Swipe Right to Spike

Analysis and modeling of spiking neurons

2019-01-08

#isiCNI2019

Slides:

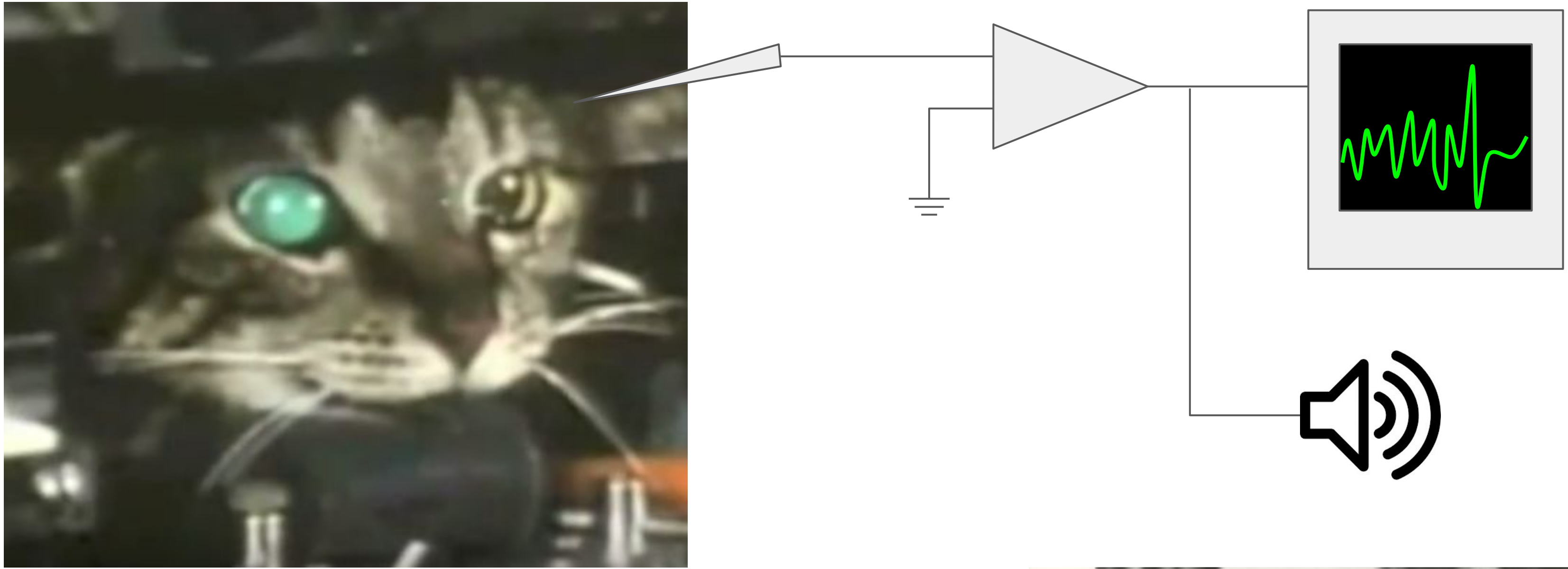
https://github.com/rkp8000/imbizo_2019_spikes_tutorial

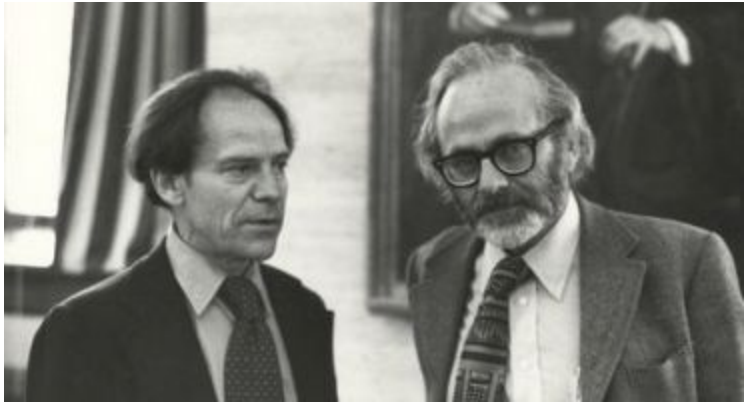
Outline

- Crash course in 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.

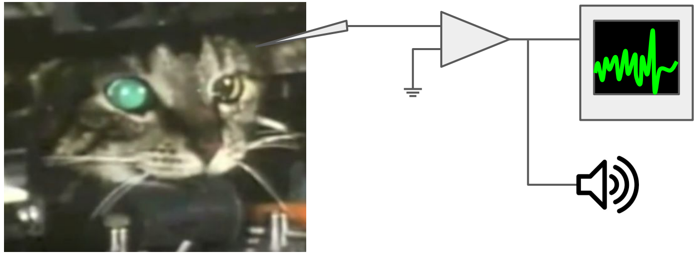
Outline

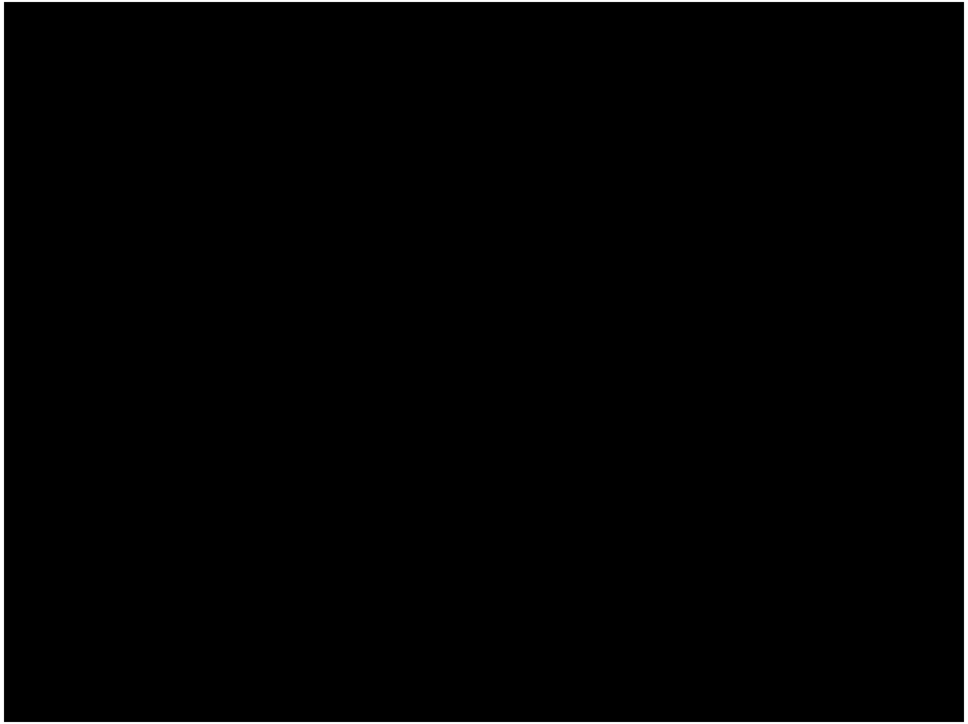
- Crash course in action potentials.
- Basic spike train analysis.
- Spiking neuron models.
- Short problem set time.
- Advanced spike train analysis.
- Other spike-based concepts.
- Full problem set time.





Hubel and Wiesel 1959



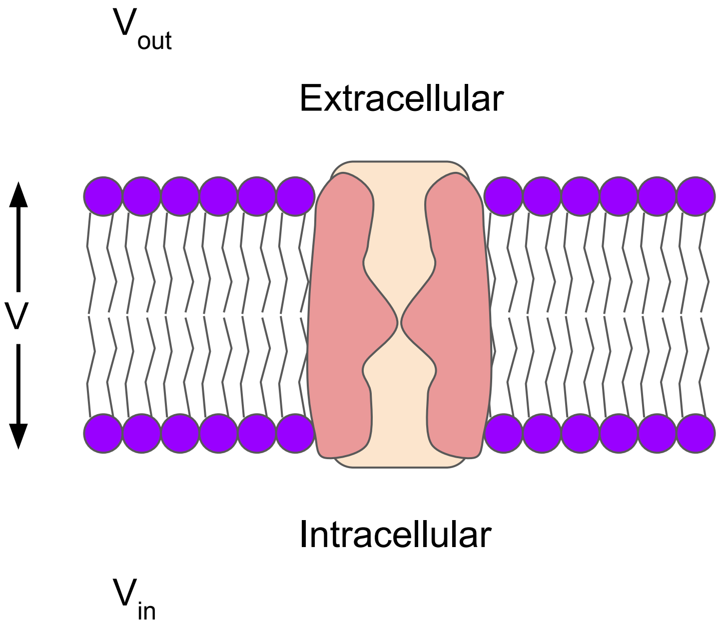


Hubel and Wiesel 1959

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

Spike generation and detection

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

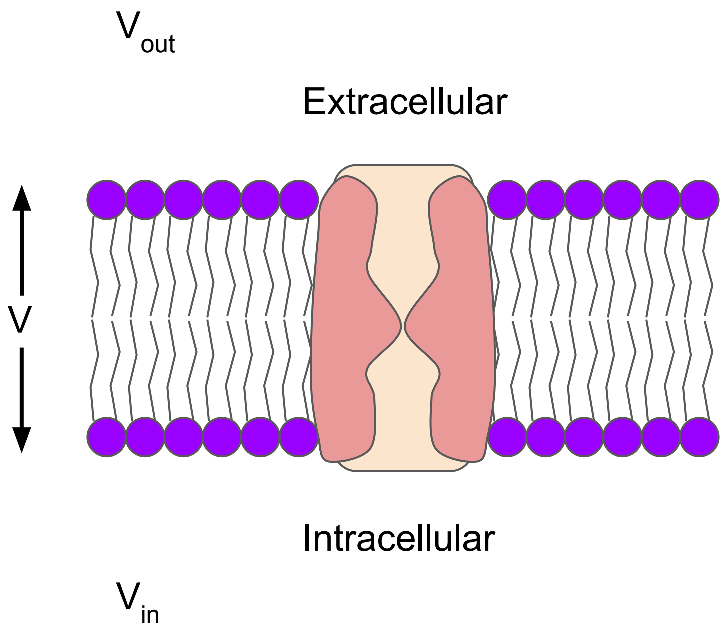


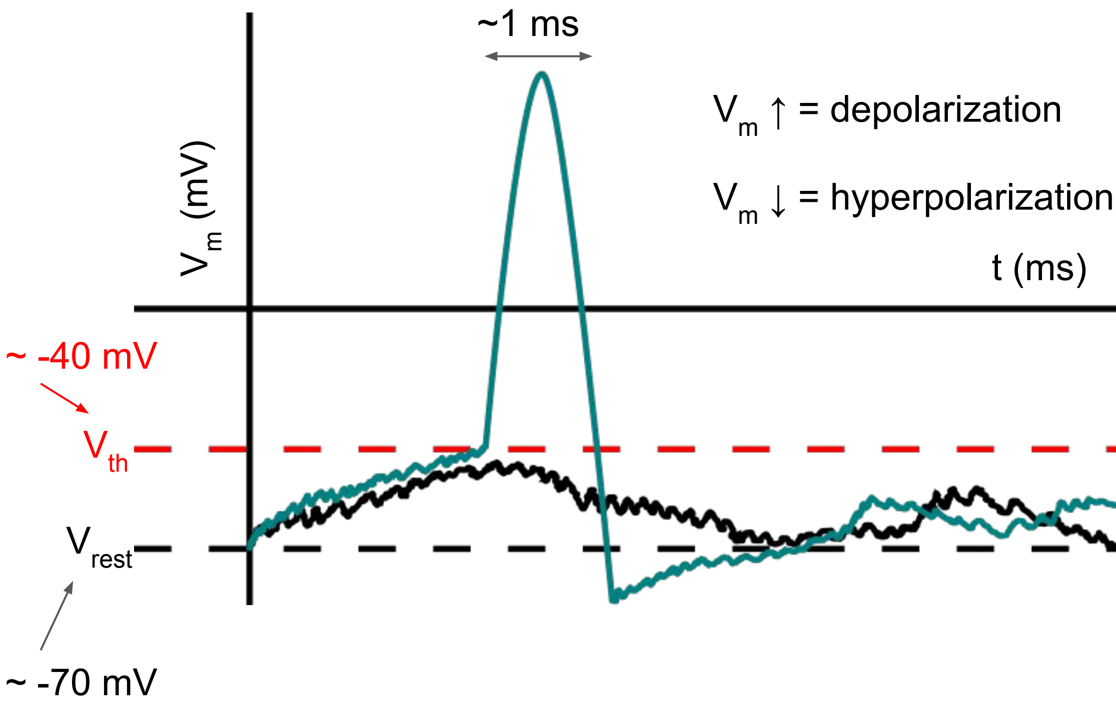
Typical resting $V_m = V_{rest} \sim -70$ mV

Spike generation and detection

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

Action potential = ***spike*** = rapid increase and decrease in neuronal membrane potential.

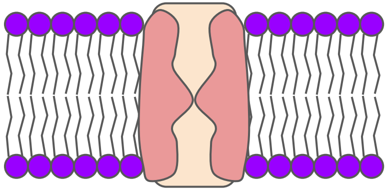


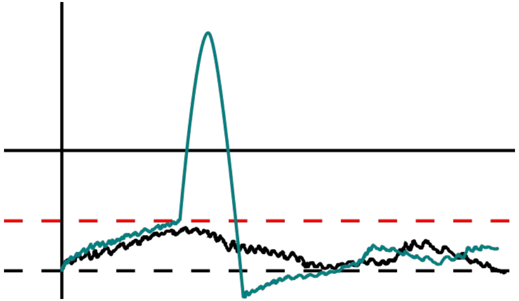


Spike generation and detection

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

Action potential = ***spike*** = rapid increase and decrease in neuronal membrane potential.



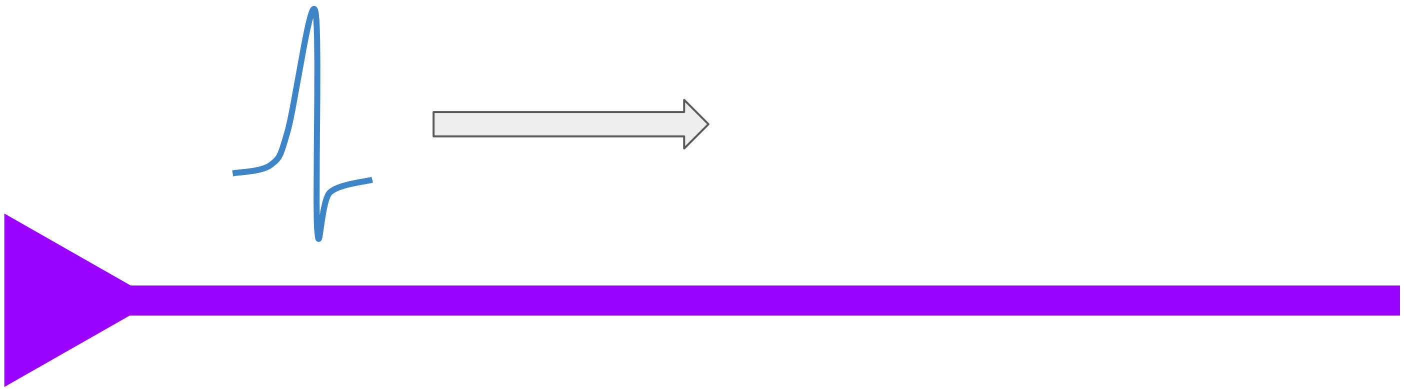


Bryant and Segundo, 1976.

Spike generation and detection

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

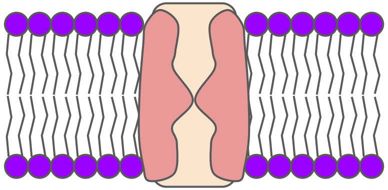
Action potential = ***spike*** = rapid increase and decrease in neuronal membrane potential.

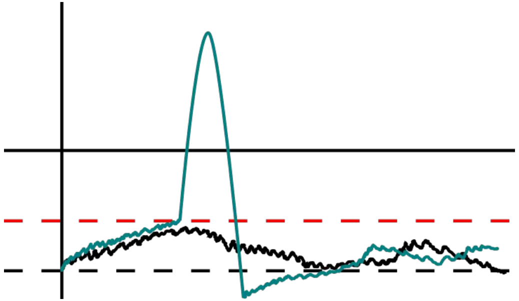


Spike generation and detection

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

Action potential = ***spike*** = rapid increase and decrease in neuronal membrane potential.



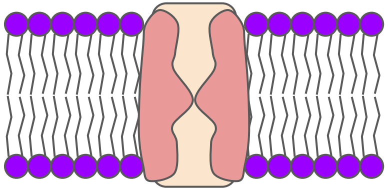


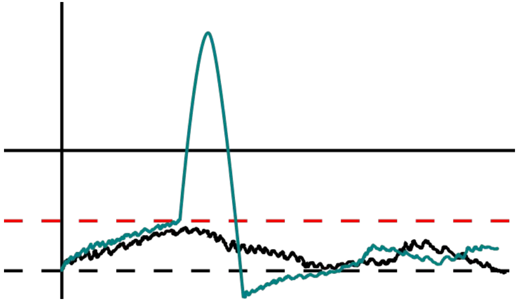
Bryant and Segundo, 1976.

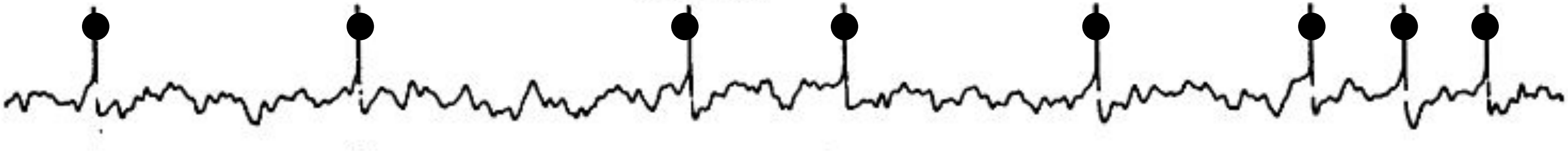
Spike generation and detection

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

Action potential = ***spike*** = rapid increase and decrease in neuronal membrane potential.





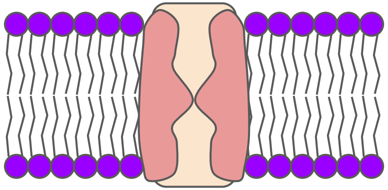


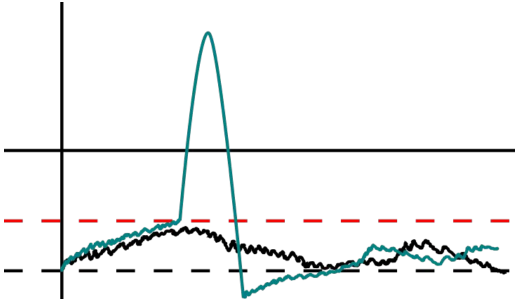
Bryant and Segundo, 1976.

