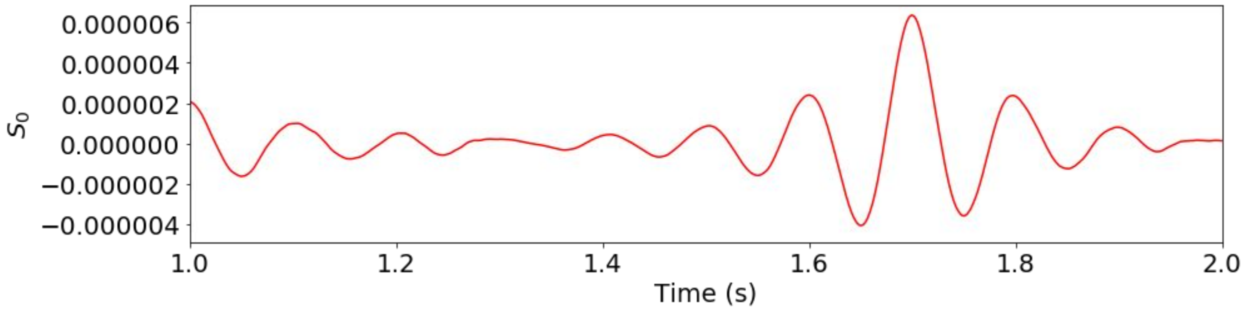
Interlude: Linear filtering

Given a time-series (or image, movie, etc), how do we look for specific “features”?



Interlude: Linear filtering





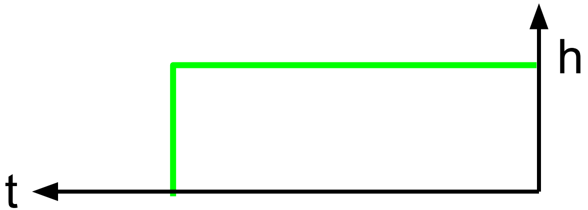
$$s_0(t) = \int_0^T h(\tau)s(t-\tau)d\tau$$

Discretization: $s_0(t) = \mathbf{h}^T \mathbf{s}(t) \equiv \mathbf{h} \cdot \mathbf{s}(t)$

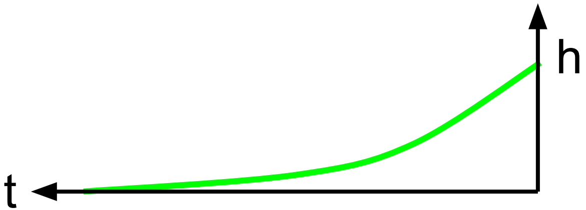
Interlude: Linear filtering

Common linear filter computations:

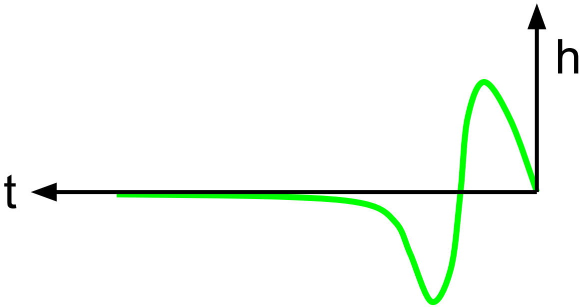
Moving average



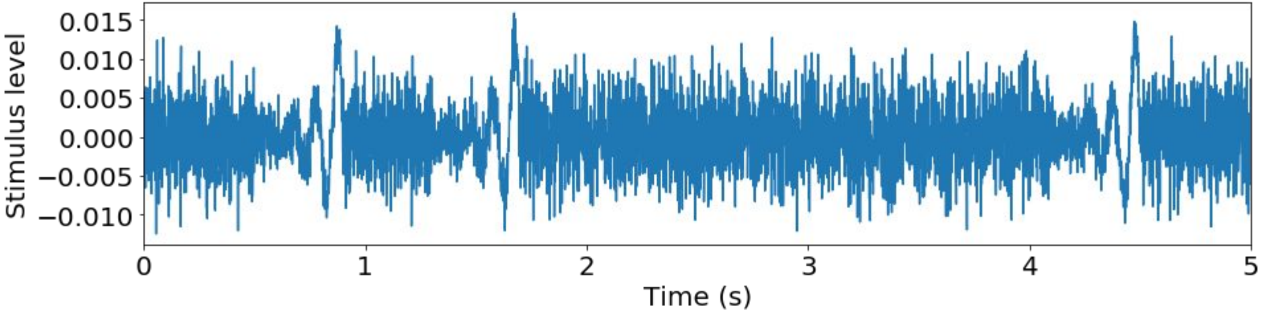
Leaky moving average

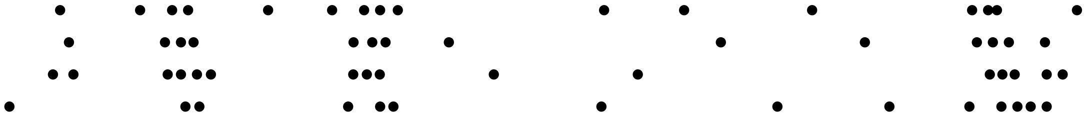


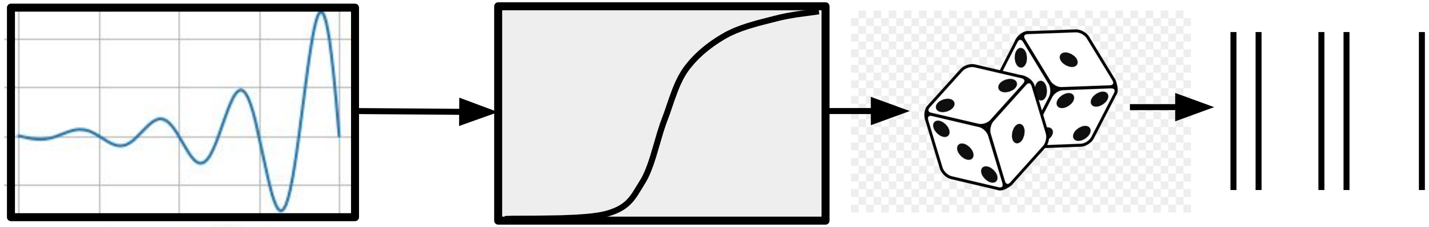
Differentiator



Spiking neuron models: the linear-nonlinear-Poisson (LNP) neuron







$$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$$

$$r(t) = g(s_0(t))$$

$$p_{spk}(t) = r(t)\Delta t$$

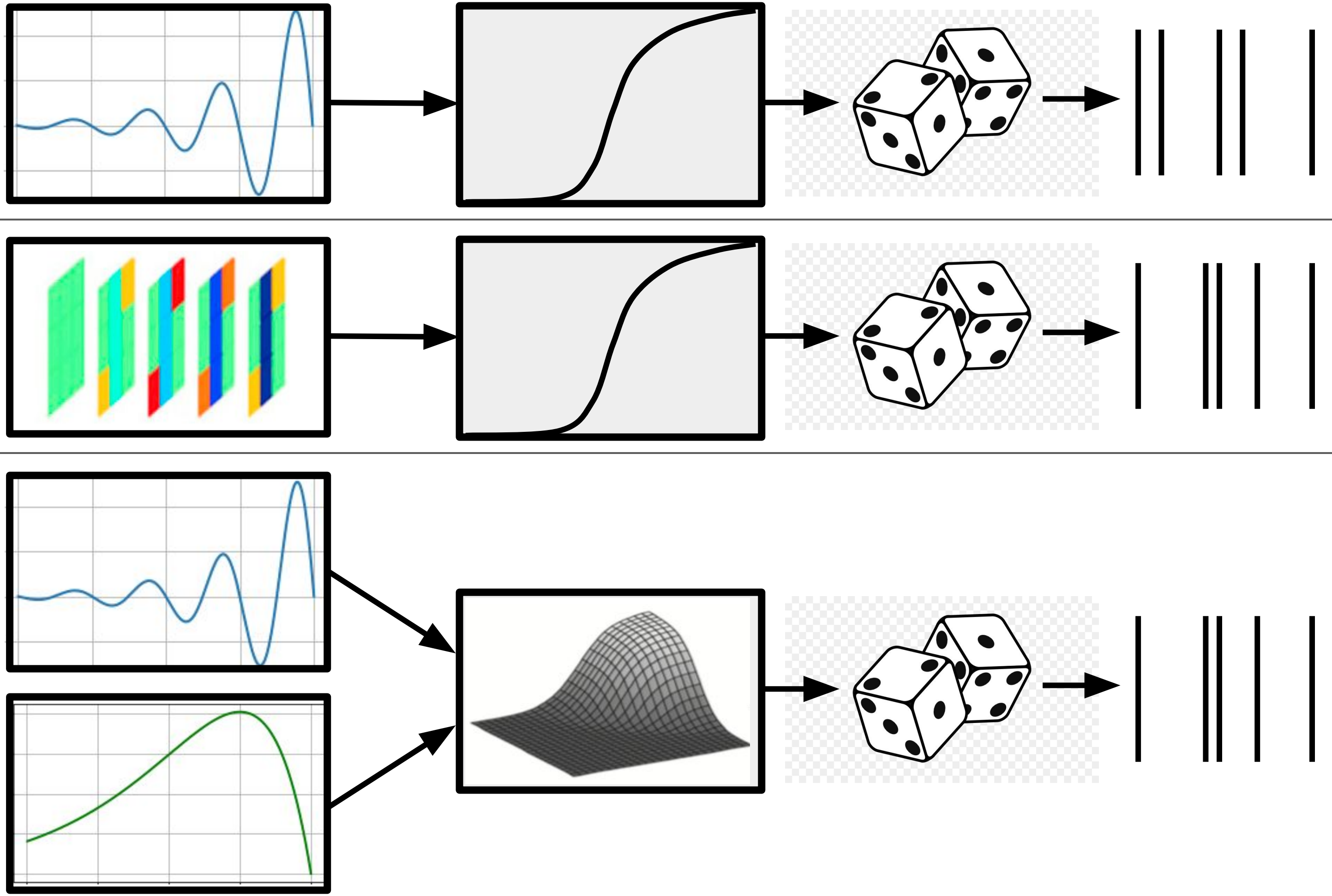
$$y(t) \sim \mathrm{Bernoulli}(p_{spk}(t))$$