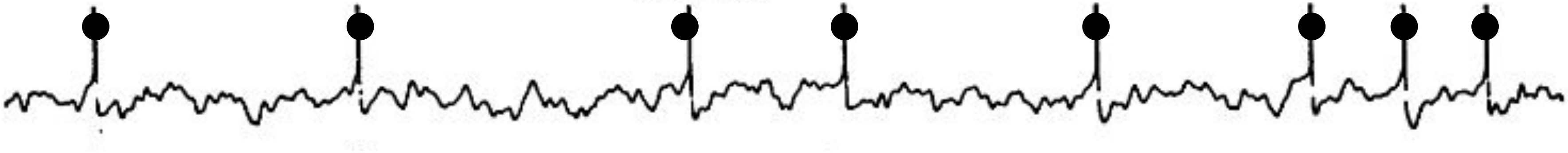
Spike generation and detection

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

Action potential = ***spike*** = rapid increase and decrease in neuronal membrane potential.







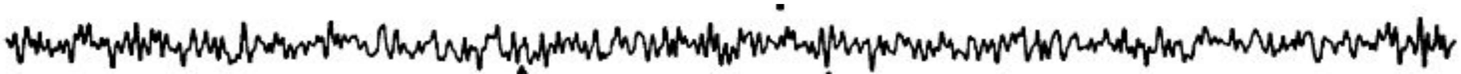
00000**1**000000000000**1**0000000000000000 **1**0000000**1**00000000000**1**0000000000**1**0000**1**000**1**000

Bryant and Segundo, 1976.

Outline

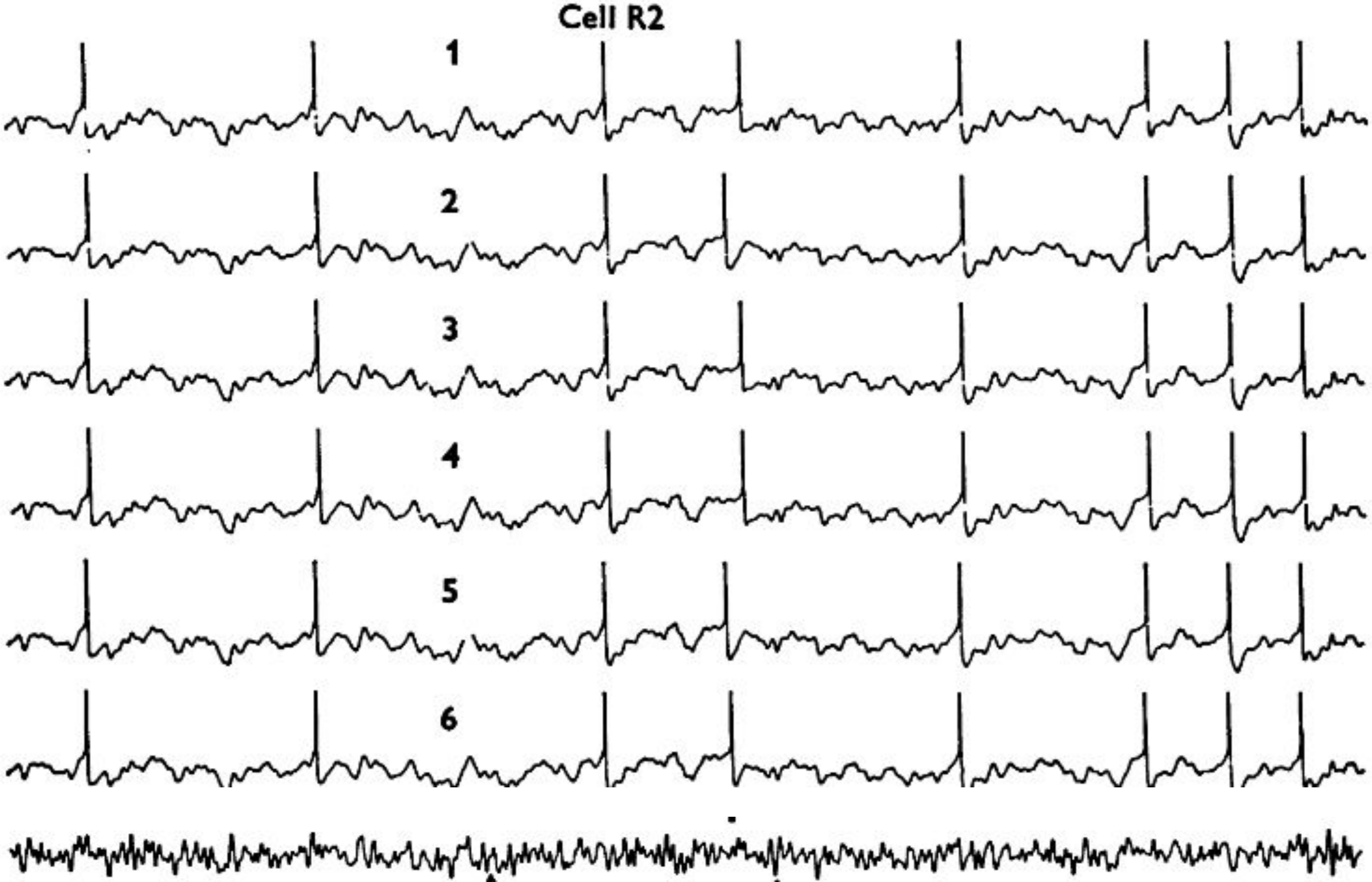
- Crash course in action potentials.
- Basic spike train analysis.
- Spiking neuron models.
- Short problem set time.
- Advanced spike train analysis.
- Other spike-based concepts.
- Full problem set time.

Spiking basics: raster plots and PSTHs



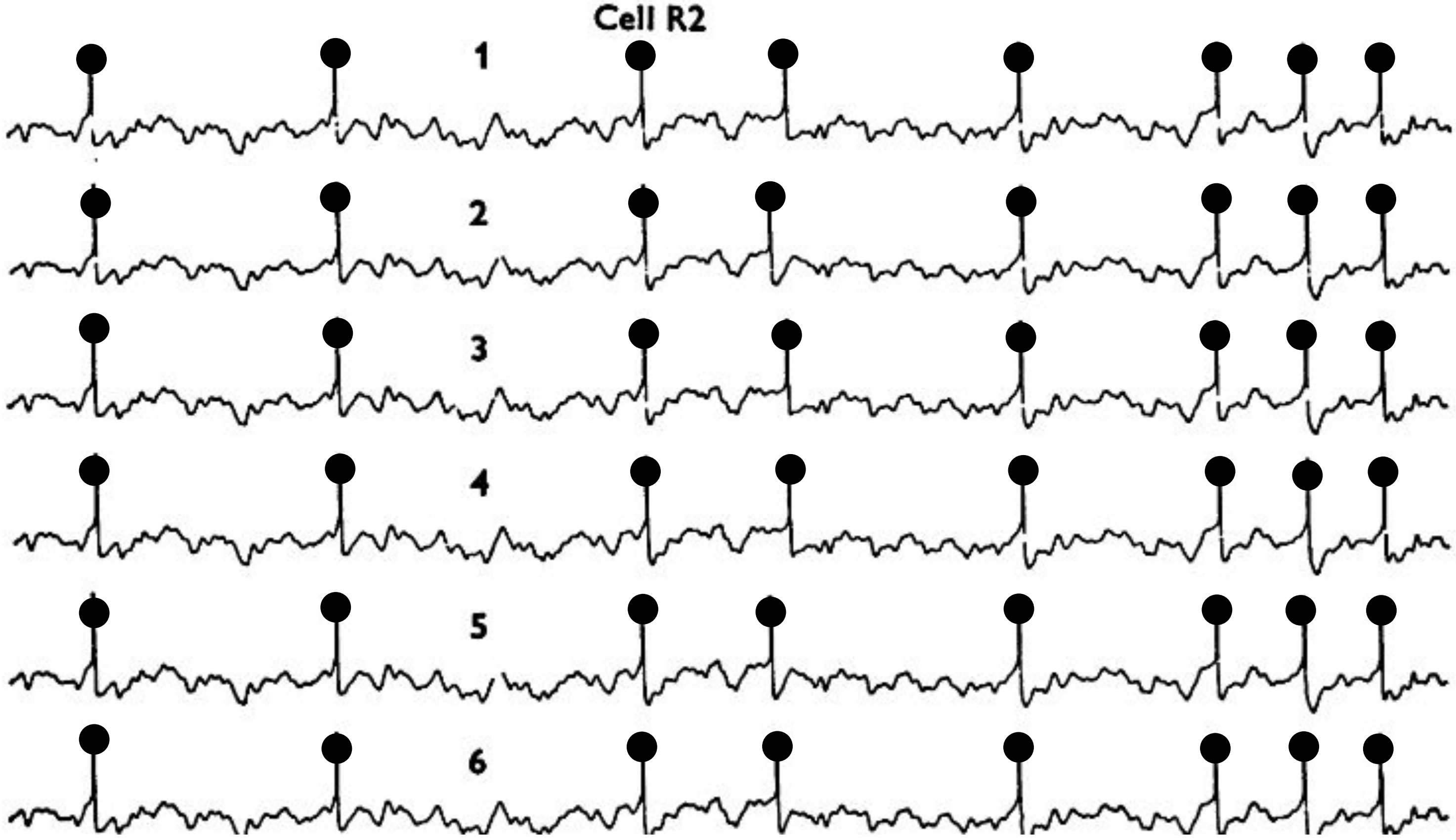
Bryant and Segundo, 1976.

Spiking basics: raster plots and PSTHs



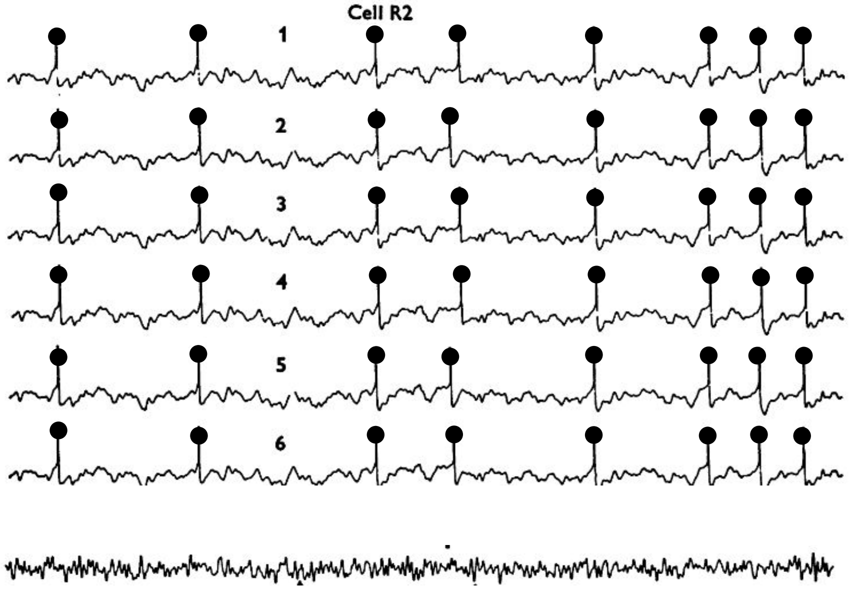
Bryant and Segundo, 1976.

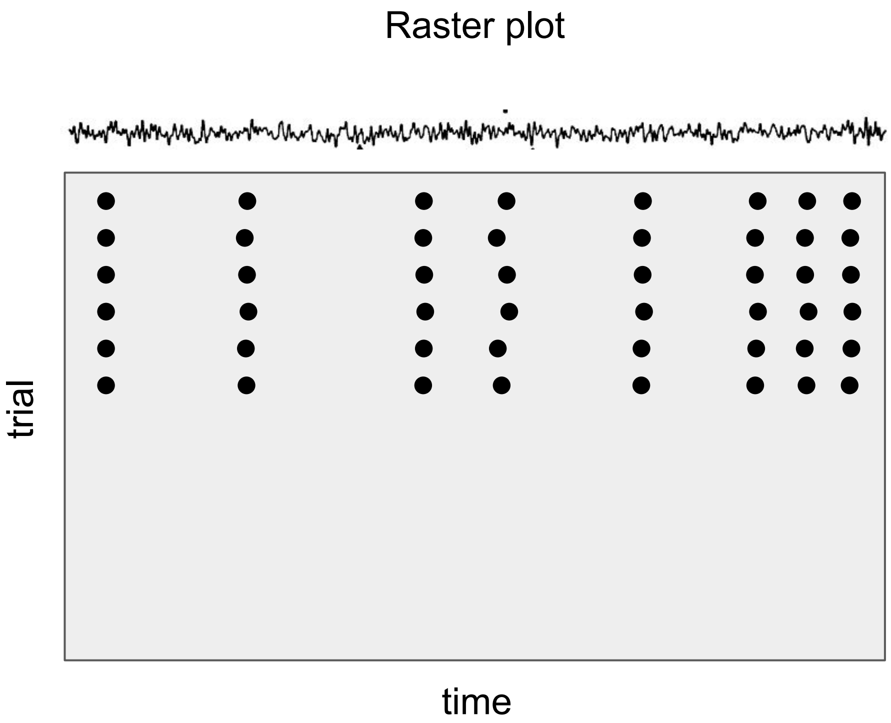
Spiking basics: raster plots and PSTHs



Bryant and Segundo, 1976.

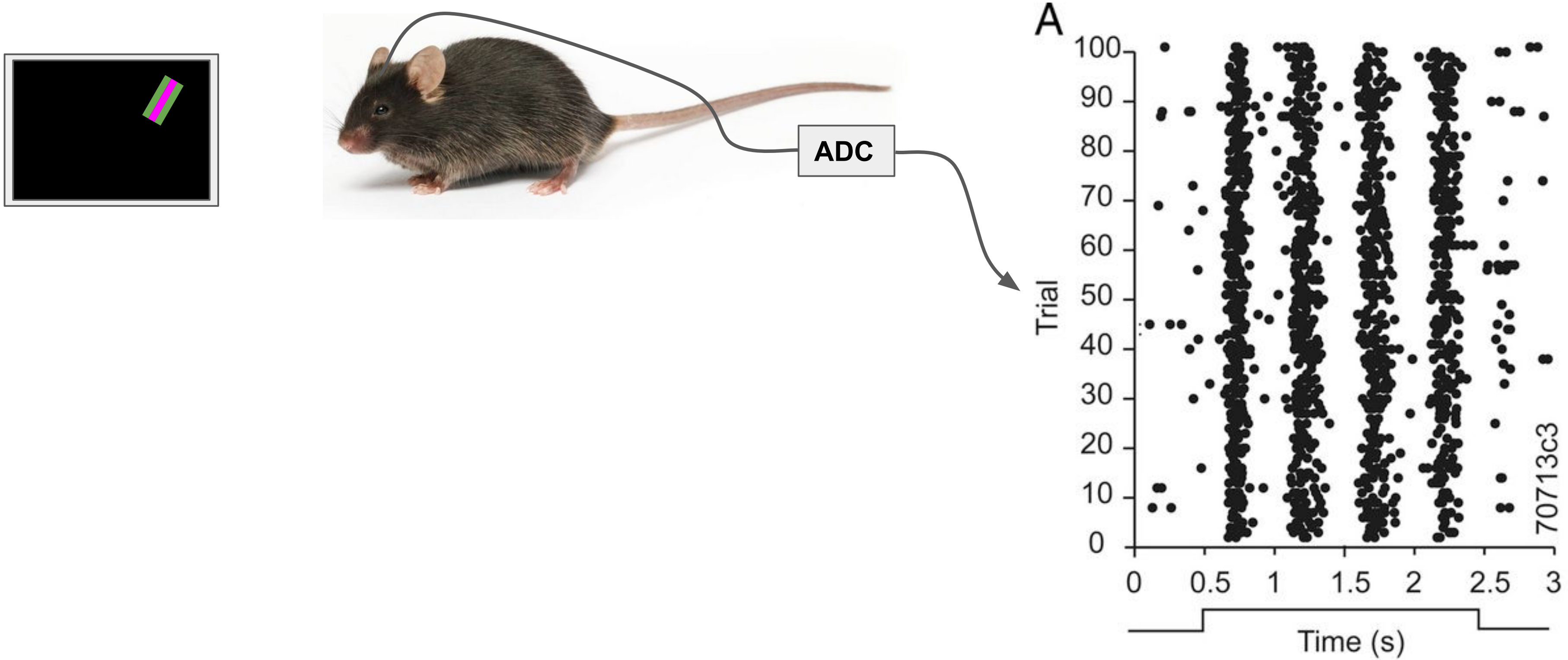
Spiking basics: raster plots and PSTHs





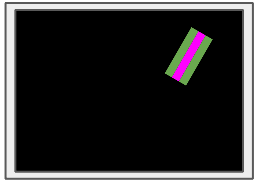
Bryant and Segundo, 1976.

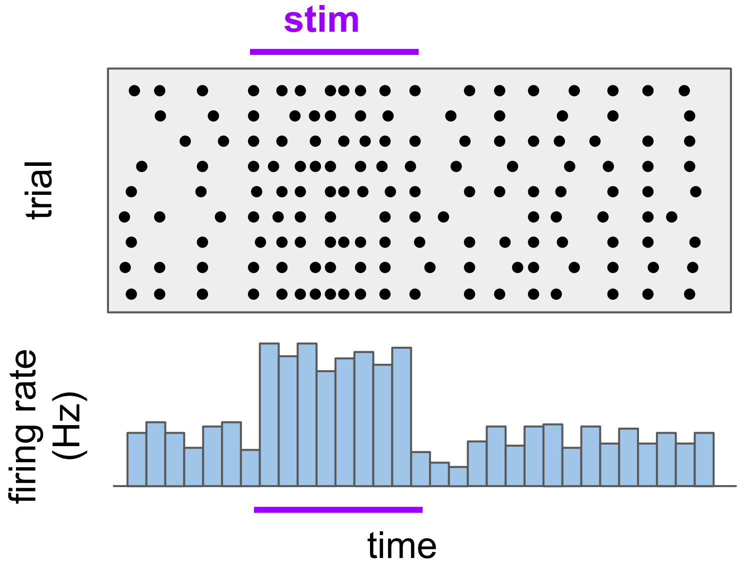
Spiking basics: raster plots and PSTHs



Gao, Deangelis, Burkhalter 2010

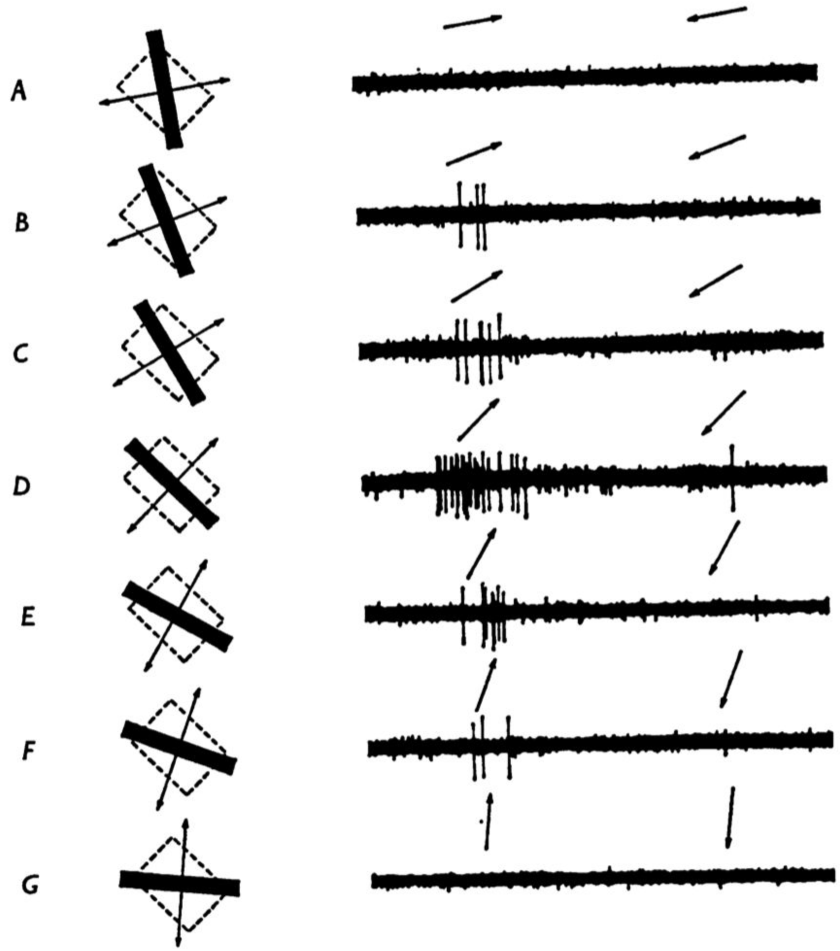
Spiking basics: raster plots and PSTHs



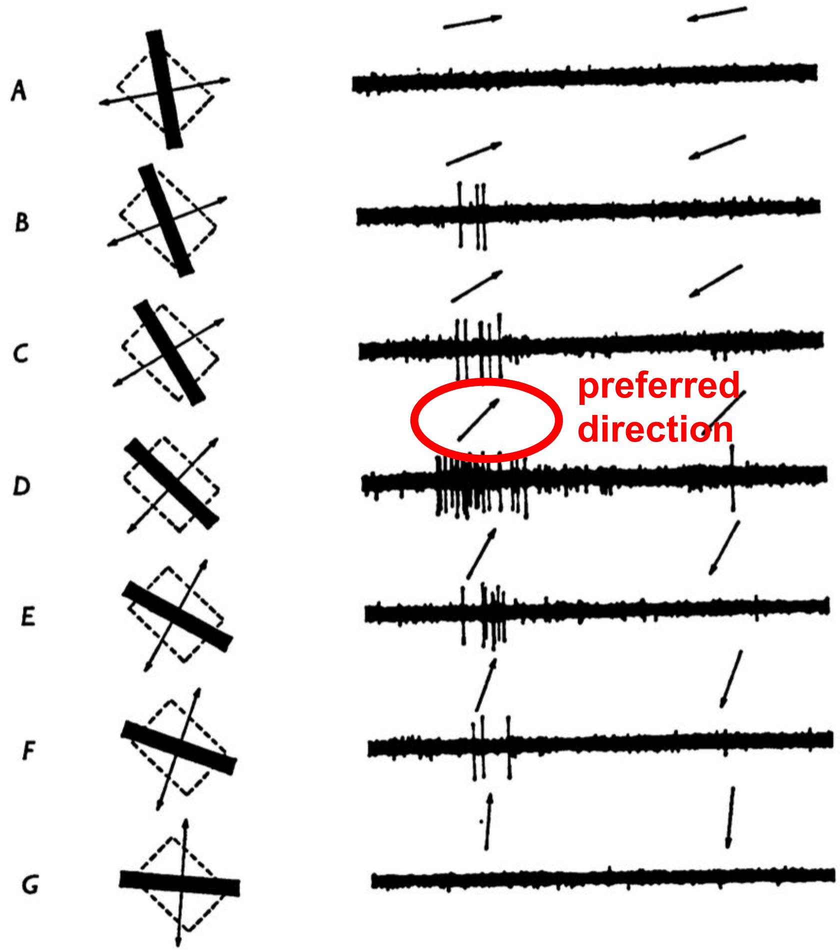


peristimulus time histogram

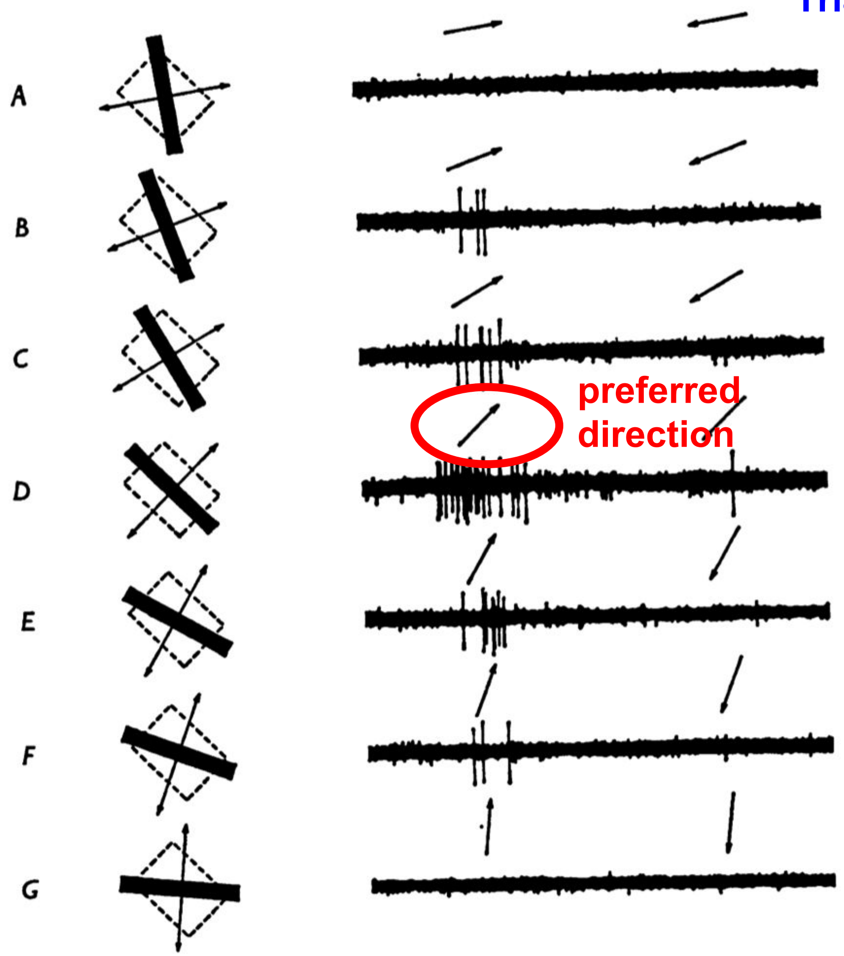
Spiking basics: tuning curves



Spiking basics: tuning curves



Spiking basics: tuning curves

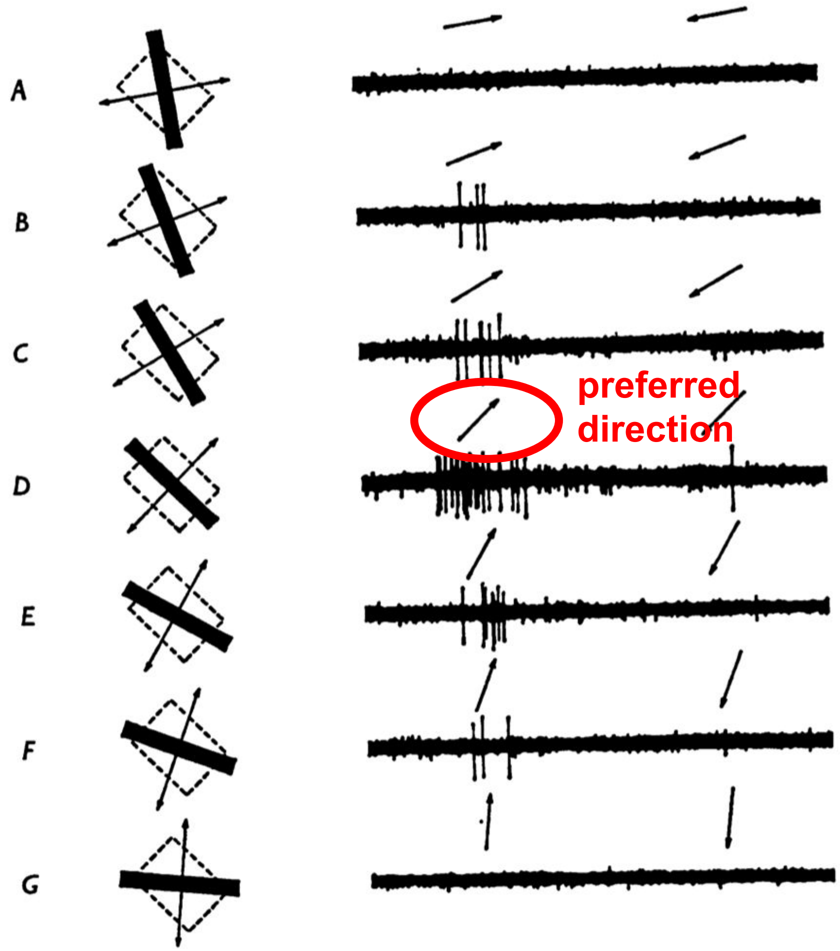


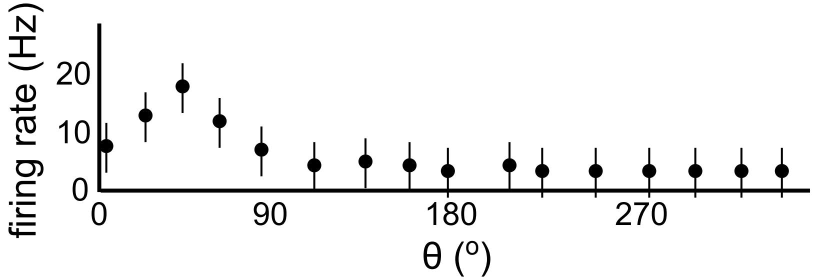
Trial	1	2	3	...
	0	0	0	...
	2	1	3	...
	6	8	5	...
	20	23	18	...
	10	7	8	...
		⋮		

spike counts

Hubel and Wiesel, 1968.

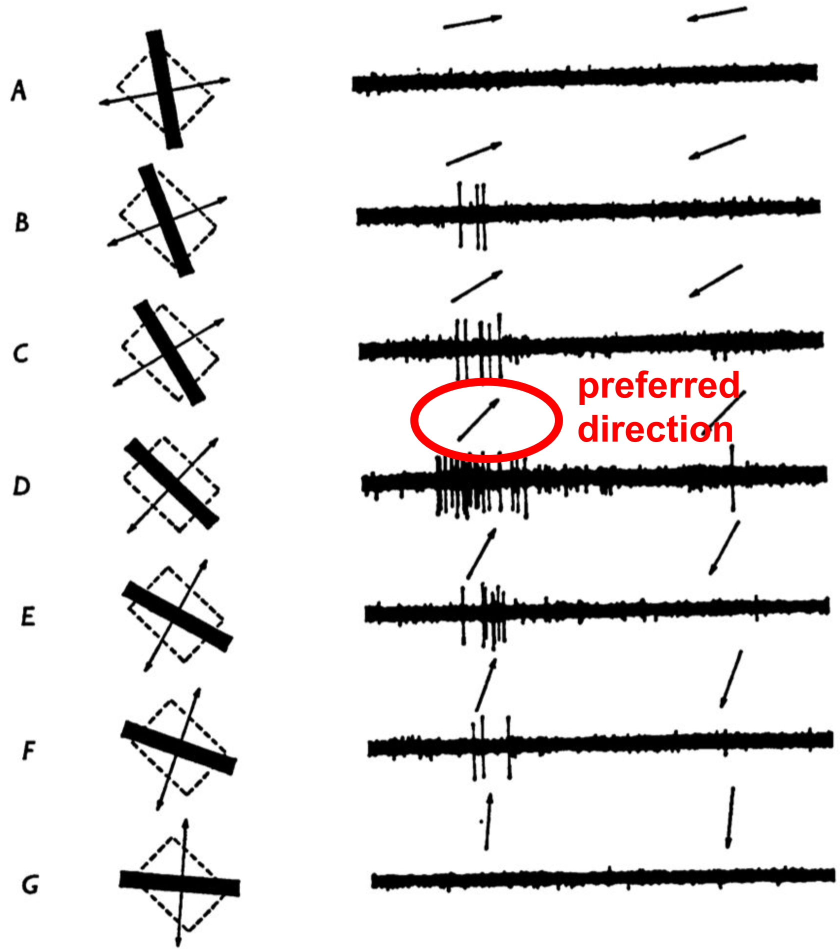
Spiking basics: tuning curves

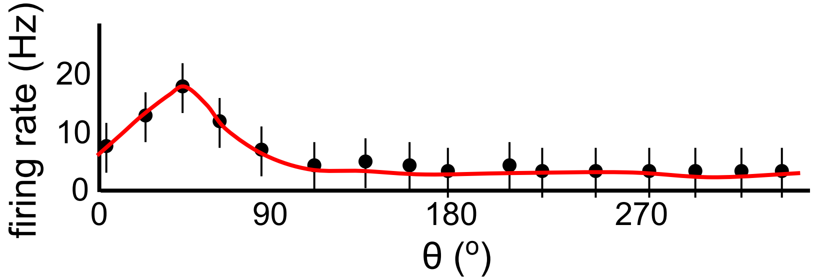




Hubel and Wiesel, 1968.

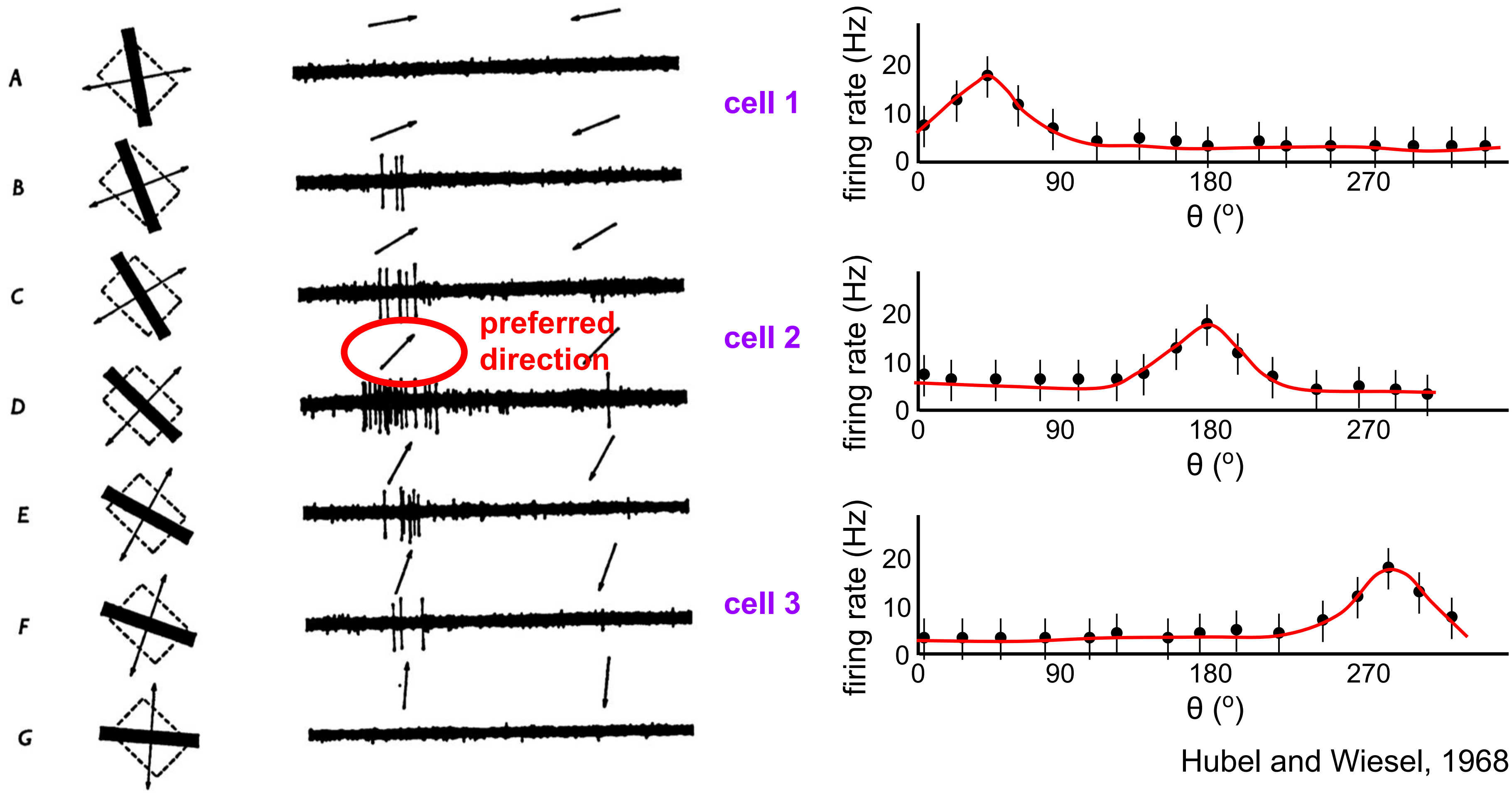
Spiking basics: tuning curves





Hubel and Wiesel, 1968.

Spiking basics: tuning curves



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?***

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).

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).

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

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).