Spiking neuron models: the linear-nonlinear-Poisson (LNP) neuron

Scalar stim, single filter

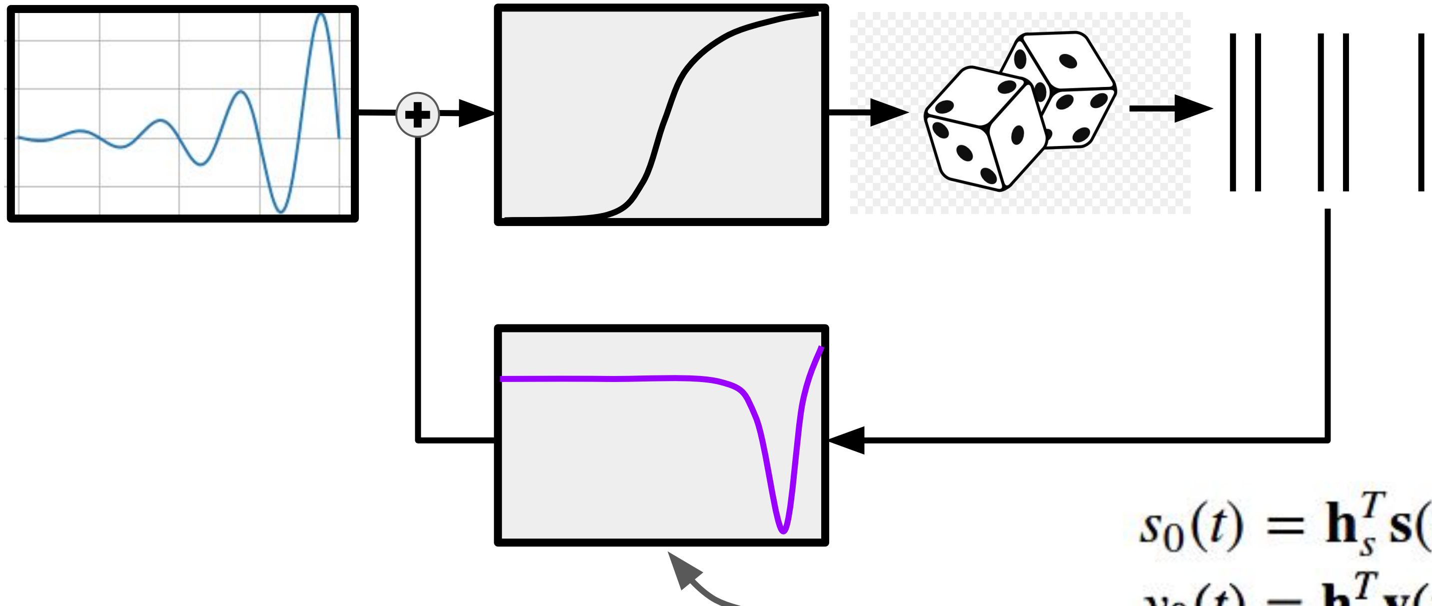
Vector stim, single filter

Scalar or vector stim, multiple filters



Spiking neuron models: the generalized linear model

Paninski 2004
Pillow 2008



How can we account for spike history?

Introduce "spike-history" filter $\mathbf{h}_y(t)$.

$$s_0(t) = \mathbf{h}_s^T \mathbf{s}(t)$$

$$y_0(t) = \mathbf{h}_y^T \mathbf{y}(t)$$

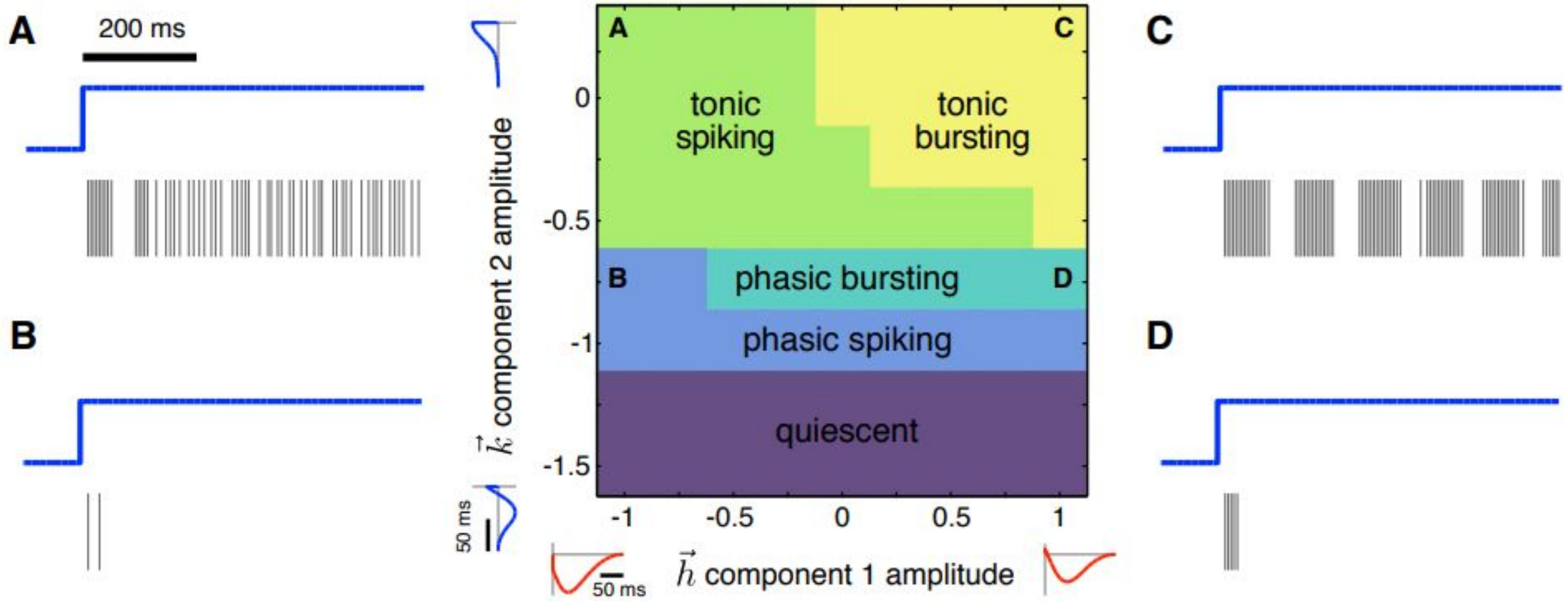
$$r(t) = g\left(\mathbf{h}_s^T \mathbf{s}(t) + \mathbf{h}_y^T \mathbf{y}(t) + b\right)$$

$$p_{spk}(t) = r(t)\Delta t$$

$$y(t) \sim \text{Bernoulli}(p_{spk}(t))$$

Spiking neuron models: the generalized linear model

GLMs can reproduce a wide diversity of behaviors.

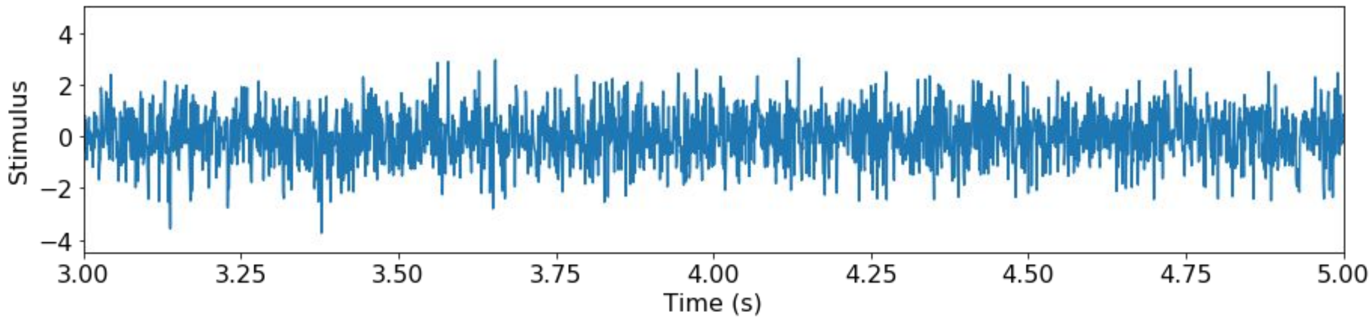


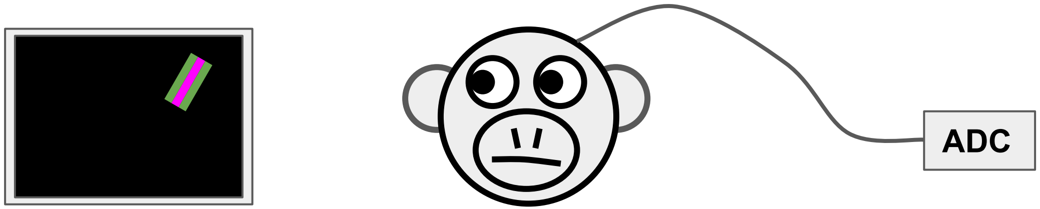
Weber and Pillow 2016

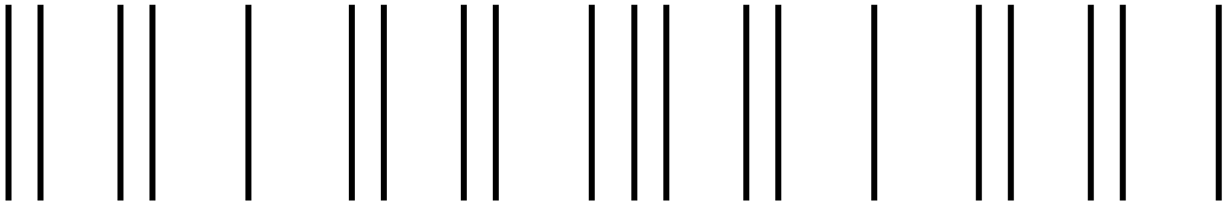
Outline

- Review of action potentials.
- Basic spike train analysis.
- Spiking neuron models.
- Short problem set time.
- Advanced spike train analysis.
- Other spike-based concepts.
- Full problem set time.