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

$$p(k_{spks}|r, T) = \text{Poisson}(k_{spks}|\lambda = rT)$$

Spiking basics: the inter-spike interval distribution

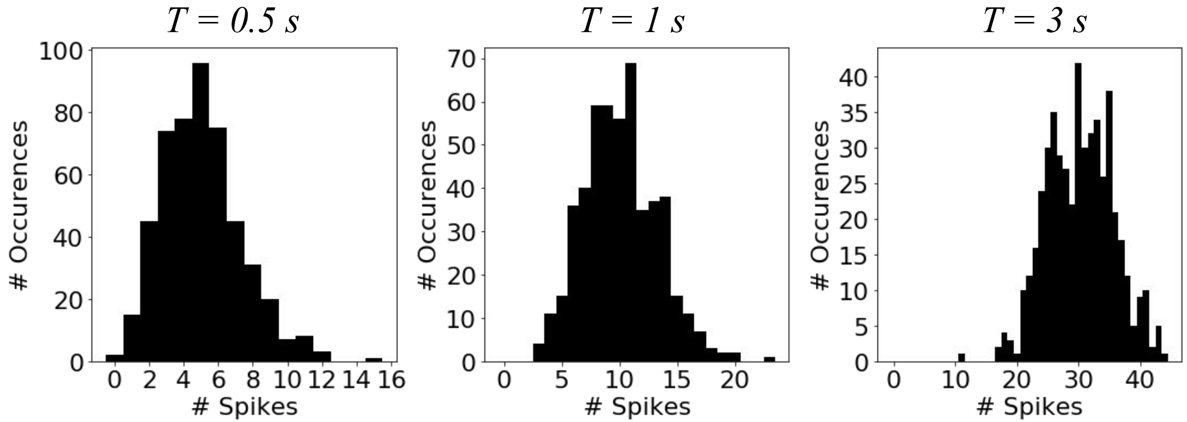
Unless all inputs fixed, spike times generally quite variable: ***what distribution underlies this variability?***

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

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

$$p(k_{spks}|r, T) = \mathrm{Poisson}(k_{spks}|\lambda = rT)$$

r = 10 Hz:



Spiking basics: the inter-spike interval distribution

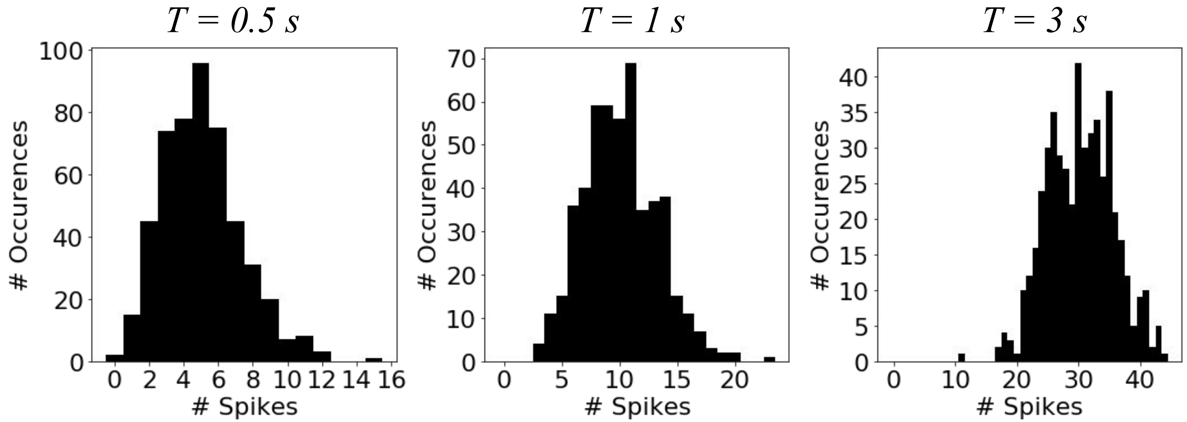
Unless all inputs fixed, spike times generally quite variable: ***what distribution underlies this variability?***

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

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

$$p(k_{spks}|r, T) = \text{Poisson}(k_{spks}|\lambda = rT)$$

r = 10 Hz:



Spiking basics: the inter-spike interval distribution

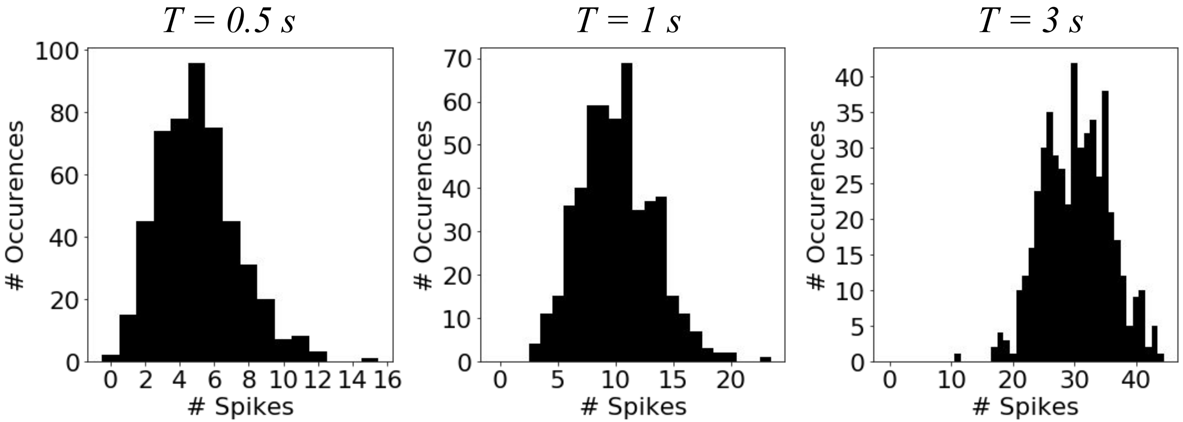
Unless all inputs fixed, spike times generally quite variable: ***what distribution underlies this variability?***

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

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

$$p(k_{spks}|r,T) = \text{Poisson}(k_{spks}|\lambda = rT)$$

r = 10 Hz:

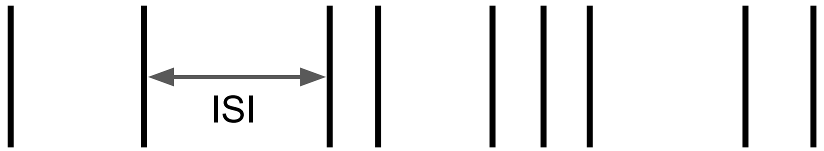


Spiking basics: the inter-spike interval distribution

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

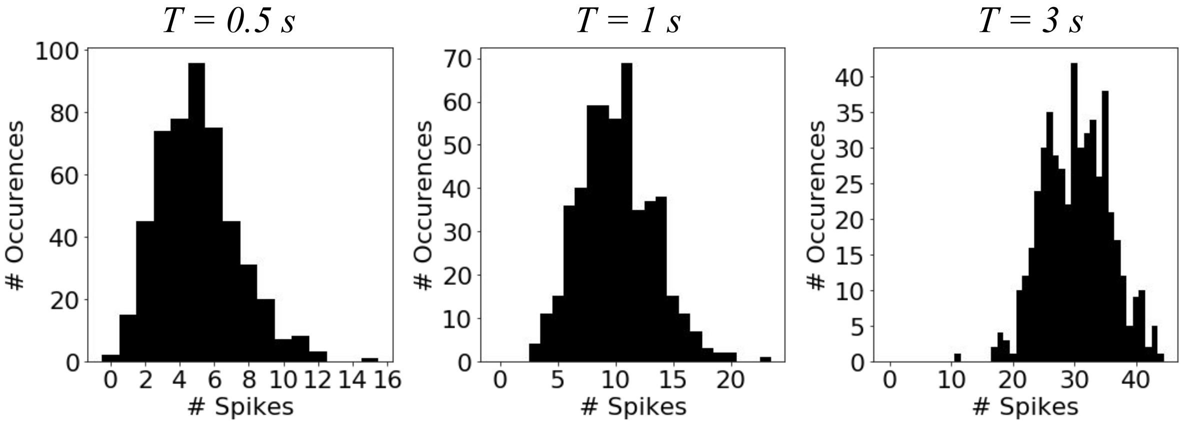
“Most random” spiking = ***Poisson-distributed*** spike counts (all spikes conditionally independent given rate).

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



$$p(k_{spks}|r, T) = \text{Poisson}(k_{spks}|\lambda = rT)$$

r = 10 Hz:



Spiking basics: the inter-spike interval distribution

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

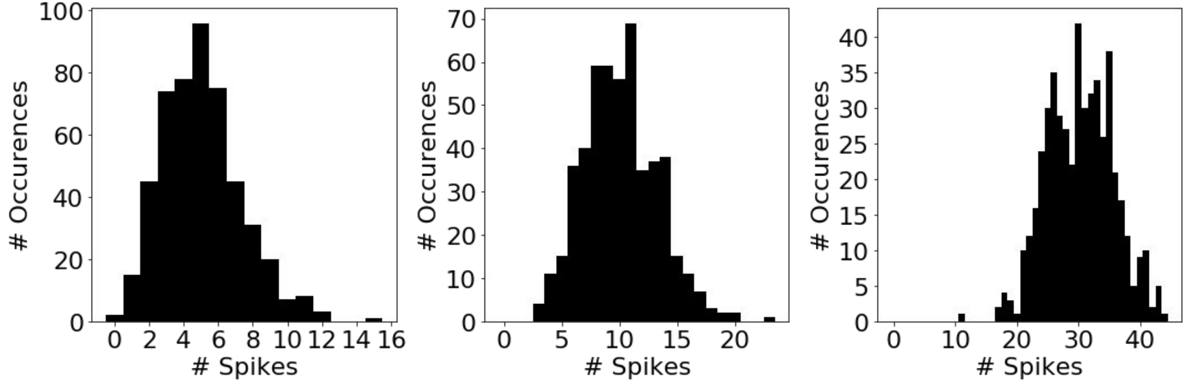
"Most random" spiking = ***Poisson-distributed*** spike counts (all spikes conditionally independent given rate).

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

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

r = 10 Hz:

T = 0.5 s *T = 1 s* *T = 3 s*



Spiking basics: the inter-spike interval distribution

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

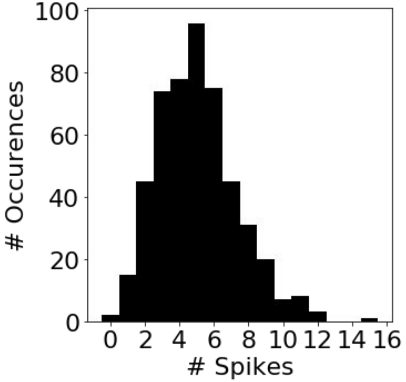
"Most random" spiking = ***Poisson-distributed*** spike counts (all spikes conditionally independent given rate).

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

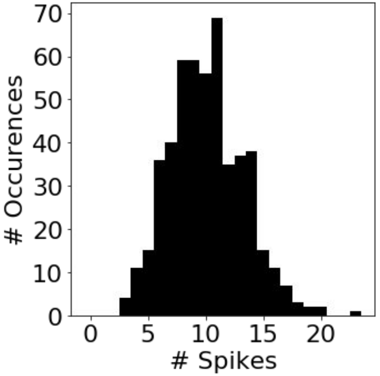
$$p(k_{spks}|r,T) = \text{Poisson}(k_{spks}|\lambda = rT) \qquad P(ISI) = r\exp(-rISI)$$

r = 10 Hz:

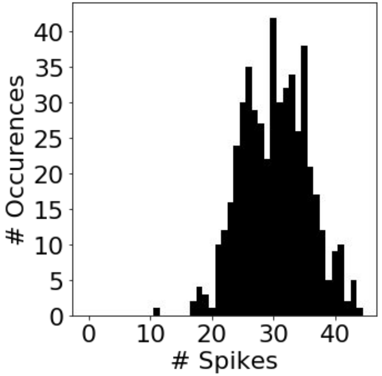
T = 0.5 s

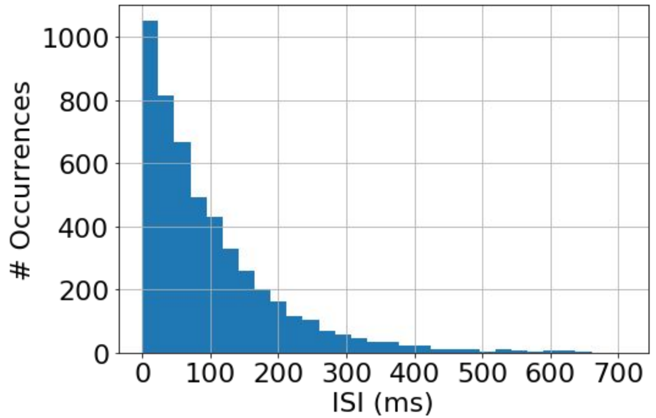


T = 1 s



T = 3 s

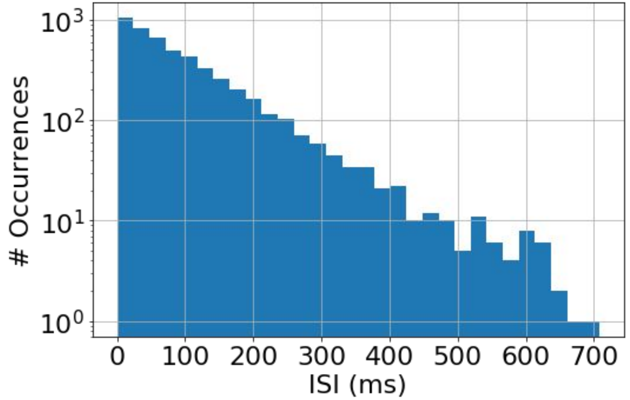




Spiking basics: the inter-spike interval distribution

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

“Most random” spiking = ***Poisson-distributed*** spike counts.

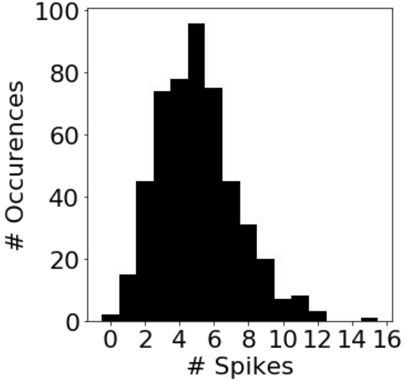


$$\mathrm{Poisson}(k|\lambda) = \frac{\lambda^k e^{-\lambda}}{k!}$$

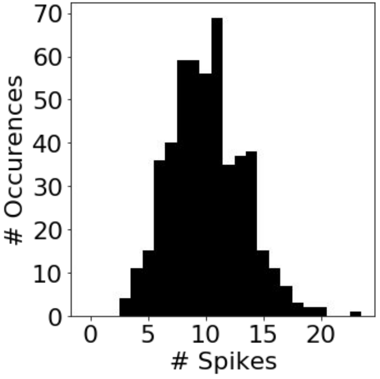
$$p(k_{spks}|r, T) = \mathrm{Poisson}(k_{spks}|\lambda = rT)$$

r = 10 Hz:

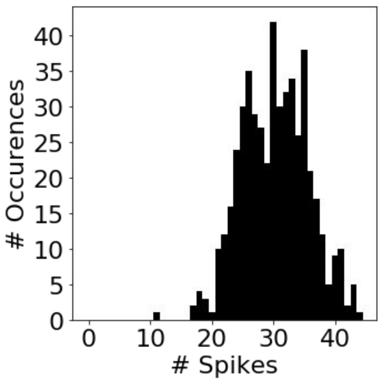
T = 0.5 s

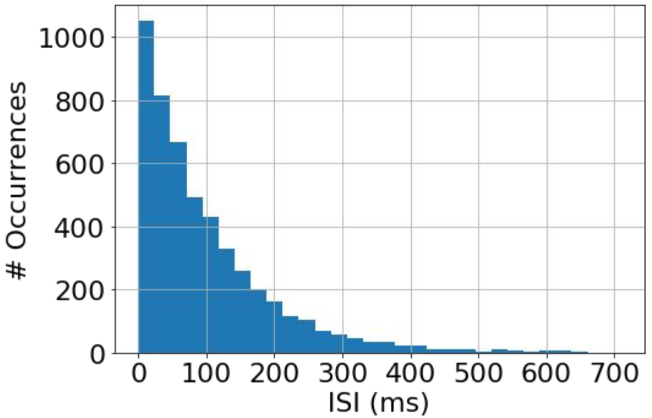


T = 1 s



T = 3 s





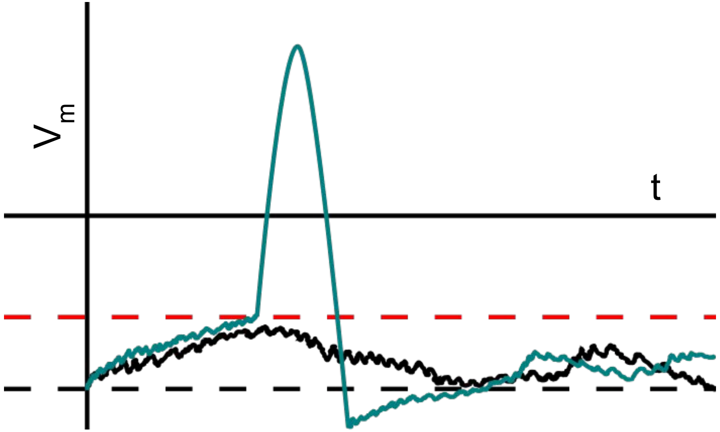
Outline

- Crash course in 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.

Spiking neuron models

Hodgkin-Huxley model

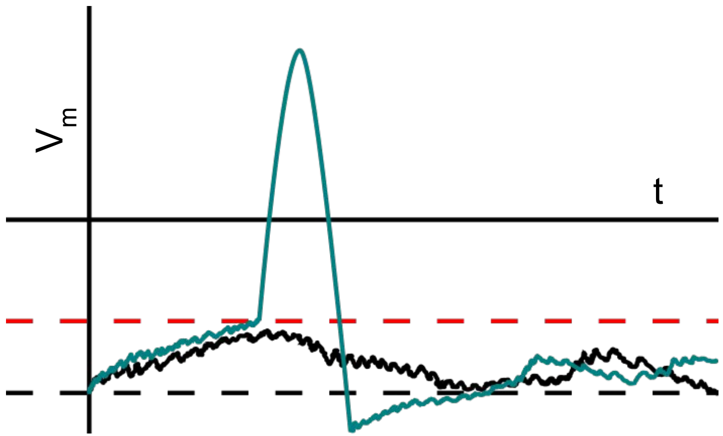
$$\begin{cases} \dfrac{dV_m}{dt} = \dfrac{I}{C_m} - \dfrac{\bar{g}_K n^4}{C_m}(V_m - V_K) - \dfrac{\bar{g}_{Na} m^3 h}{C_m}(V_m - V_{Na}) - \dfrac{\bar{g}_l}{C_m}(V_m - V_l) \\ \dfrac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n \\ \dfrac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m \\ \dfrac{dh}{dt}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



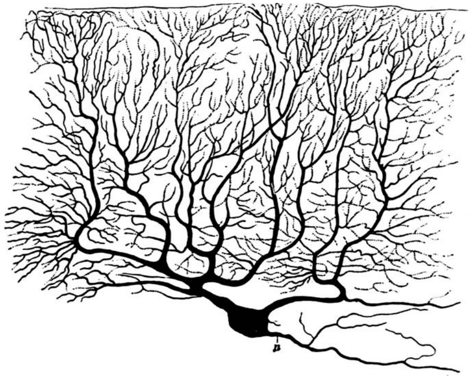
Spiking neuron models

Hodgkin-Huxley model

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



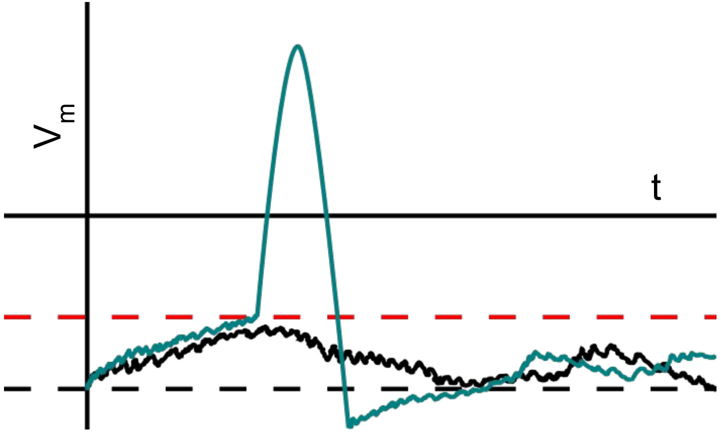
Realistic neuron morphology!



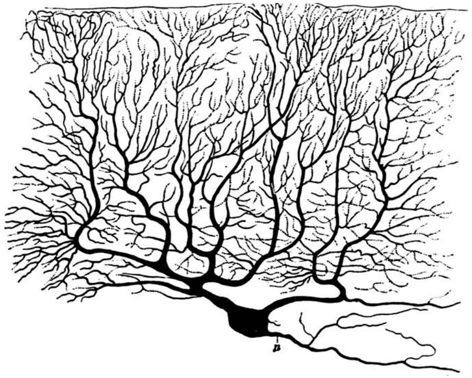
Spiking neuron models

Hodgkin-Huxley model

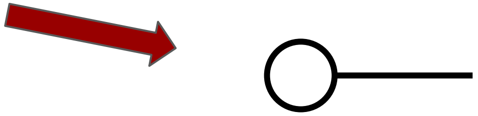
$$\begin{cases} \dfrac{dV_m}{dt} = \dfrac{I}{C_m} - \dfrac{\bar{g}_K n^4}{C_m}(V_m - V_K) - \dfrac{\bar{g}_{Na} m^3 h}{C_m}(V_m - V_{Na}) - \dfrac{\bar{g}_l}{C_m}(V_m - V_l) \\ \dfrac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n \\ \dfrac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m \\ \dfrac{dh}{dt}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



Realistic neuron morphology!



Can we simplify?



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

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

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

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

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

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

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

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

discretize

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

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

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

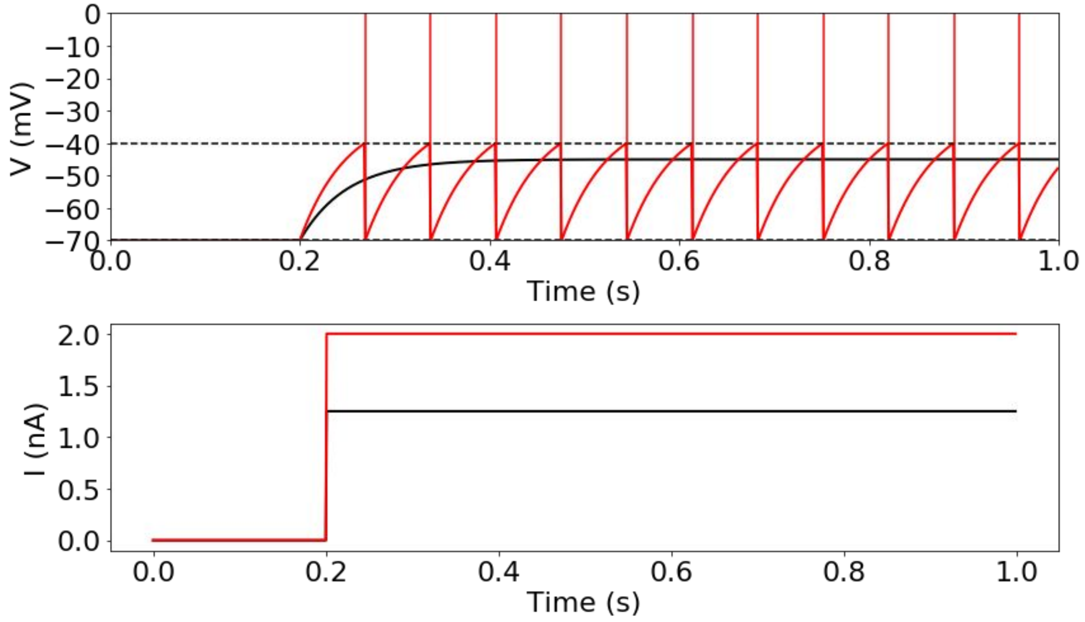
$$\tau \frac{dV}{dt} = -(V(t) - V_{leak}) + RI(t)$$

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

discretize

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

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



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

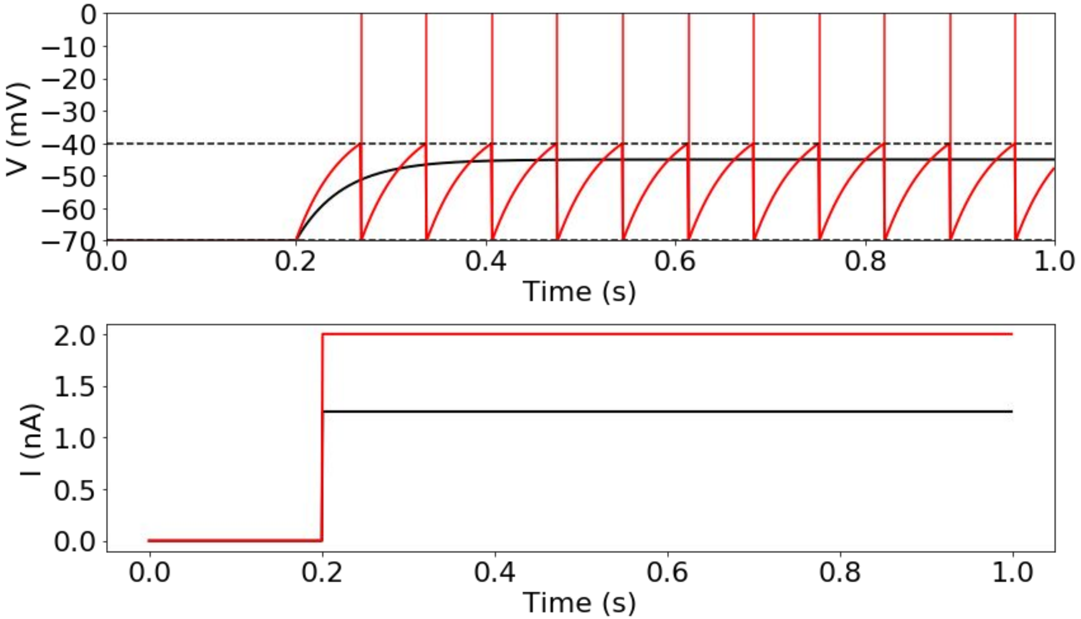
$$\tau \frac{dV}{dt} = -(V(t) - V_{leak}) + RI(t)$$

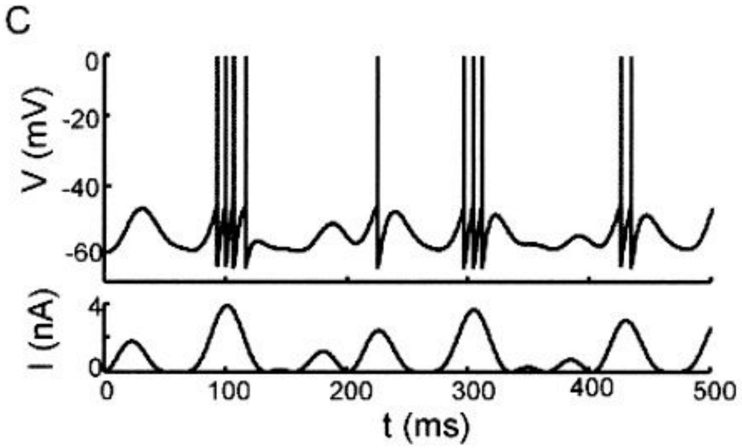
discretize

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

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

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





Abbott 1999

Spiking neuron models: modeling synapses

Presynaptic spikes as sum of delta functions

$$y(t) = \delta(t - t_{spk}^0) + \delta(t - t_{spk}^1) + \dots \delta(t - t_{spk}^n)$$

Current-based synapses

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

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

Conductance-based synapses

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

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

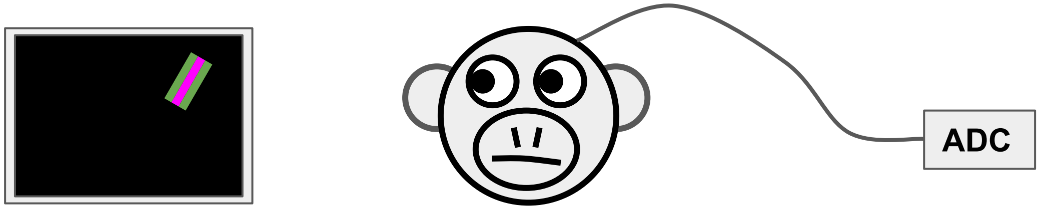
$$g_{syn}(t) = w \sum_{t_{spk}^k} \alpha(t - t_{spk}^k)$$

Problem set part 1

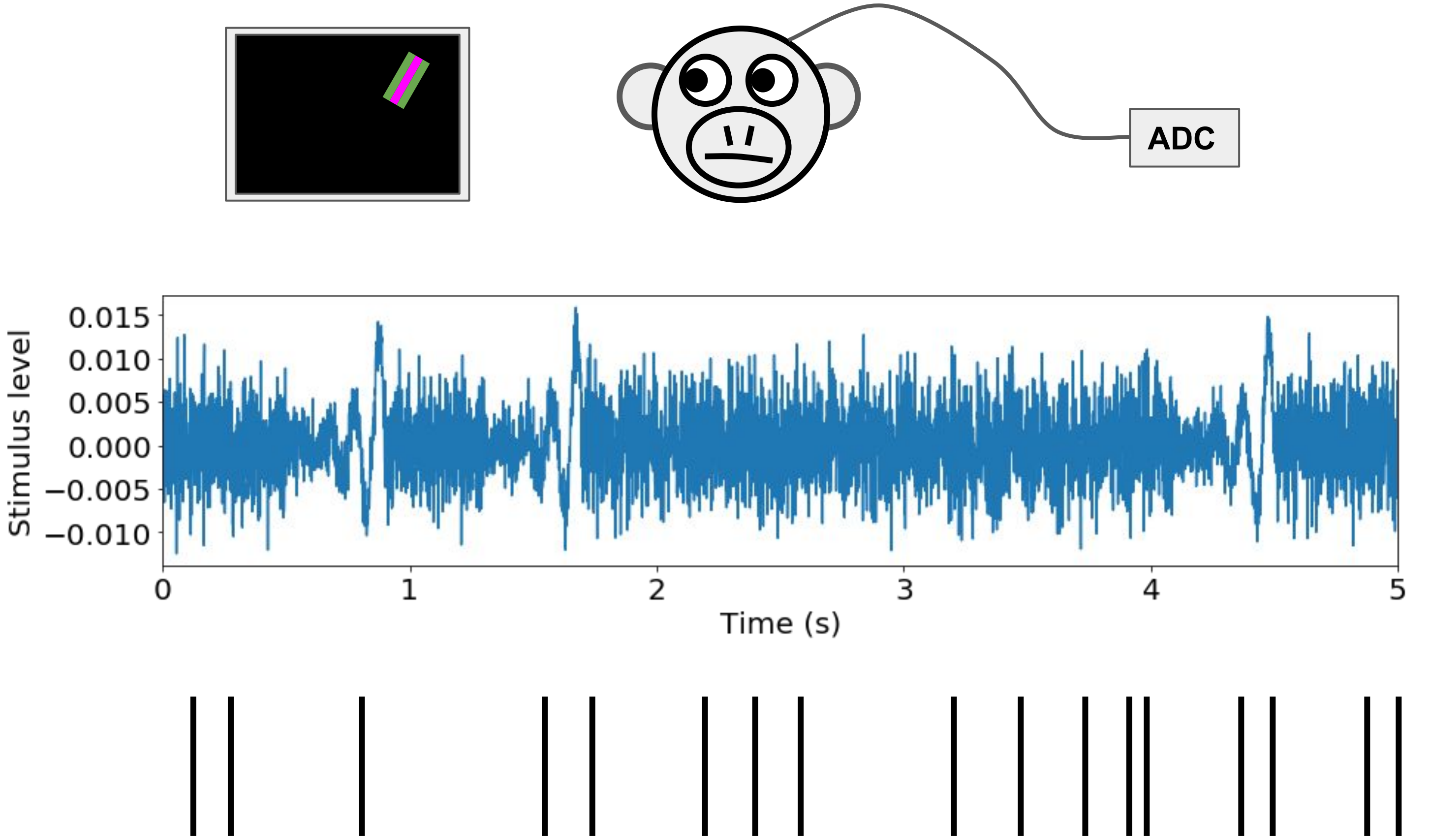
https://github.com/rkp8000/imbizo_2019_spikes_tutorial

problems_1.ipynb

General neural response models

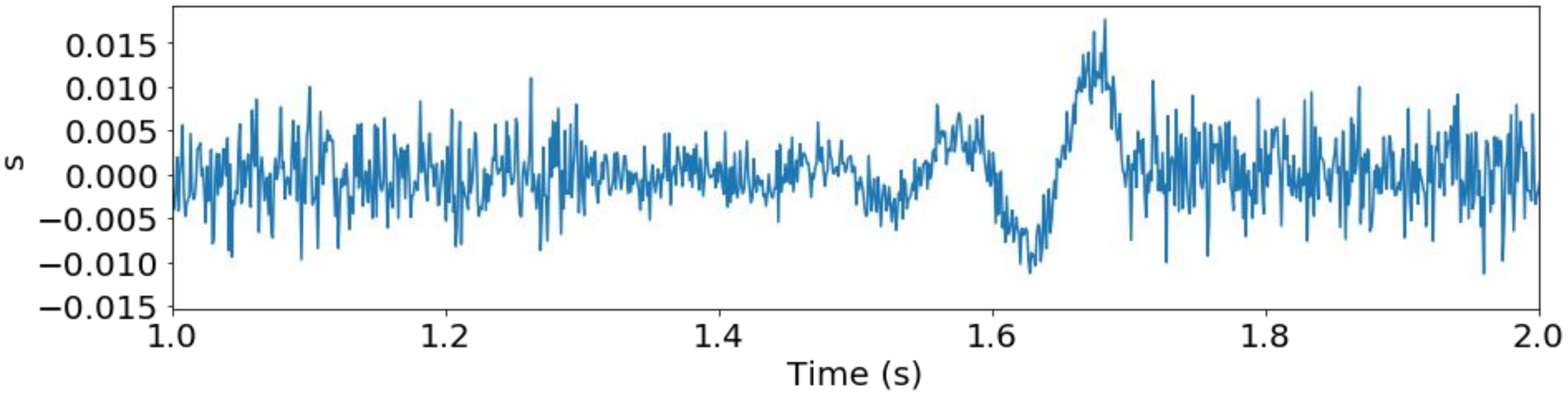


General neural response models



Interlude: Linear filtering

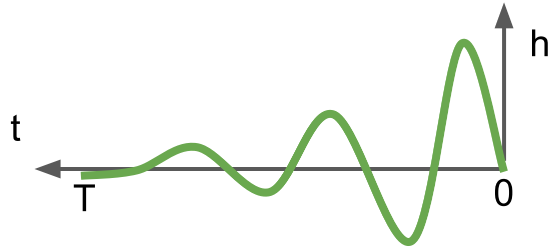
Given a time-series, how do we look for specific “features”?



How do we detect this feature?

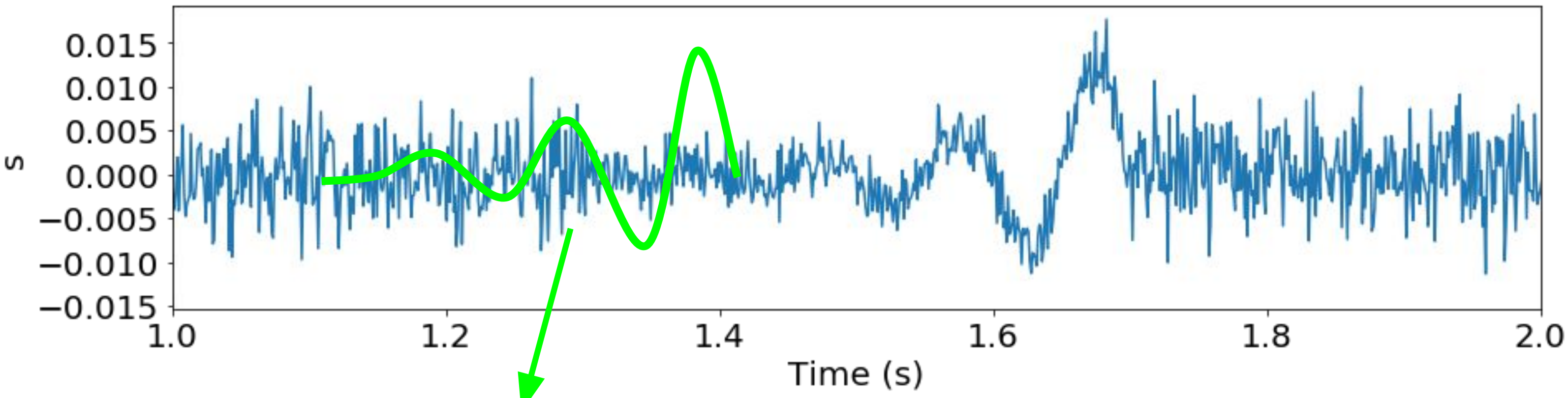
Answer:

1. Create “filter” with same shape as target feature.



Interlude: Linear filtering

Given a time-series, how do we look for specific “features”?