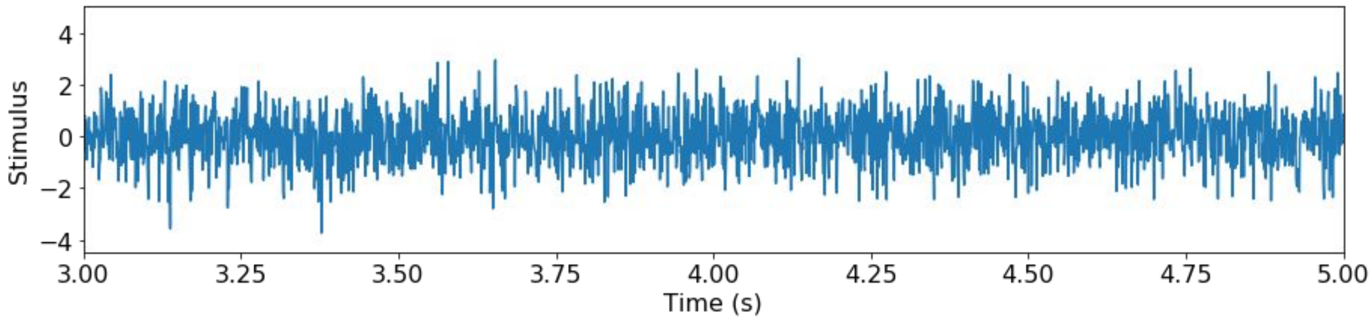
Spike train analysis: how do we identify filters?

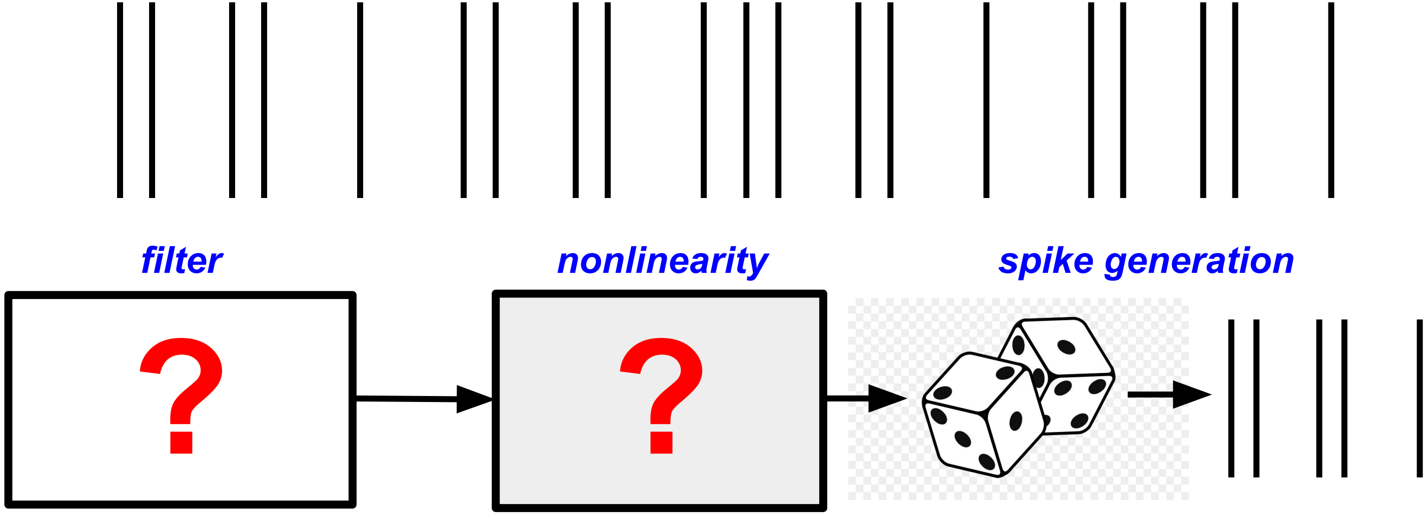




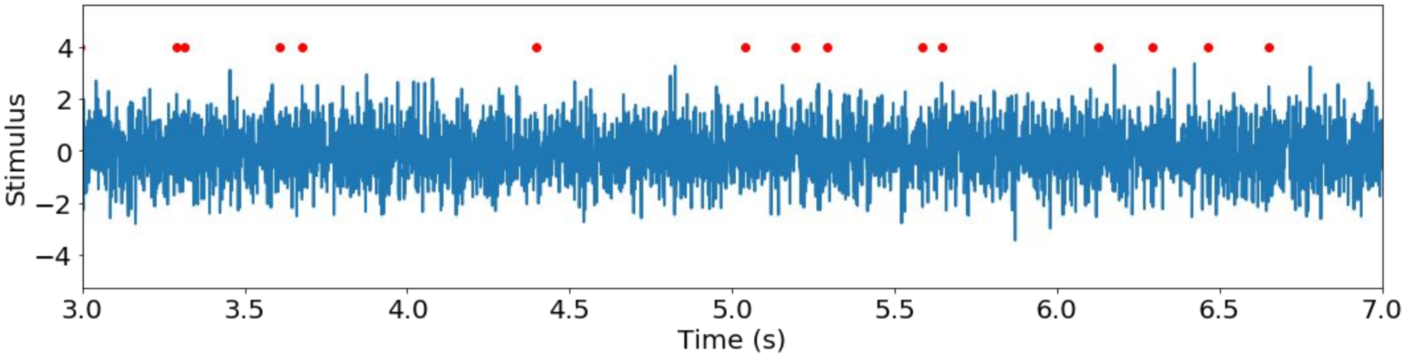


Spike train analysis: how do we identify filters?



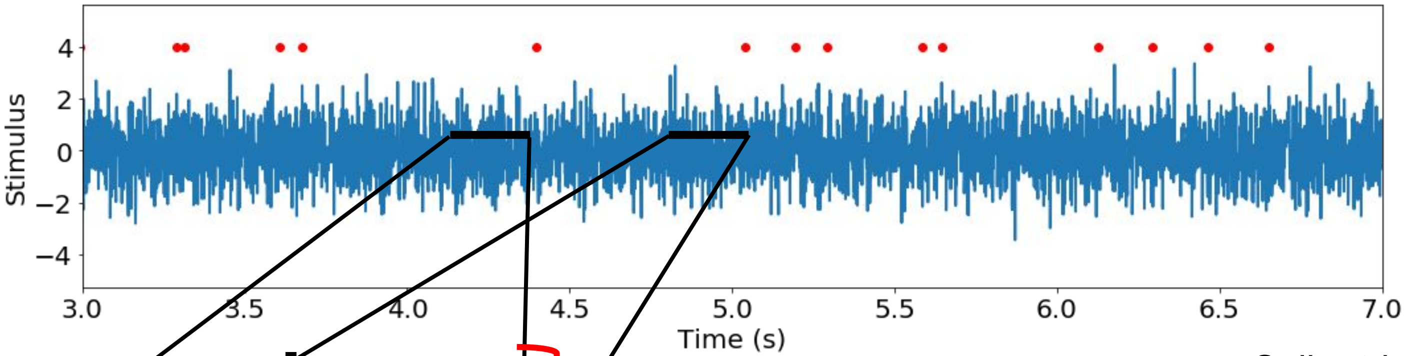


Spike train analysis: the spike-triggered average



Approach:
Identify average stimulus pattern preceding spike.

Spike train analysis: the spike-triggered average



⋮

(.129, -.053, ..., -2.73, 1.33)

(-1.93, 1.22, ..., -1.88, 0.76)

⋮

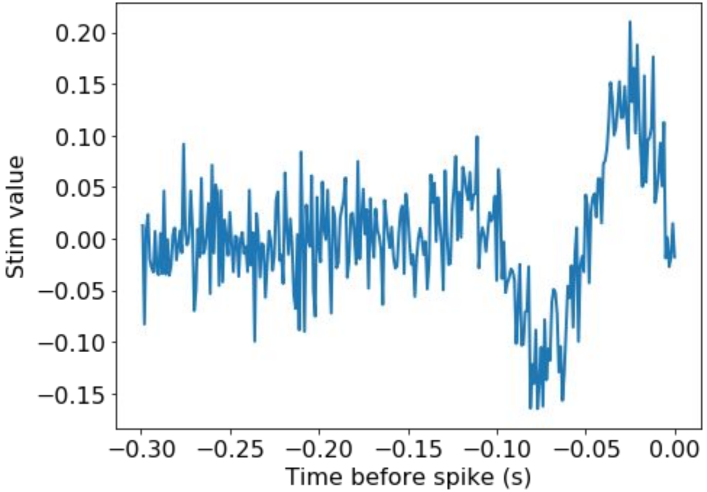
Spike-triggered ensemble

(-0.34, 0.63, ..., -1.91, 0.97)

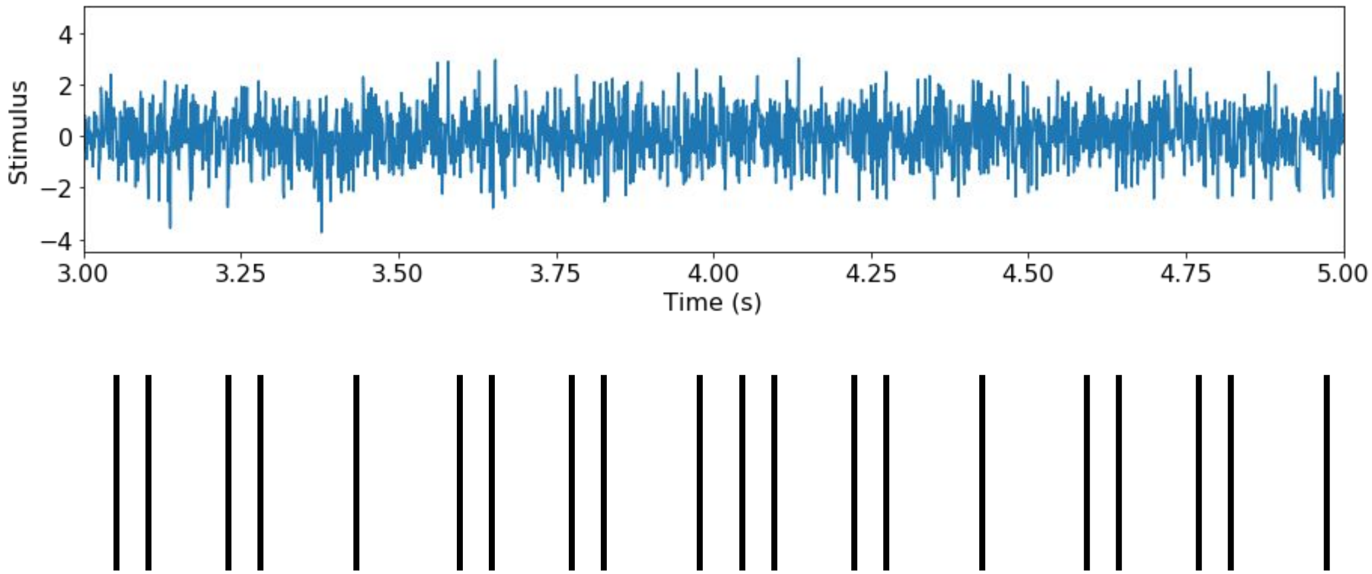
$$s_{sta}(\tau) = \frac{1}{N_{spk}} \sum_{t_{spk}} s(t_{spk} - \tau)$$

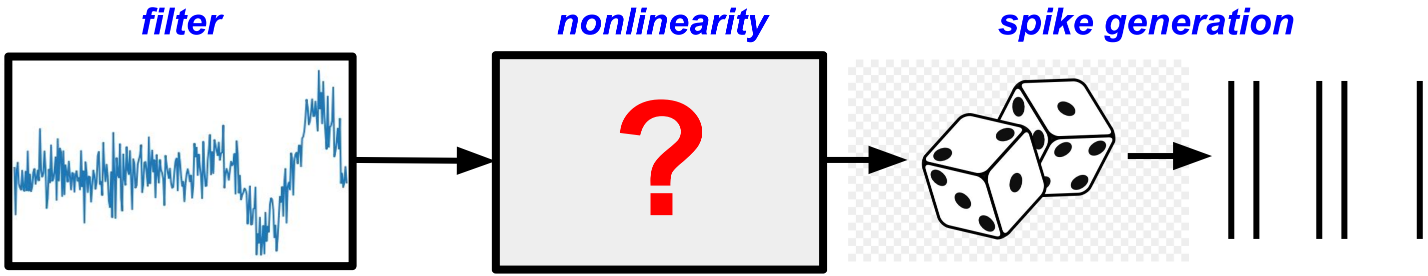
Spike-triggered average

Spike-triggered average (STA)



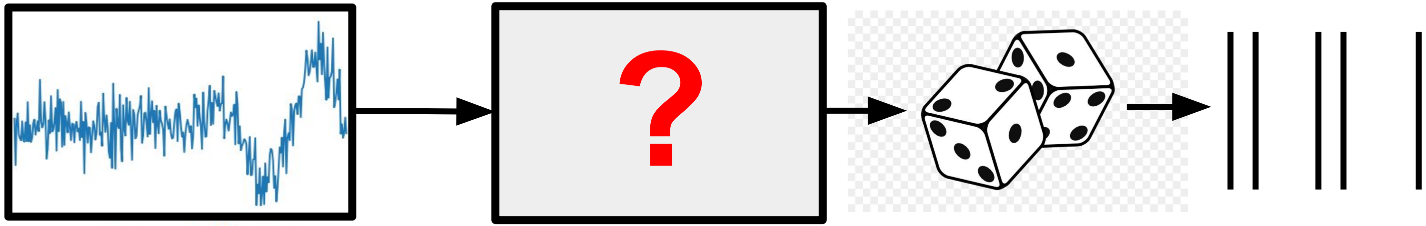
Spike train analysis: the spike-triggered average





Spike train analysis: the spike-triggered average

filter ***nonlinearity*** ***spike generation***



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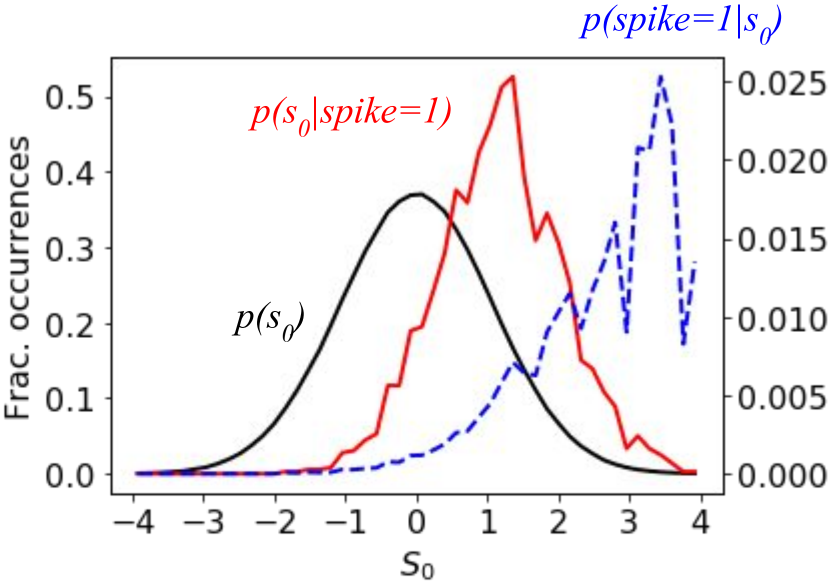
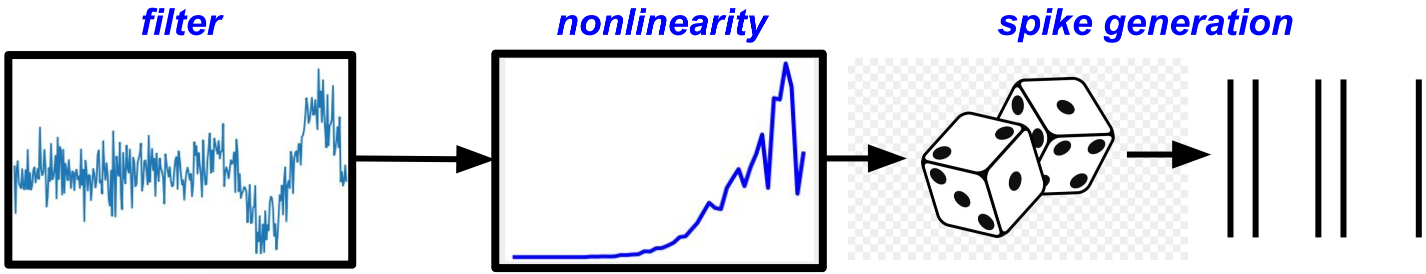
$$y(t) \sim \text{Bernoulli}(p_{spk}(t))$$

$$p(spike = 1|s_0) = \frac{p(s_0|spike = 1)p(spike = 1)}{p(s_0)}$$



Spike train analysis: the spike-triggered average



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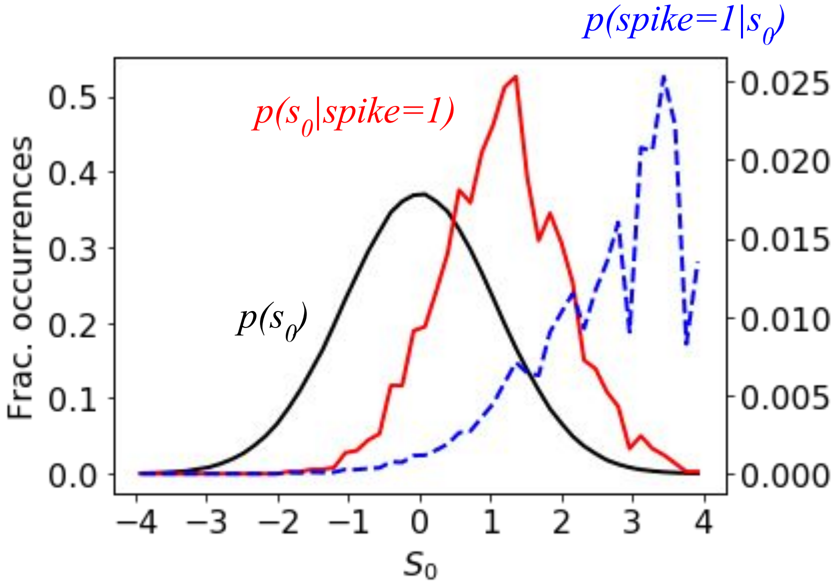
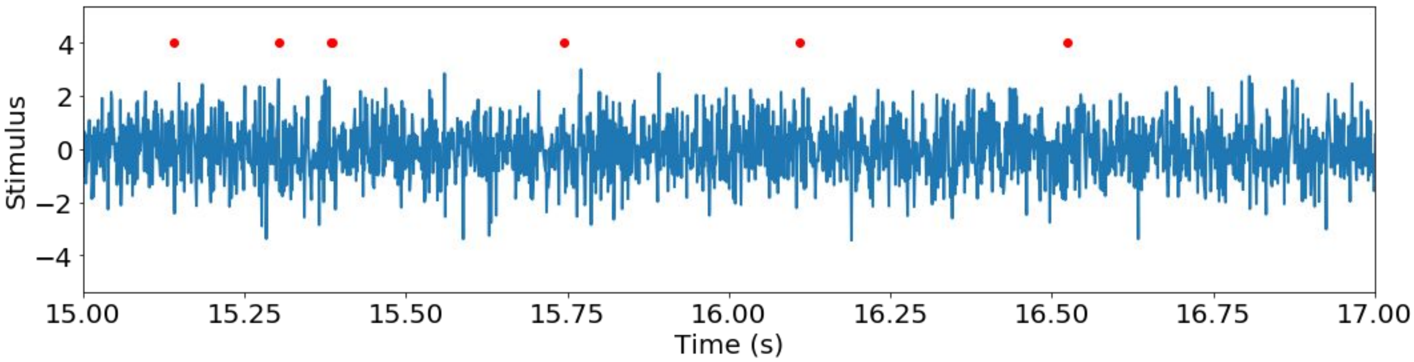
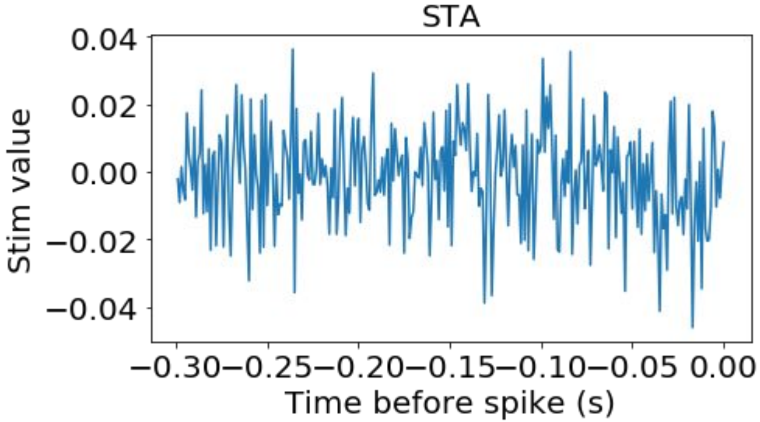


Spike train analysis: the spike-triggered average

Will spike-triggered average always be informative?