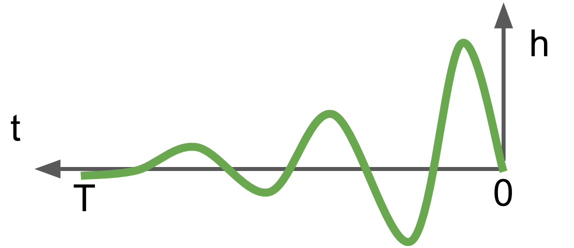


$\int_0^T h(\tau)s(t-\tau)d\tau$ ~ 0

Answer:

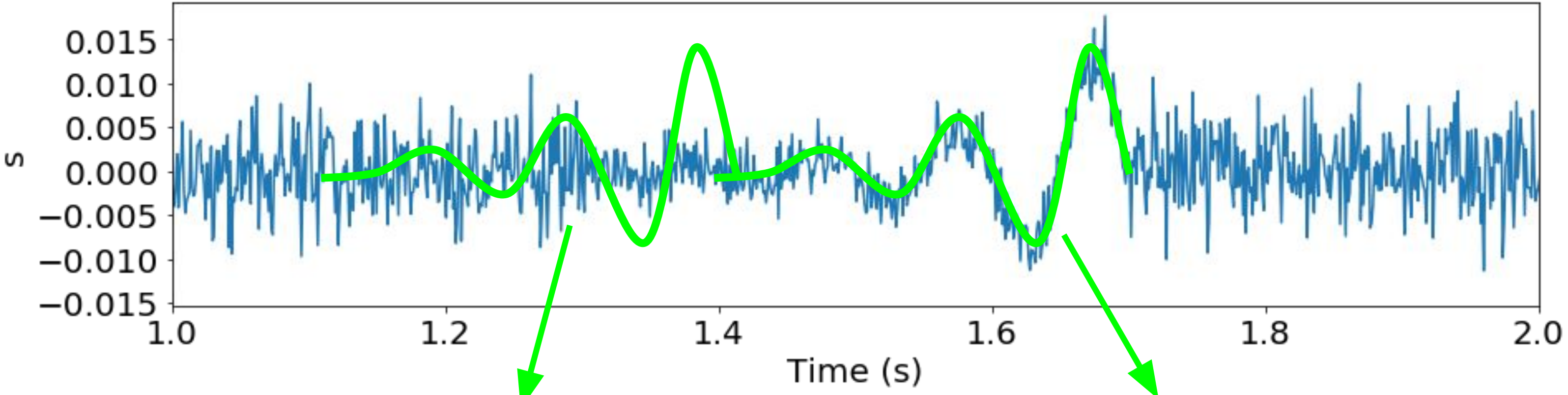
1. Create “filter” with same shape as target feature.

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



Interlude: Linear filtering

Given a time-series, how do we look for specific “features”?



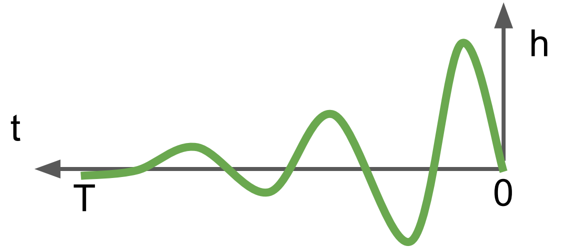
$\int_0^T h(\tau)s(t-\tau)d\tau \sim 0$

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

Answer:

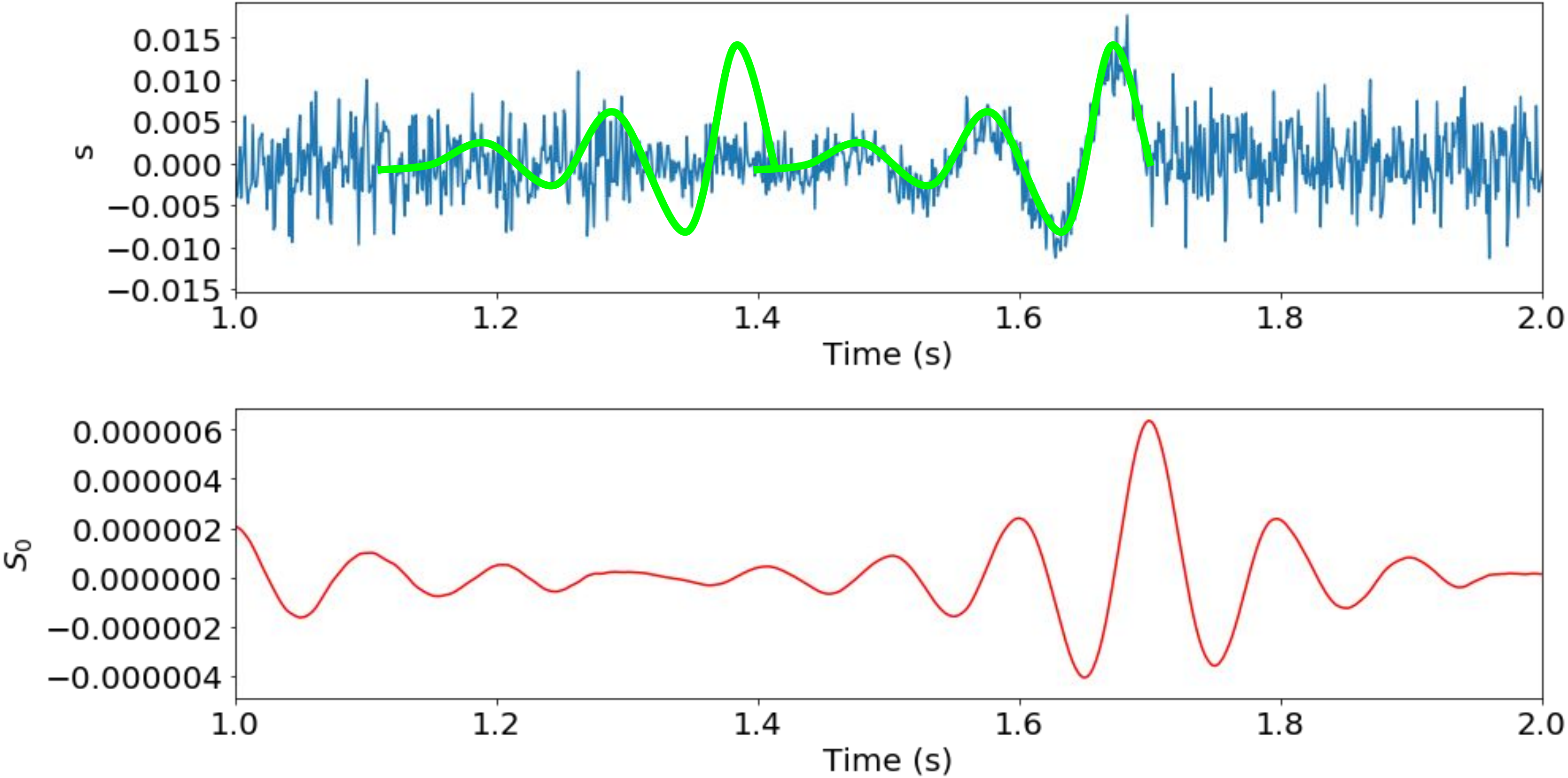
1. Create “filter” with same shape as target feature.

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

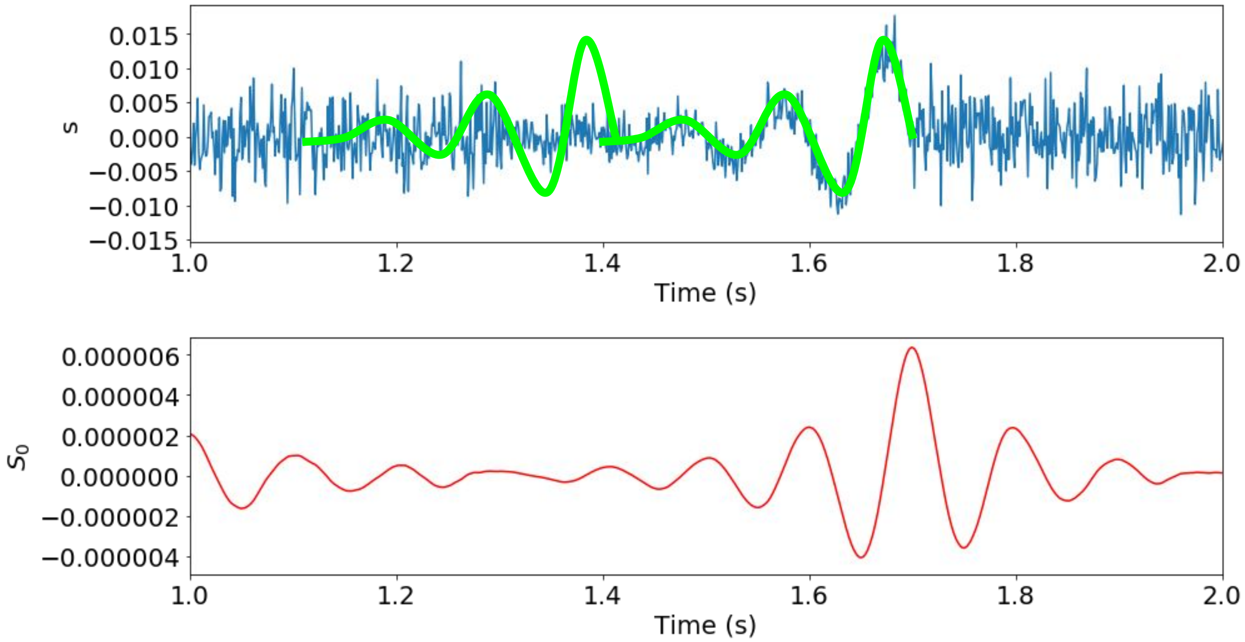


Interlude: Linear filtering

Given a time-series, how do we look for specific “features”?

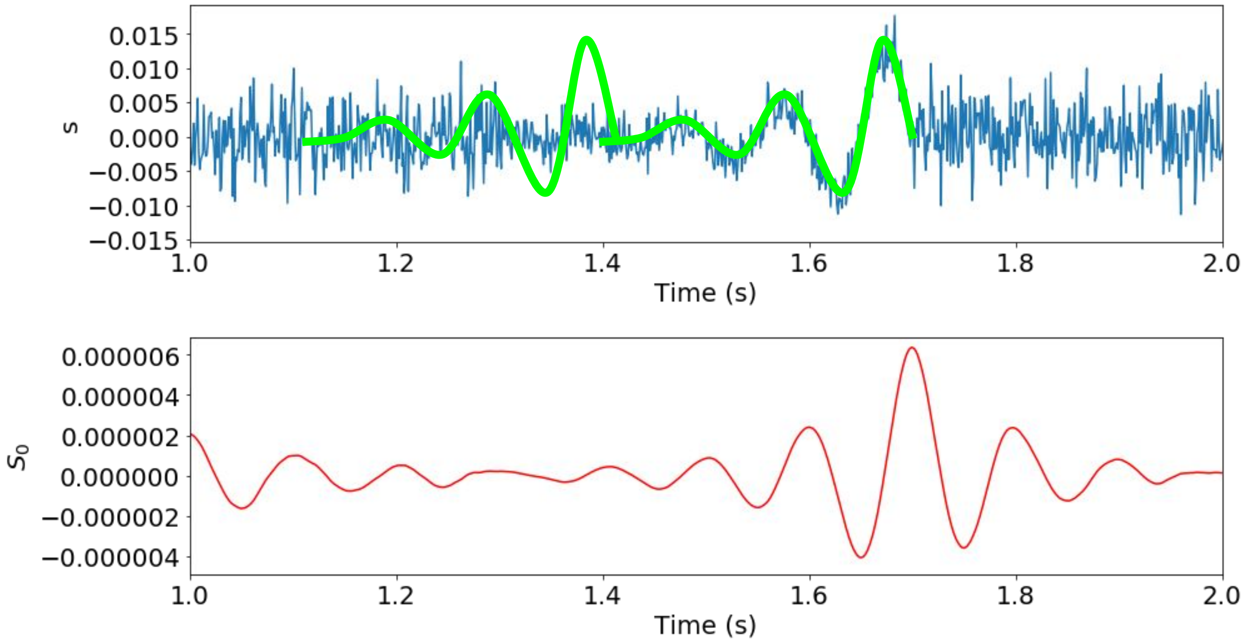


Interlude: Linear filtering



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

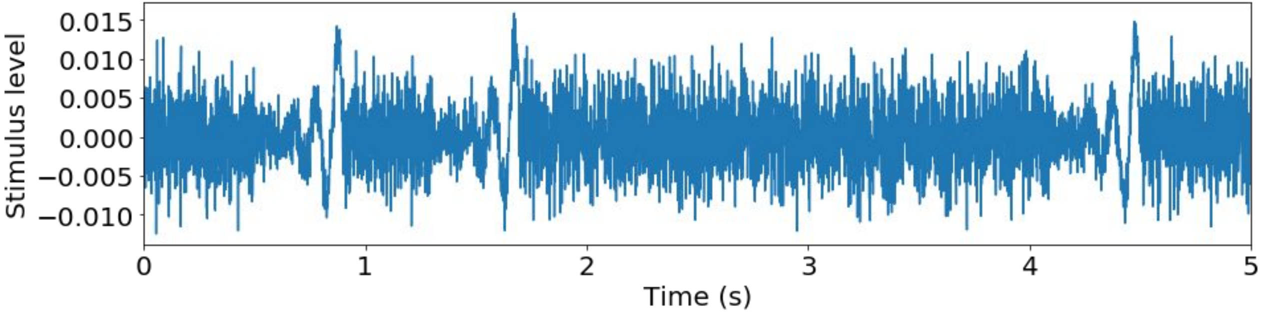
Interlude: Linear filtering

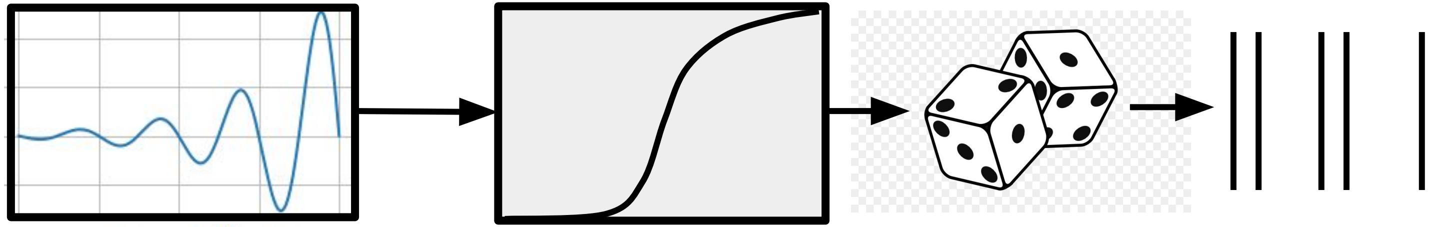


$$s_0(t) = \int_0^T h(\tau)s(t-\tau)d\tau$$

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

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





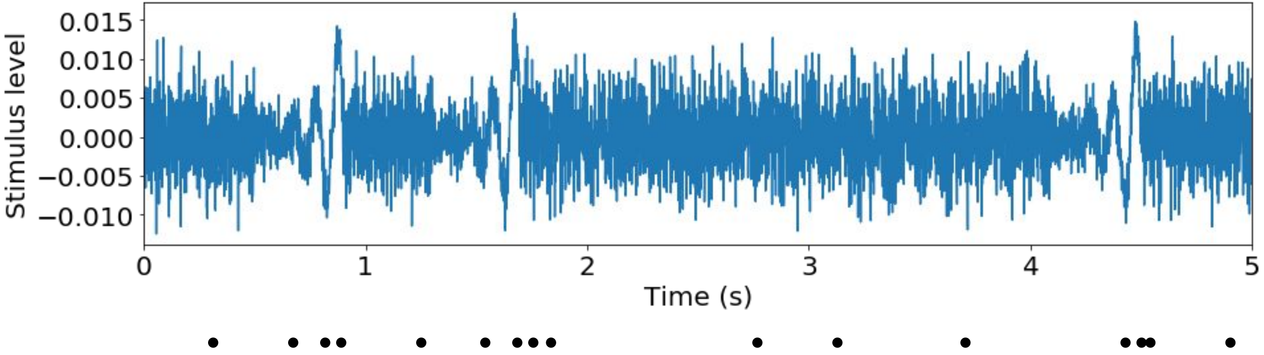
$$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$$

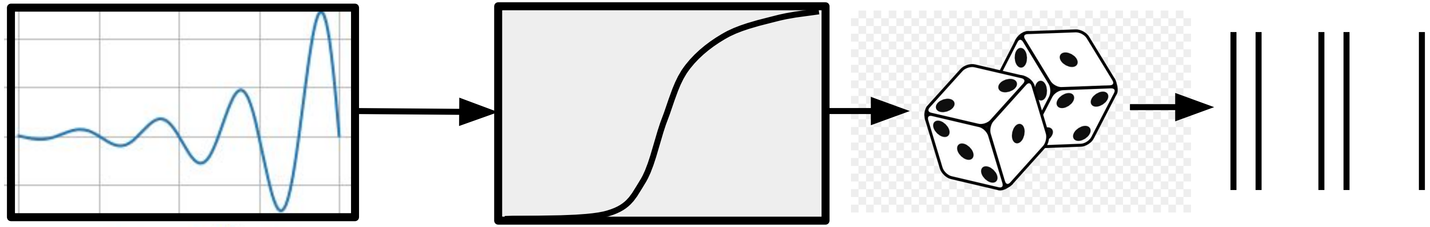
$$r(t) = g(s_0(t))$$

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

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

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





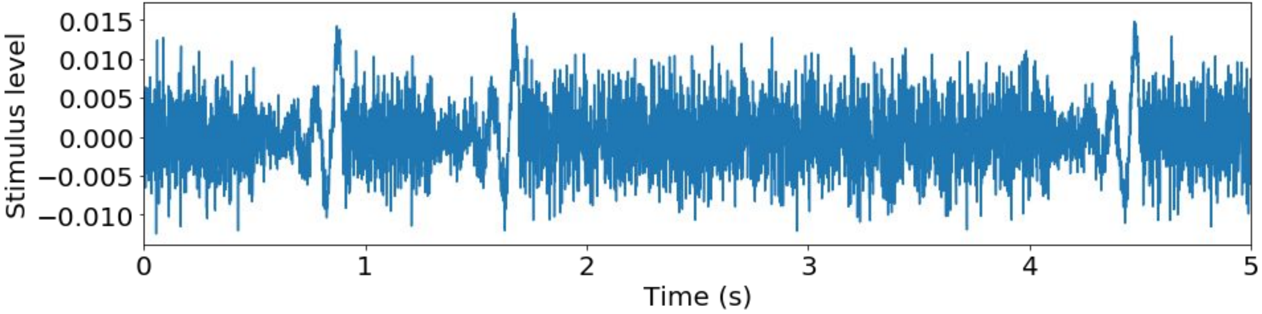
$$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$$