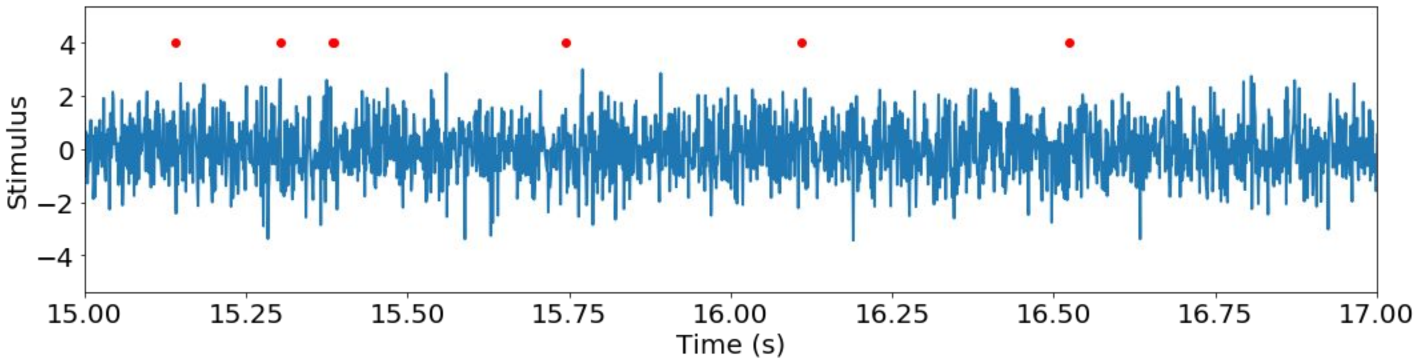
Spike train analysis: spike-triggered covariance analysis





STA not very interesting. What next?

Spike train analysis: spike-triggered covariance analysis



⋮

(.129, -.053, ..., -2.73, 1.33)

(-1.93, 1.22, ..., -1.88, 0.76)

⋮

Spike-triggered ensemble

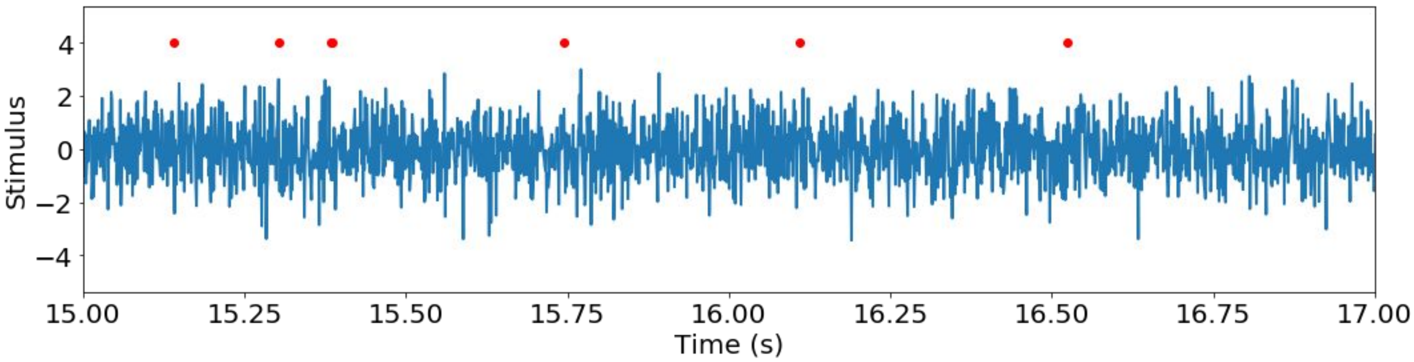
STA asks how ***first-order*** structure of spike-triggered ensemble differs from prior.

Now ask: how does ***second-order*** structure of spike-triggered ensemble differ from prior?

Recall:

first-order structure = mean
second-order structure = covariance

Spike train analysis: spike-triggered covariance analysis

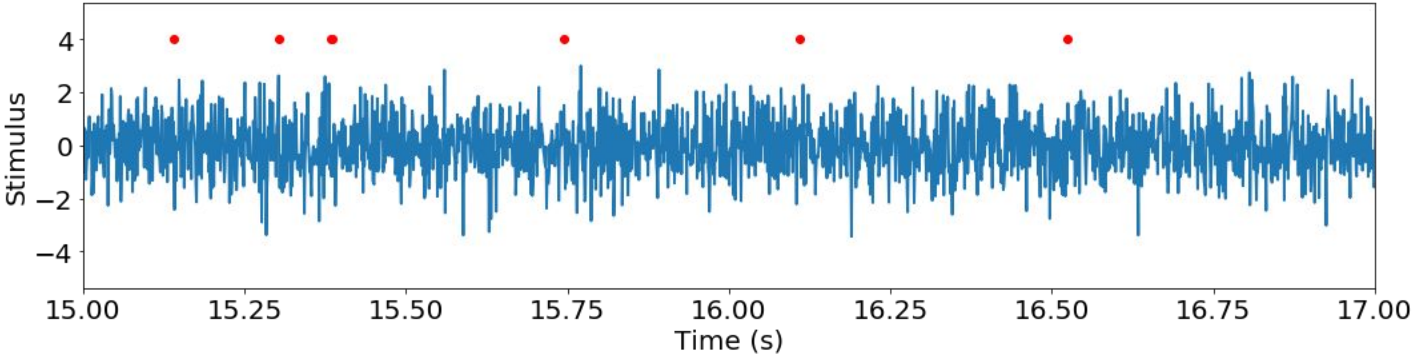


$$\left.\begin{array}{c} \vdots \\ (.129, -.053, \ldots, -2.73, 1.33) \\ (-1.93, 1.22, \ldots, -1.88, 0.76) \\ \vdots \end{array}\right\} \text{Spike-triggered ensemble}$$

Key idea:

1. Calculate ***covariance*** K^{spk} of spike-triggered ensemble.
2. Calculate ***covariance*** K^{pr} of prior ensemble.
3. Ask: where do K^{spk} and K^{pr} differ most?

Spike train analysis: spike-triggered covariance analysis



⋮

(.129, -.053, ..., -2.73, 1.33)

(-1.93, 1.22, ..., -1.88, 0.76)

⋮

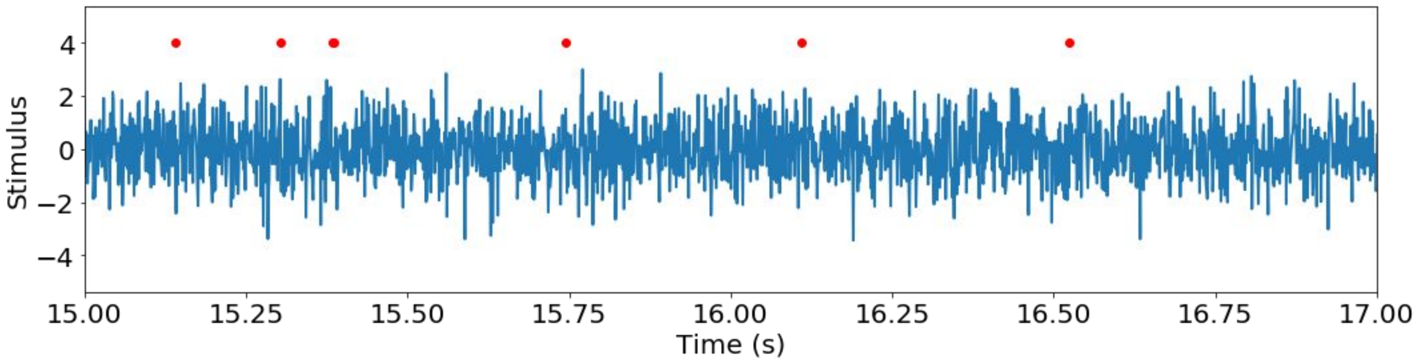
Spike-triggered ensemble

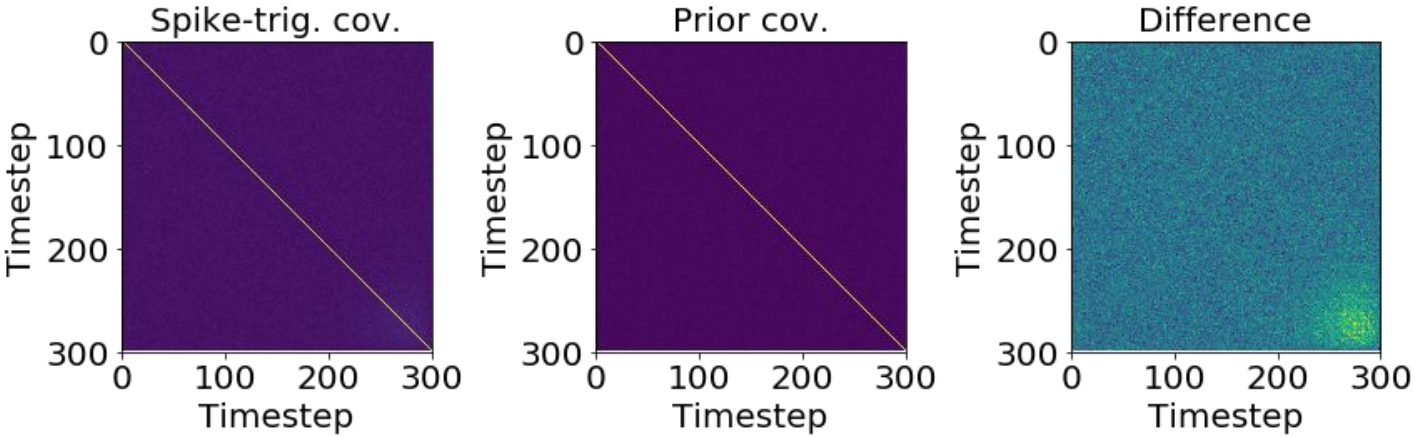
$$K^{spk}_{\tau,\tau'} = \mathrm{COV}(s(\tau), s(\tau'))$$
$$= \mathrm{E}_{t_{spk}}[(s(t_{spk} - \tau) - \mathrm{E}[s(t_{spk} - \tau)])(s(t_{spk} - \tau') - \mathrm{E}[s(t_{spk} - \tau)])]$$

$$K^{pr}_{\tau,\tau'} = \mathrm{COV}(s(\tau), s(\tau'))$$
$$= \mathrm{E}_t[(s(t - \tau) - \mathrm{E}[s(t - \tau)])(s(t - \tau') - \mathrm{E}[s(t - \tau)])]$$

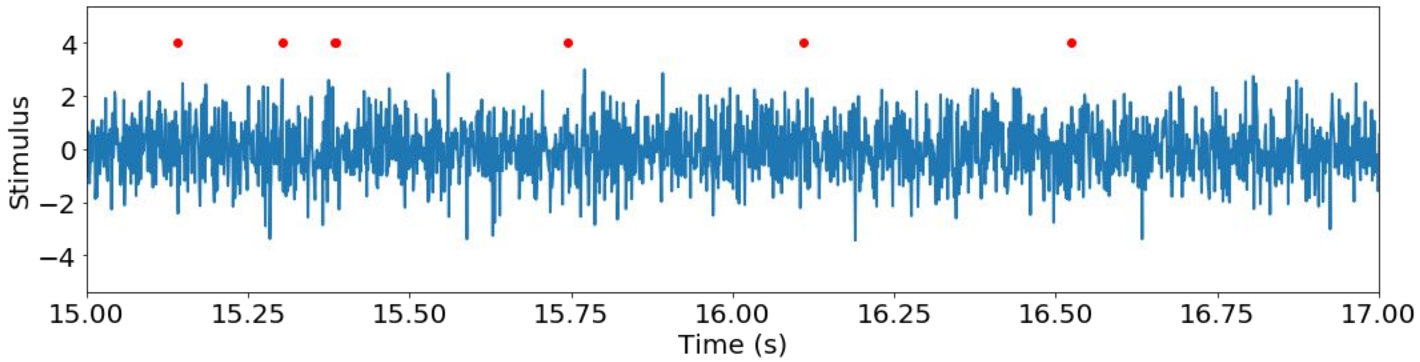
$$K^{diff} = K^{spk} - K^{pr}$$

Spike train analysis: spike-triggered covariance analysis





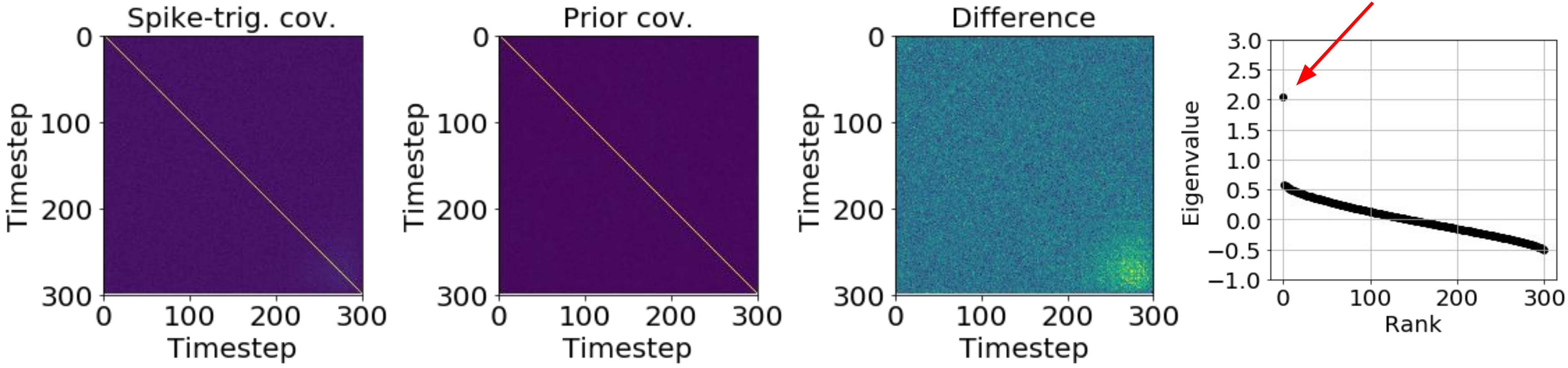
Spike train analysis: spike-triggered covariance analysis



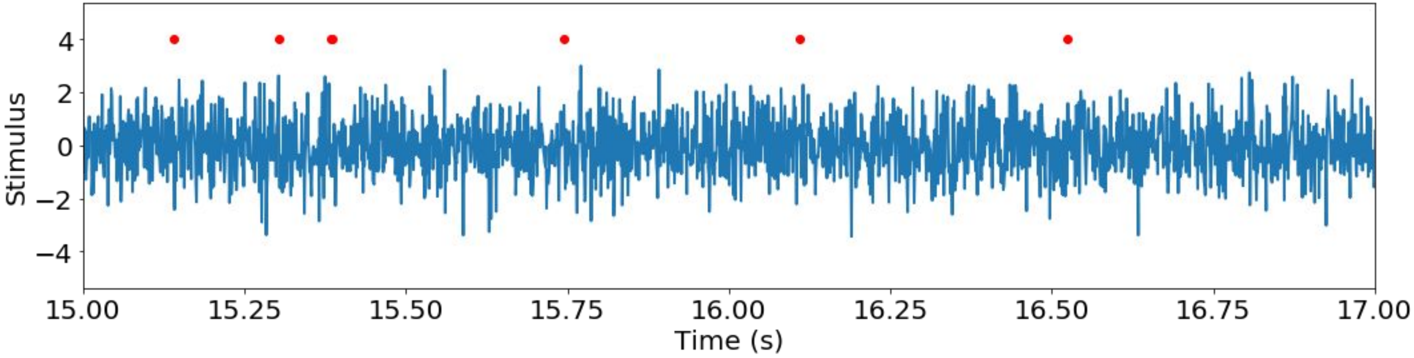
How should we quantify structure of K^{diff}?

Eigenvectors!

1 “mode” of interest



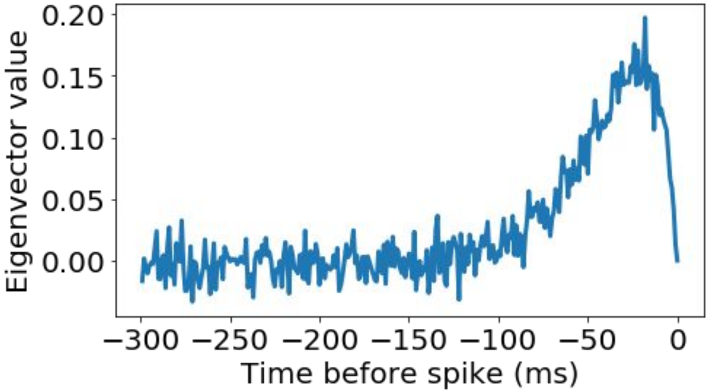
Spike train analysis: spike-triggered covariance analysis



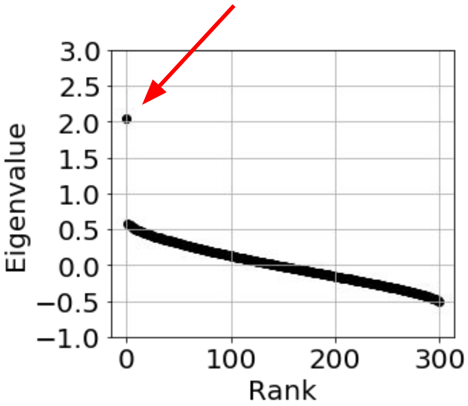
How should we quantify structure of K^{diff}?

Eigenvectors!