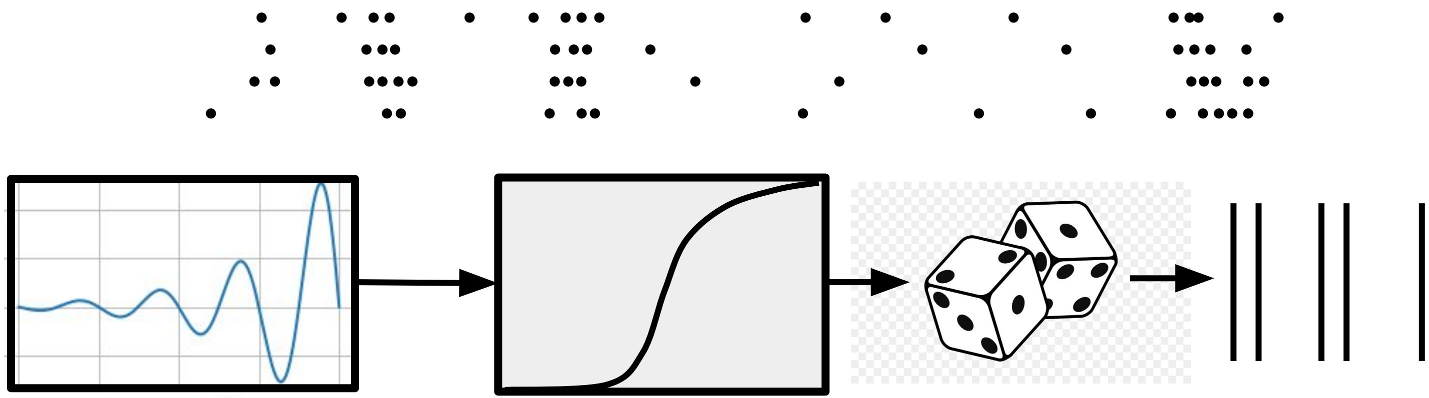
$$r(t) = g(s_0(t))$$

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

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

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





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

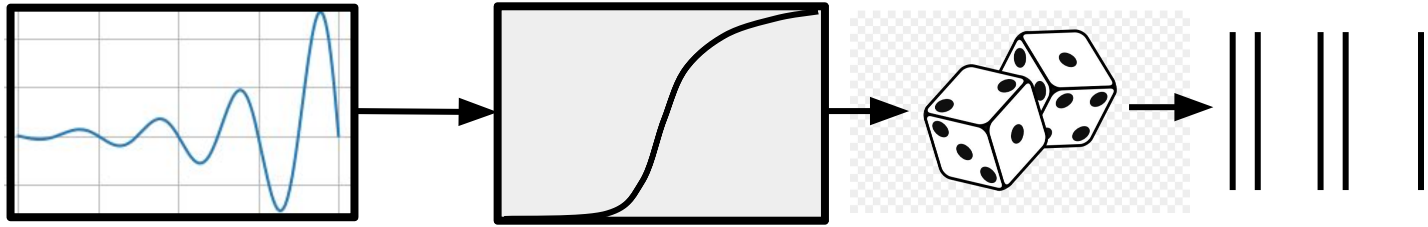
$$r(t) = g(s_0(t))$$

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

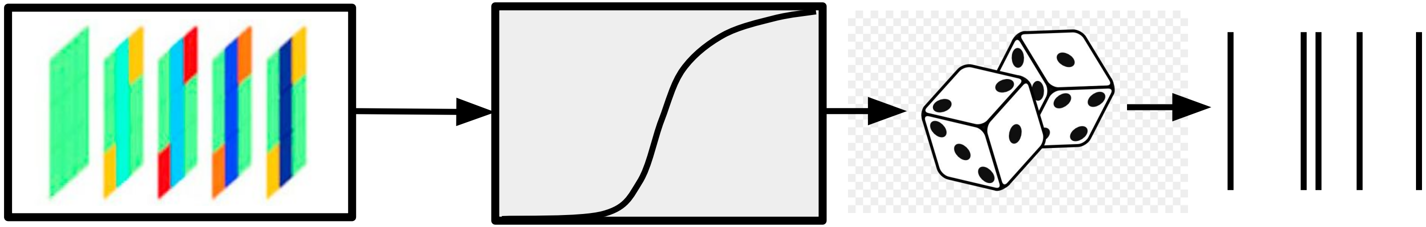
$$y(t) \sim \text{Bernoulli}(p_{spk}(t))$$

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

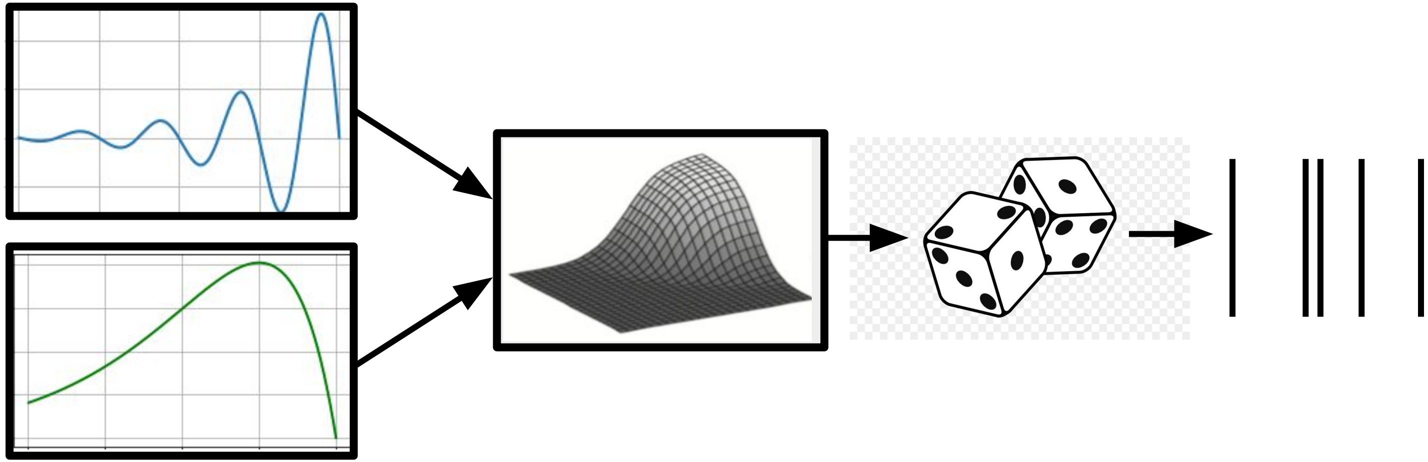
Scalar stim, single filter



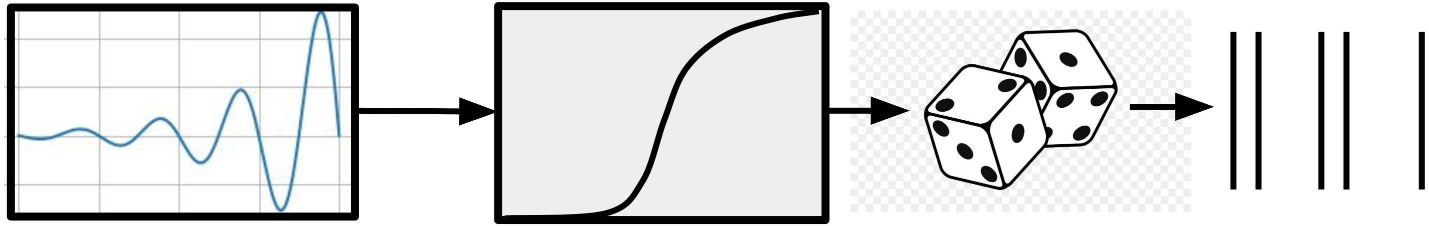
Vector stim, single filter



Scalar or vector stim, multiple filters



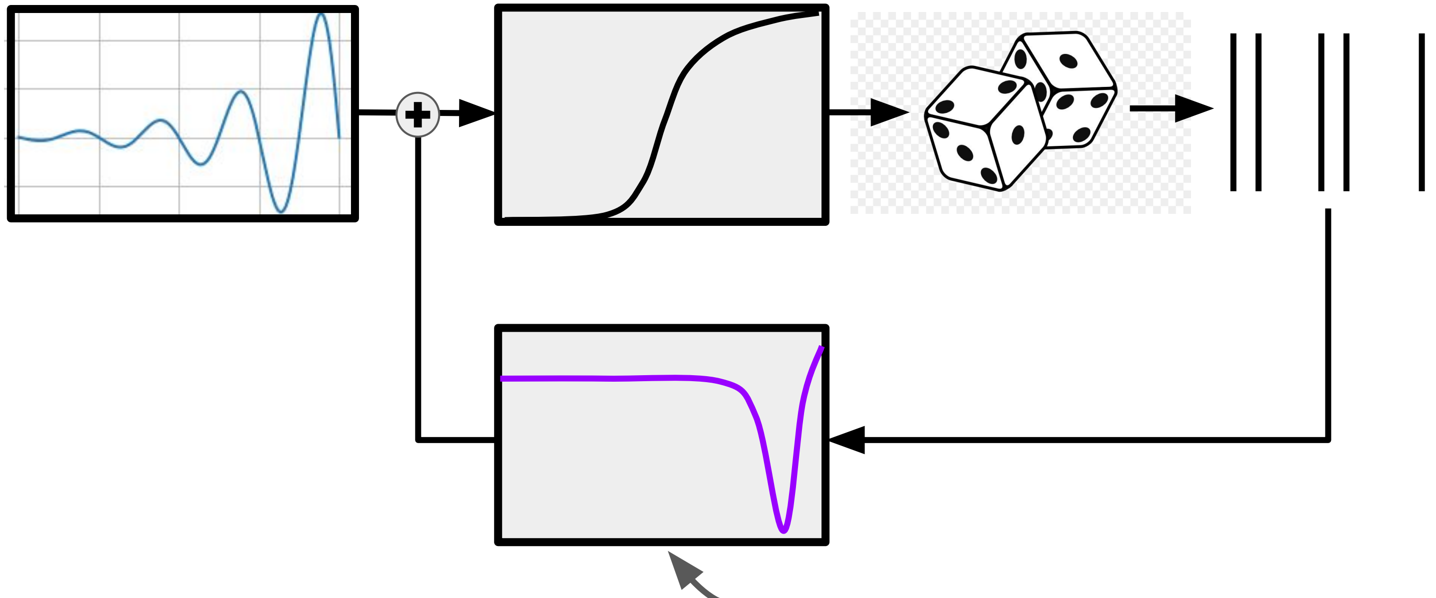
Spiking neuron models: the generalized linear model



How can we account for spike history?

Spiking neuron models: the generalized linear model

Paninski 2004
Pillow 2008

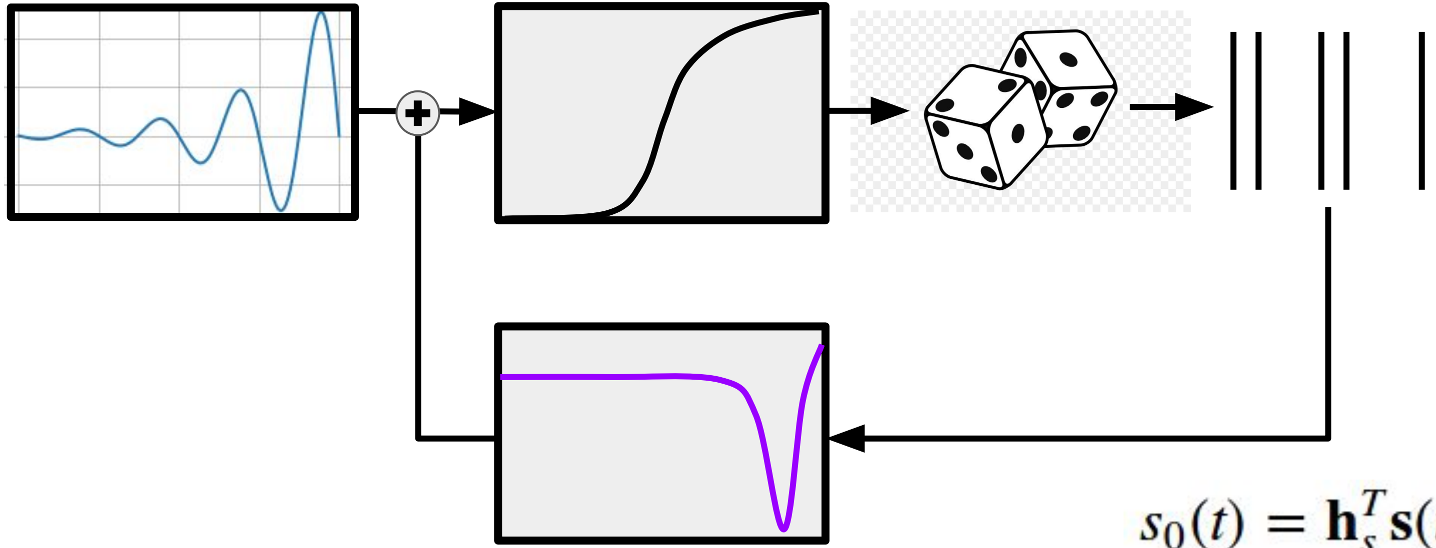


How can we account for spike history?

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

Spiking neuron models: the generalized linear model

Paninski 2004
Pillow 2008



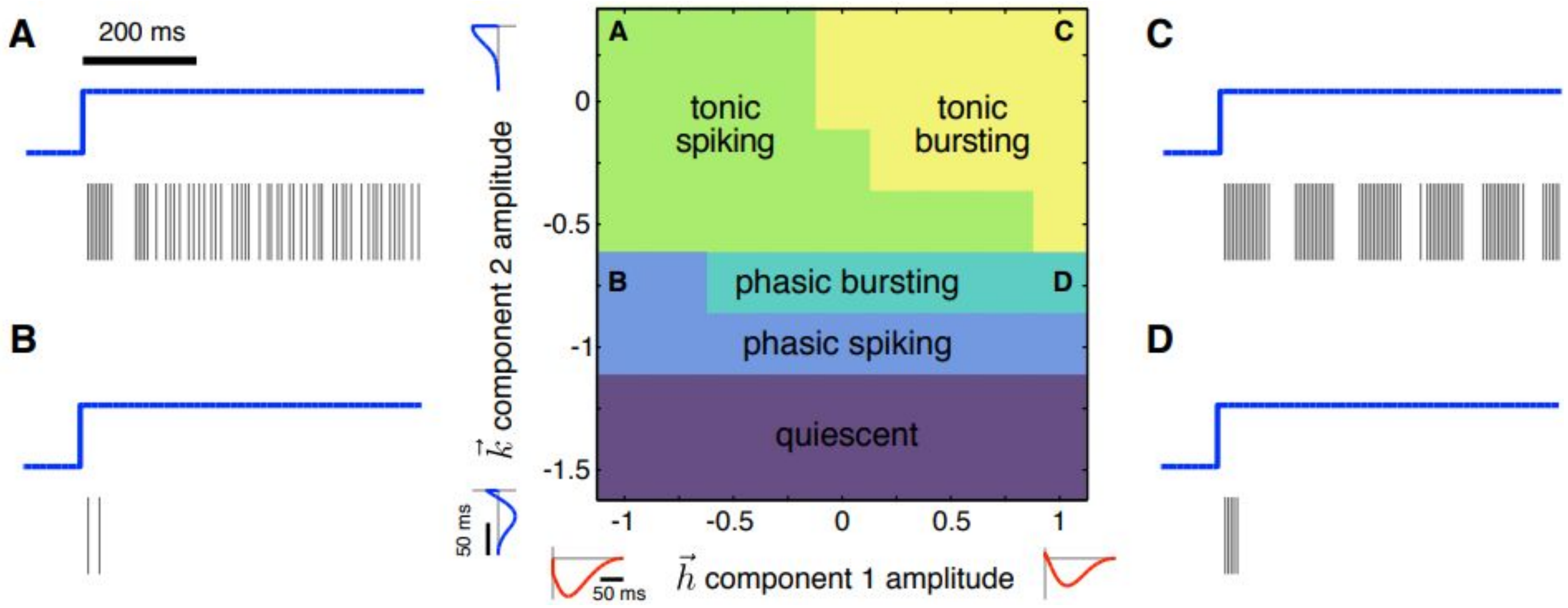
How can we account for spike history?

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.

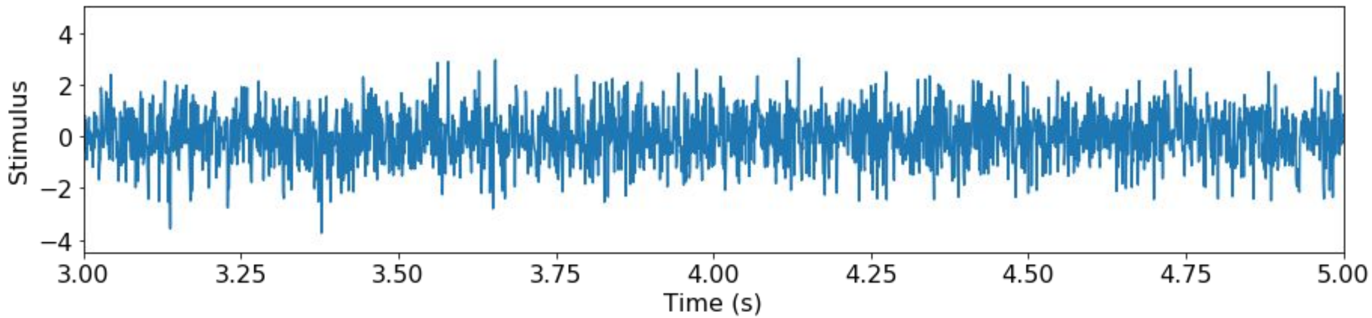


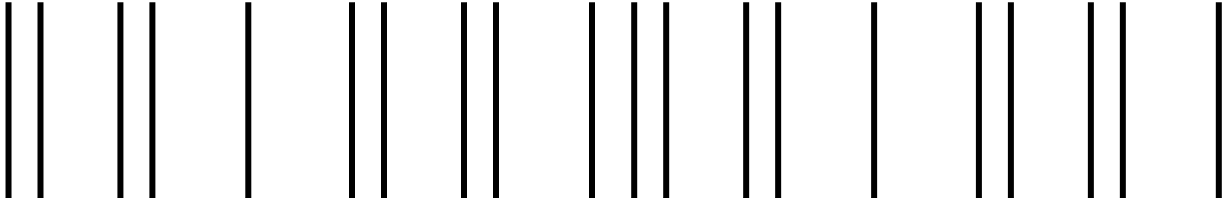
Weber and Pillow 2016

Outline

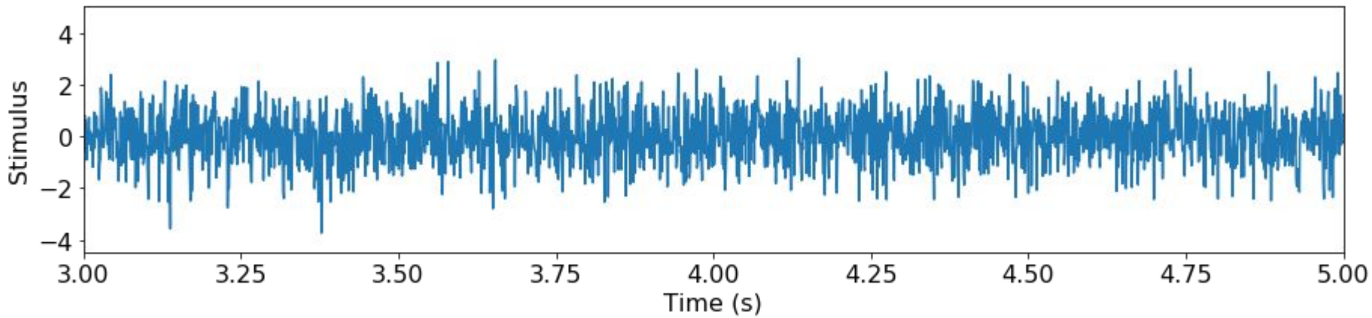
- Crash course in action potentials.
- Basic spike train analysis.
- Spiking neuron models.
- Short problem set time.
- Advanced spike train analysis.
- Other spike-based concepts.
- Full problem set time.