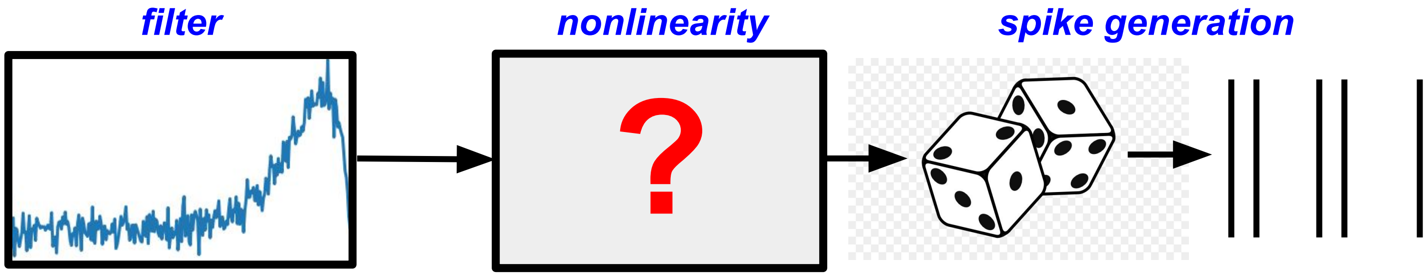
Top mode of K^{diff}

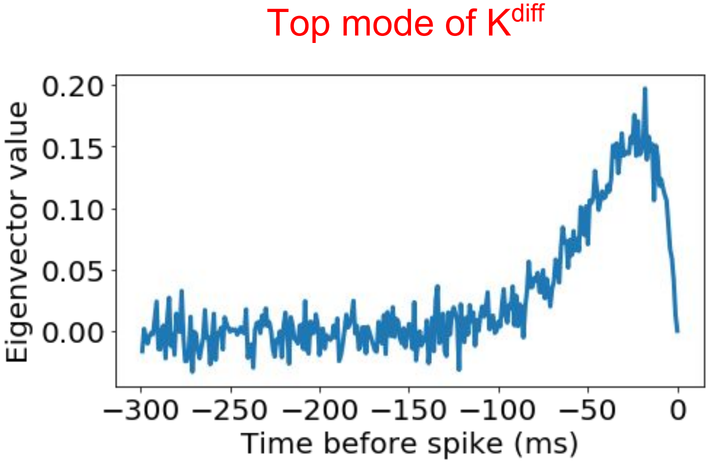


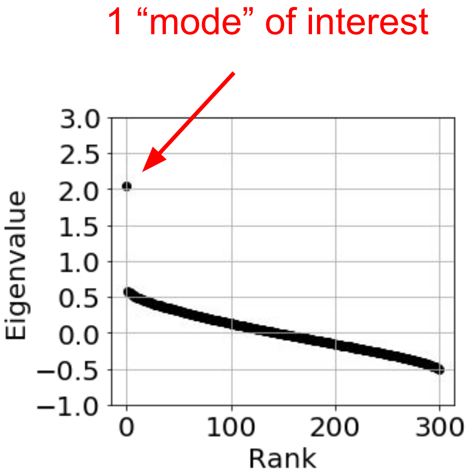
1 “mode” of interest



Spike train analysis: spike-triggered covariance analysis

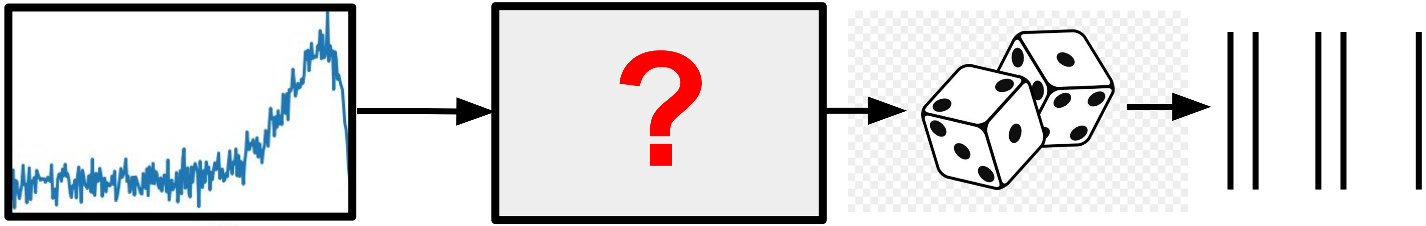






Spike train analysis: spike-triggered covariance analysis

filter *nonlinearity* *spike generation*



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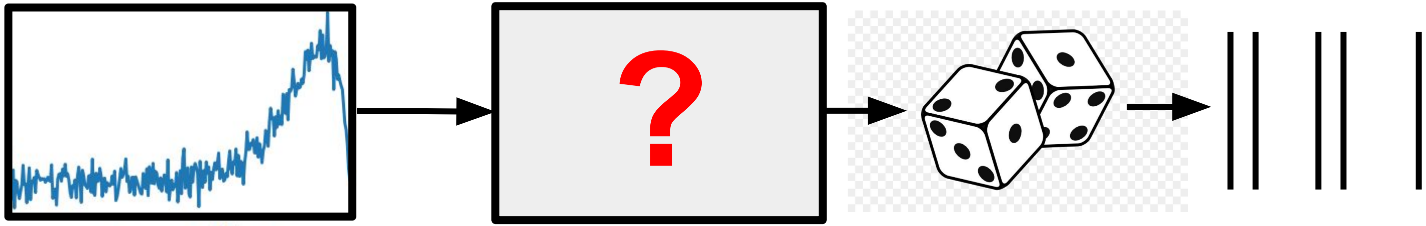
Spike train analysis: spike-triggered covariance analysis

filter | *nonlinearity* | *spike generation*



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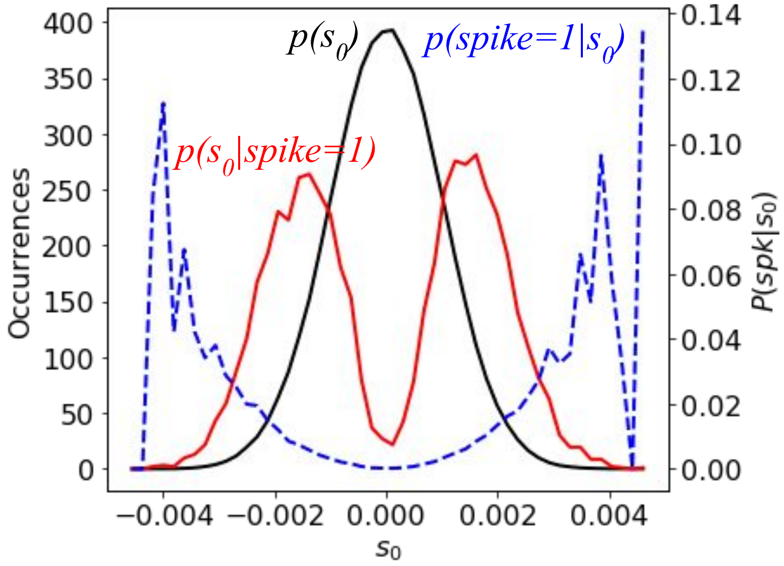
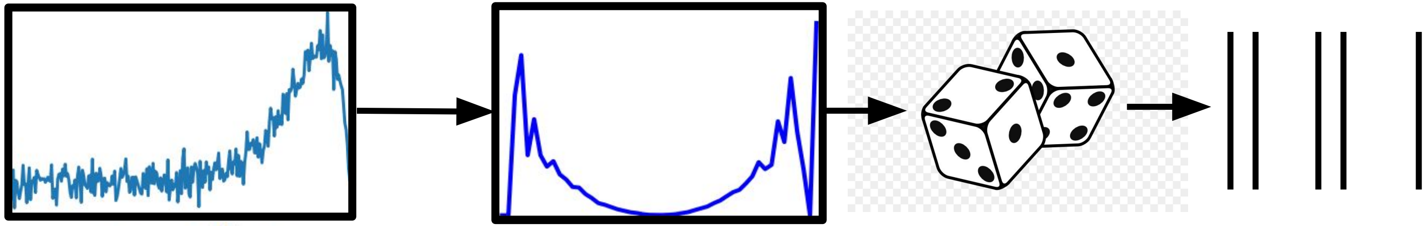


Spike train analysis: spike-triggered covariance analysis

filter *nonlinearity* *spike generation*



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$p_{spk}(t) = r(t)\Delta t$

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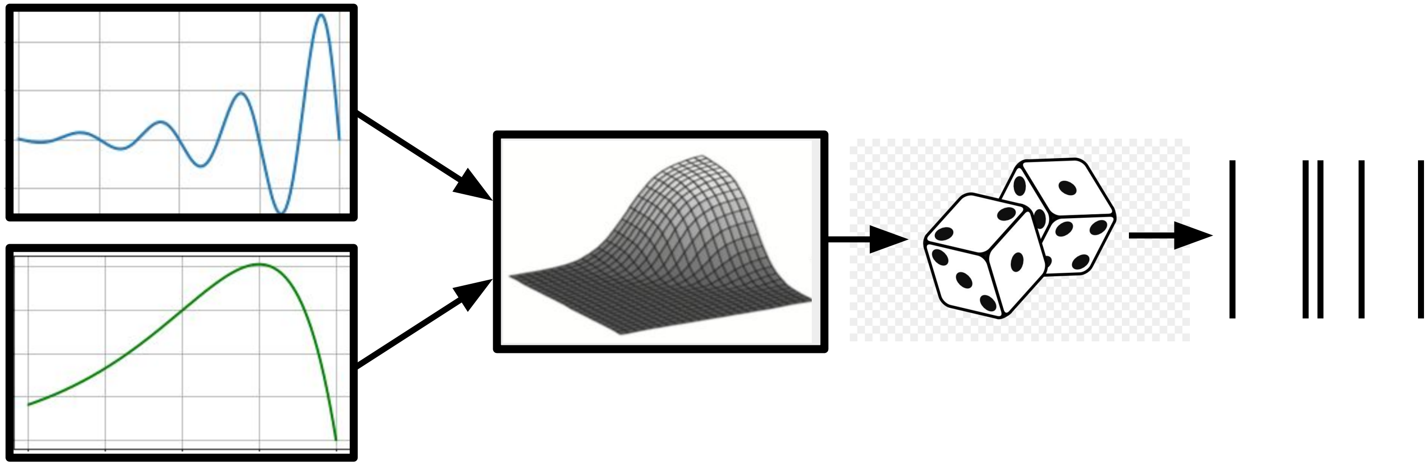
Spike train analysis: spike-triggered covariance analysis

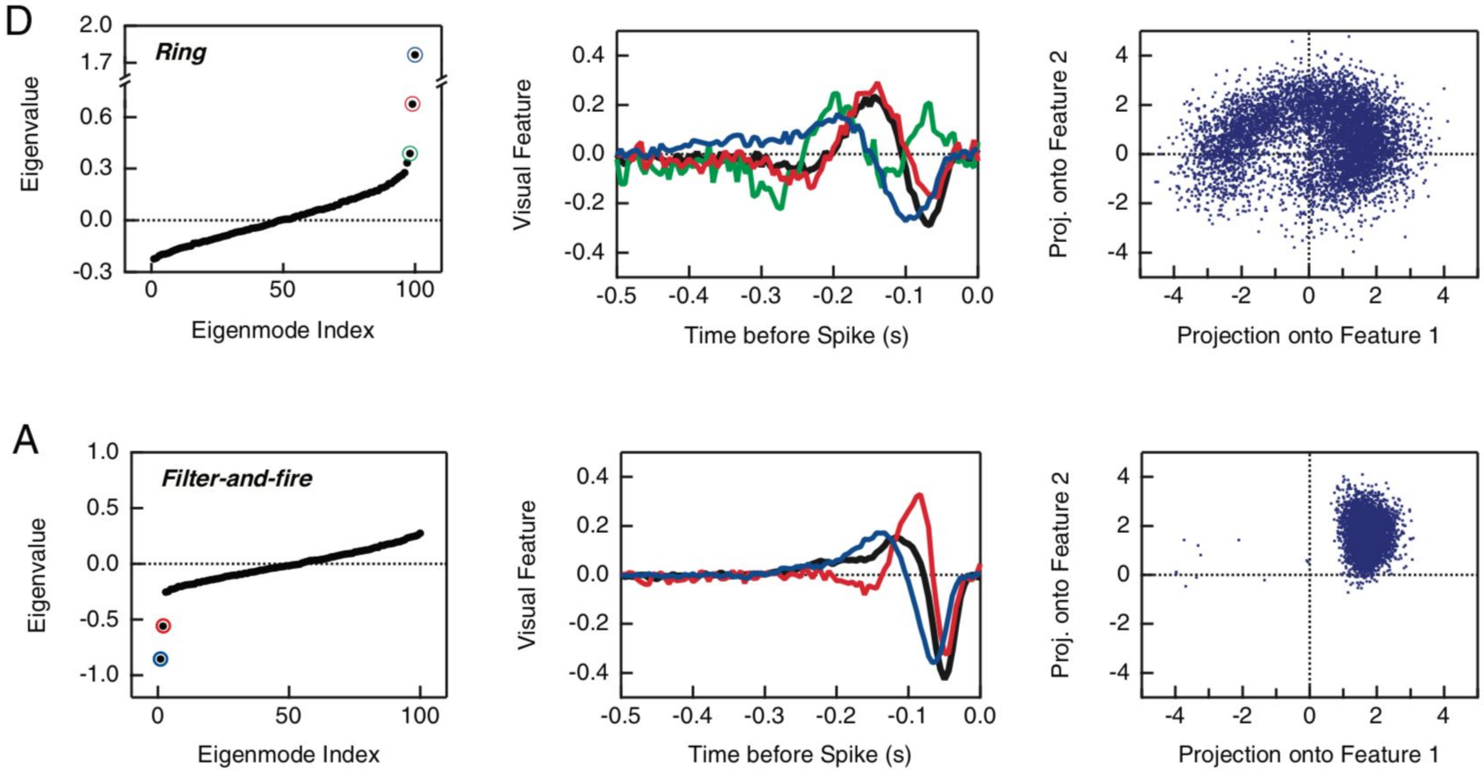
Can also have multiple top eigenmodes yielding multiple filters.

Scalar or vector stim,
multiple filters



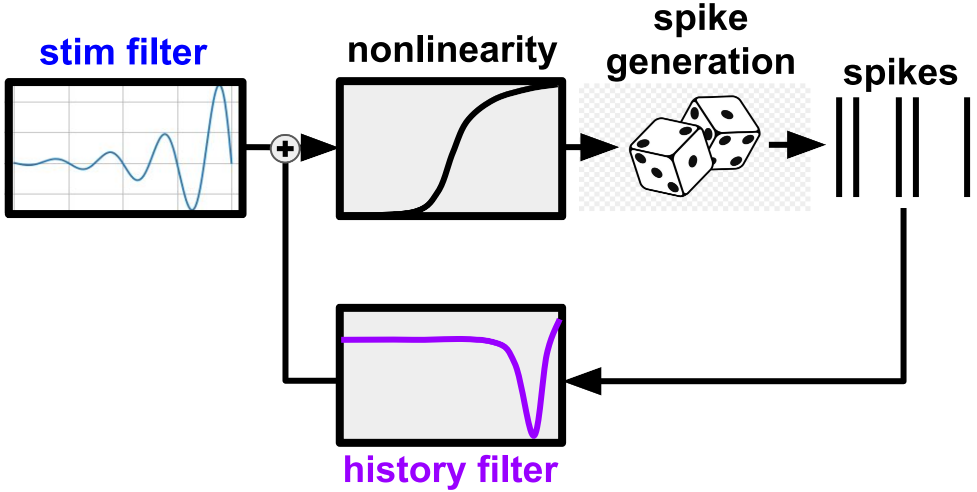
Spike train analysis: spike-triggered covariance analysis

Salamander retinal ganglion cells



Fairhall et al. 2006

Spike train analysis: generalized linear models



spike train generation

$$s_0(t) = \mathbf{h}_0^T \mathbf{s}(t)$$

$$y_0(t) = \mathbf{h}_y^T \mathbf{y}(t)$$

$$r(t) = g\left(\mathbf{h}_0^T \mathbf{s}(t) + \mathbf{h}_y^T \mathbf{y}(t) + b\right)$$

$$p_{spk}(t) = r(t)\Delta t$$

$$y(t) \sim \text{Bernoulli}(p_{spk}(t))$$

maximum likelihood model fitting

$$\hat{\theta} \equiv \{\hat{\mathbf{h}}_s, \hat{\mathbf{h}}_y, \hat{b}\} = \arg\max_{\theta}\ p\left[y(t)|\theta, s(t)\right] = \arg\max_{\theta} \prod_t p\left[y(t)|r(t;\theta, s(t' < t), y(t' < t))\right]$$

$$p\left[y(t)|r(t;\theta, s(t' < t), y(t' < t)))\right] = r(t;\theta, s(t' < t), y(t' < t)))\Delta t$$

$$r(t;\theta, s(t' < t), y(t' < t))) = g(\mathbf{h}_s^T \mathbf{s}(t) + \mathbf{h}_y^T \mathbf{y}(t) + b)$$

Paninski 2004
Pillow 2008
Weber and Pillow 2016

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Spike train analysis: information in spikes

How much *information* do spikes contain about stim?
How much information do models capture?

For well sampled stim, can compute mutual info between stim and spike from spike rate alone.

$$I(r,s) = \frac{1}{T}\int_0^T dt \, \frac{r(t)}{\bar{r}} \log \frac{r(t)}{\bar{r}}$$

$$\frac{r(t)}{\bar{r}} = \frac{P(\text{spike at } t|\mathbf{s})}{P(\text{spike at } t)} = \boxed{\frac{P(\mathbf{s}|\text{spike at } t)}{P(\mathbf{s})} \rightarrow \frac{P(s_1, s_2, s_3, \ldots|\text{spike at } t)}{P(s_1, s_2, s_3, \ldots)}}$$

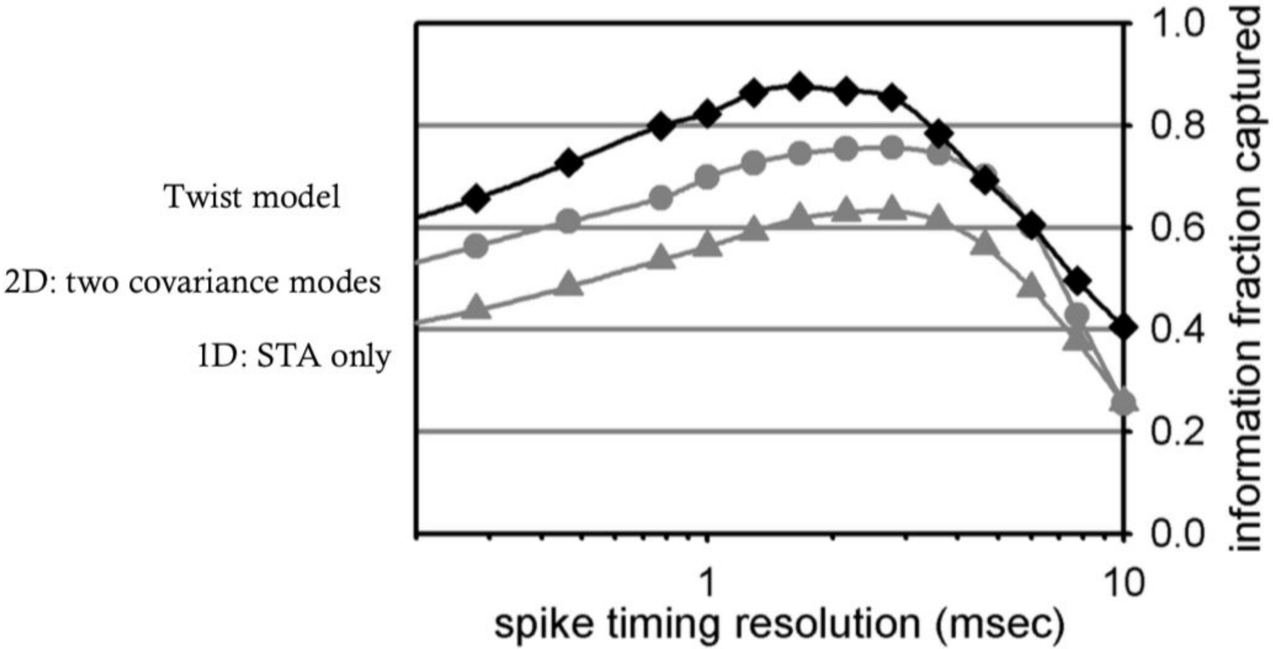
By definition   Bayes' rule   Dimensionality reduction

$$I^K_{\text{one spike}} = \int d^K s \, P(s_1, \ldots, s_K|\text{spike at } t) \log_2 \left[\frac{P(s_1, \ldots, s_K|\text{spike at } t)}{P(s_1, \ldots, s_K)}\right]$$

Brenner 2000
Aguera y Arcas, Fairhall, and Bialek 2003

Spike train analysis: information in spikes

Approximating H-H neuron with simpler models:



Aguera y Arcas, Fairhall, and Bialek 2003

Other spike-based concepts

- Comparing spike trains
- Decoding stimuli from spikes
- Nonlinear dendritic integration
- Networks of spiking neurons
- Spike sequences in networks
- Spike-timing-dependent plasticity
- Inferring network structure from spikes

Problem set part 2

https://github.com/rkp8000/imbizo_2019_spikes_tutorial

problems_2.ipynb

(Scientific Python tutorial)
(https://github.com/rkp8000/imbizo_2019_python_tutorial)

References

Free and friendly online textbooks:

- *Spiking Neuron Models* (Gerstner and Kistler 2002)
- *Theoretical Neuroscience* (Dayan and Abbott 2009)
- *Neuronal Dynamics* (Gerstner et al. 2014)

A few papers to get you started

- Bryant et al. “Spike initiation by transmembrane current: a white-noise analysis.” 1976
- Shadlen et al. “The Variable Discharge of Cortical Neurons: Implications for Connectivity, Computation, and Information Coding.” 1998
- Brunel. “Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons.” 2000
- Reinagel et al. “Temporal Coding of Visual Information in the Thalamus.” 2000
- Song et al. “Competitive Hebbian learning through spike-timing-dependent synaptic plasticity.” 2000
- Aguera y Arcas et al. “Computation in a Single Neuron: Hodgkin and Huxley Revisited.” 2003
- Slee et al. “Two-Dimensional Time Coding in the Auditory Brainstem.” 2005
- Fairhall et al. “Selectivity for Multiple Stimulus Features in Retinal Ganglion Cells.” 2005
- Victor. “Spike train metrics.” 2005
- Pillow et al. “Spatio-temporal correlations and visual signaling in a complete neuronal population.” 2008
- London et al. “Sensitivity to perturbations in vivo implies high noise and suggests rate coding in cortex”. 2010
- Weber et al. “Capturing the Dynamical Repertoire of Single Neurons with Generalized Linear Models”. 2016
- Nicola et al. “Supervised learning in spiking neural networks with FORCE training.” 2017