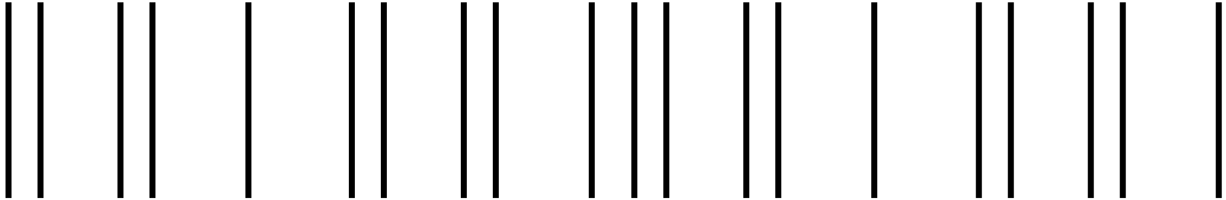
Spike train analysis: identifying filters

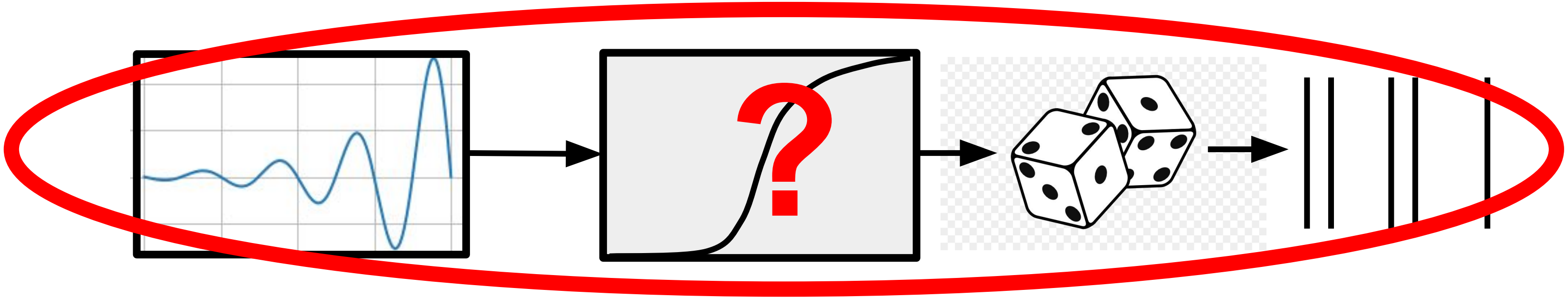




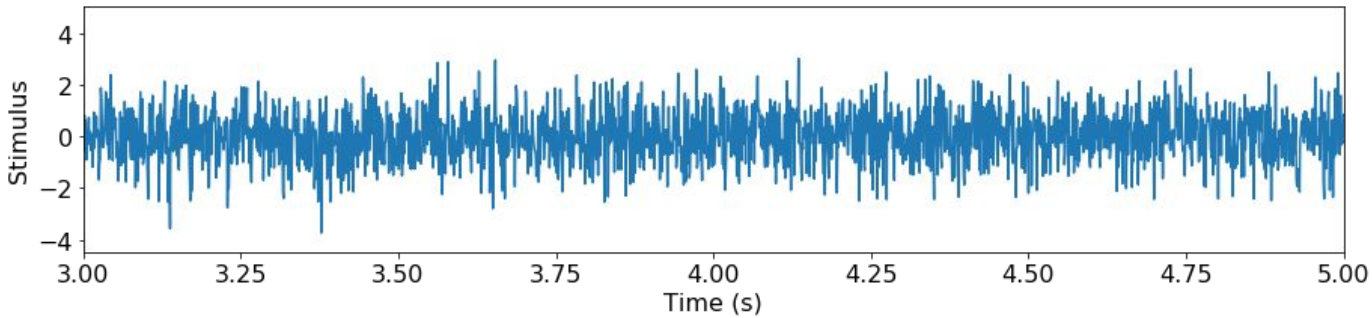
Spike train analysis: identifying filters

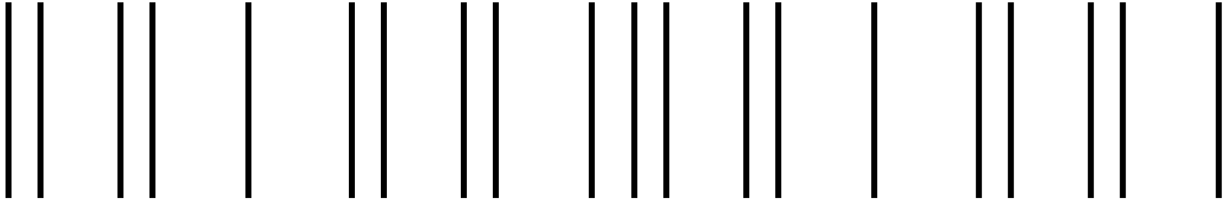


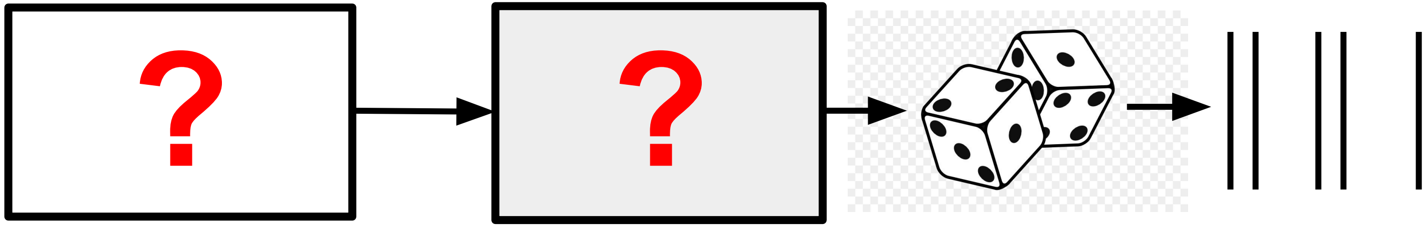




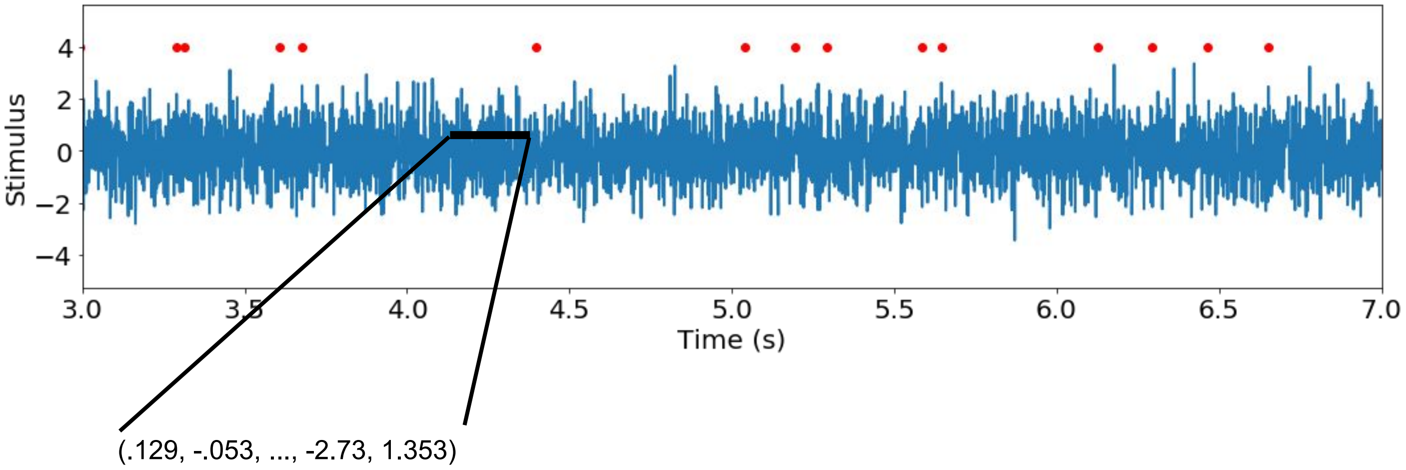
Spike train analysis: identifying filters



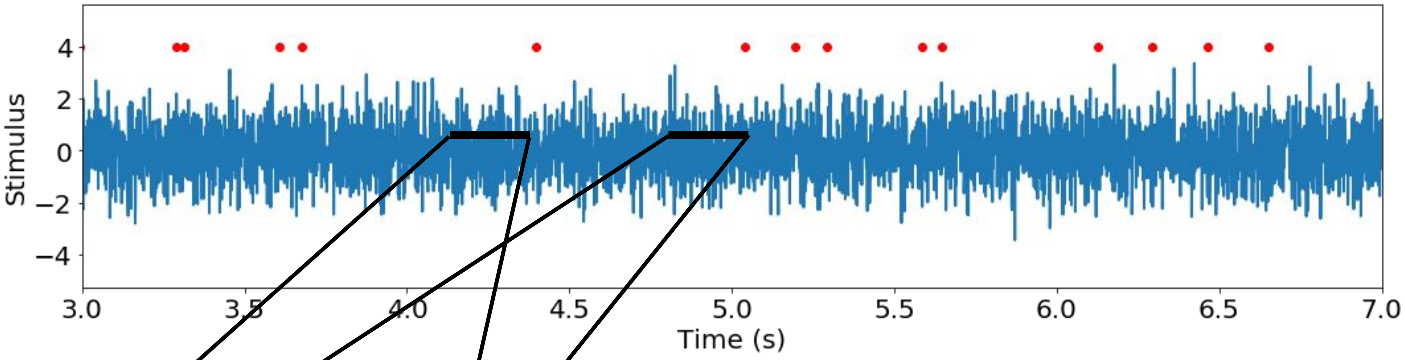




Spike train analysis: the spike-triggered average



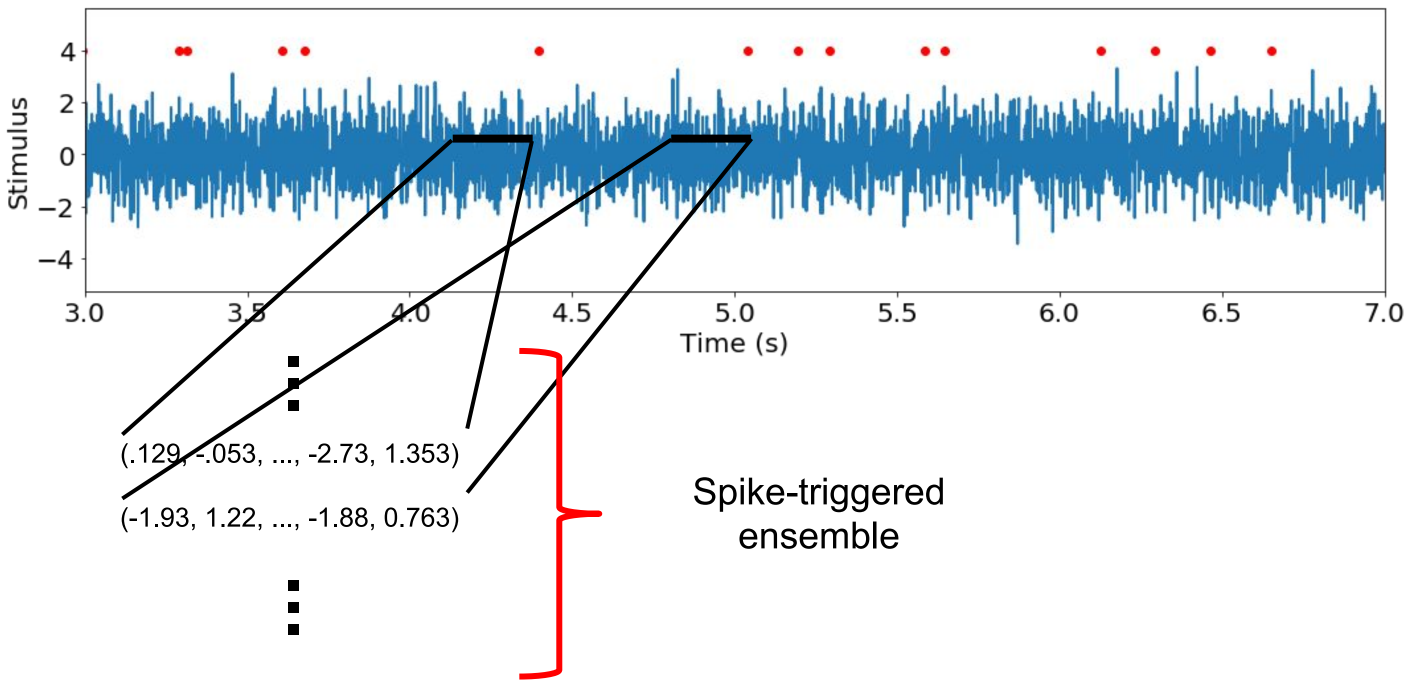
Spike train analysis: the spike-triggered average



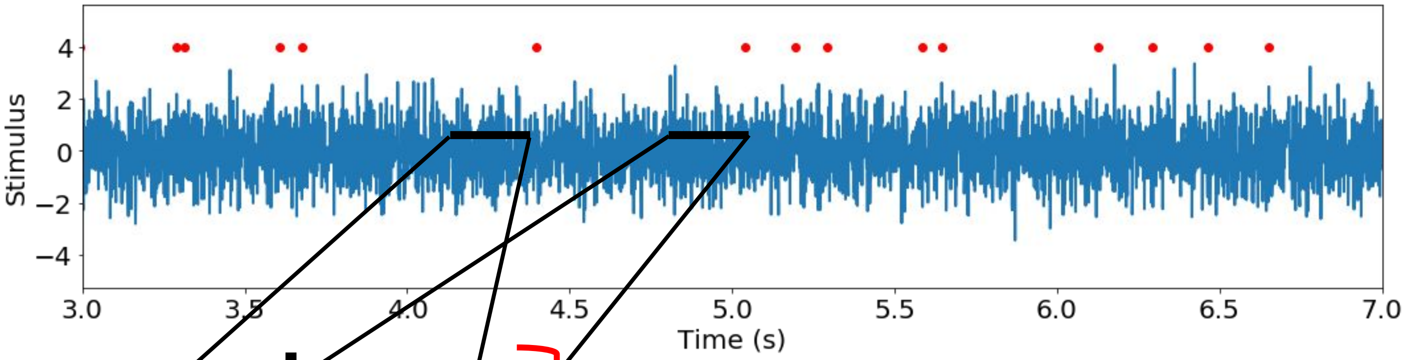
(.129, -.053, ..., -2.73, 1.353)

(-1.93, 1.22, ..., -1.88, 0.763)

Spike train analysis: the spike-triggered average



Spike train analysis: the spike-triggered average



⋮

(.129, -.053, ..., -2.73, 1.353)

(-1.93, 1.22, ..., -1.88, 0.763)

⋮

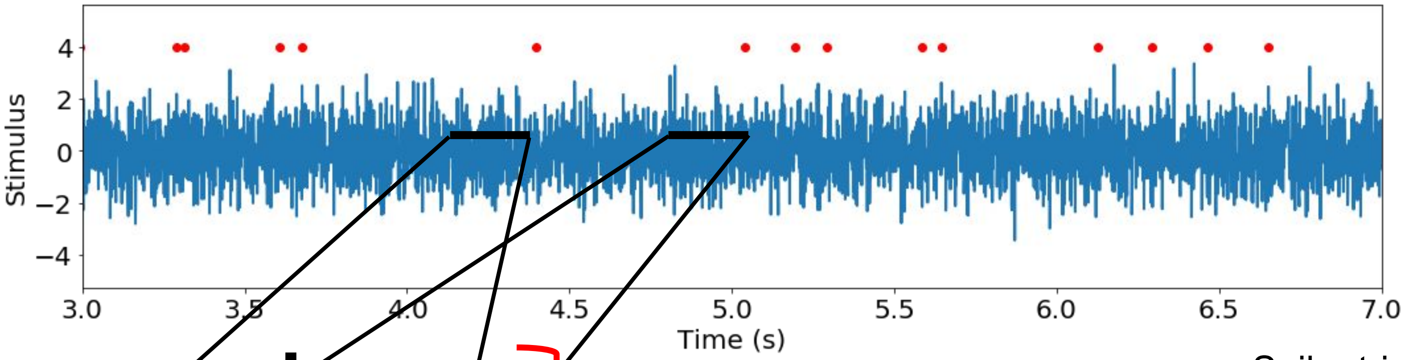
Spike-triggered ensemble

(-1.93, 1.22, ..., -1.88, 0.763)

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

Spike-triggered average

Spike train analysis: the spike-triggered average



(.129, -.053, ..., -2.73, 1.353)

(-1.93, 1.22, ..., -1.88, 0.763)

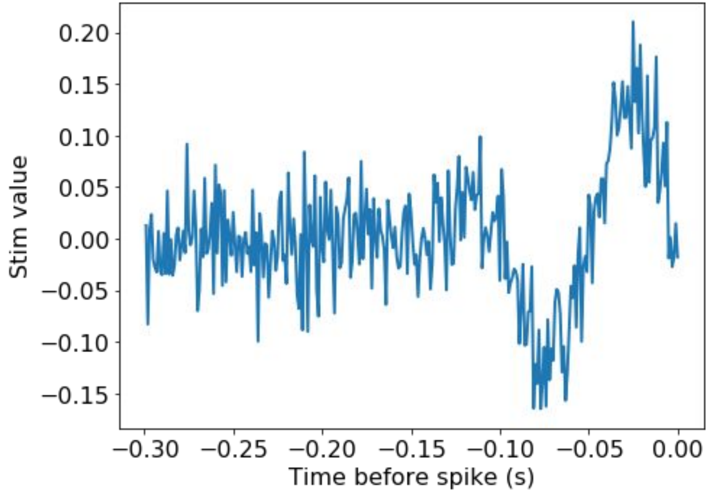
Spike-triggered ensemble

(-1.93, 1.22, ..., -1.88, 0.763)

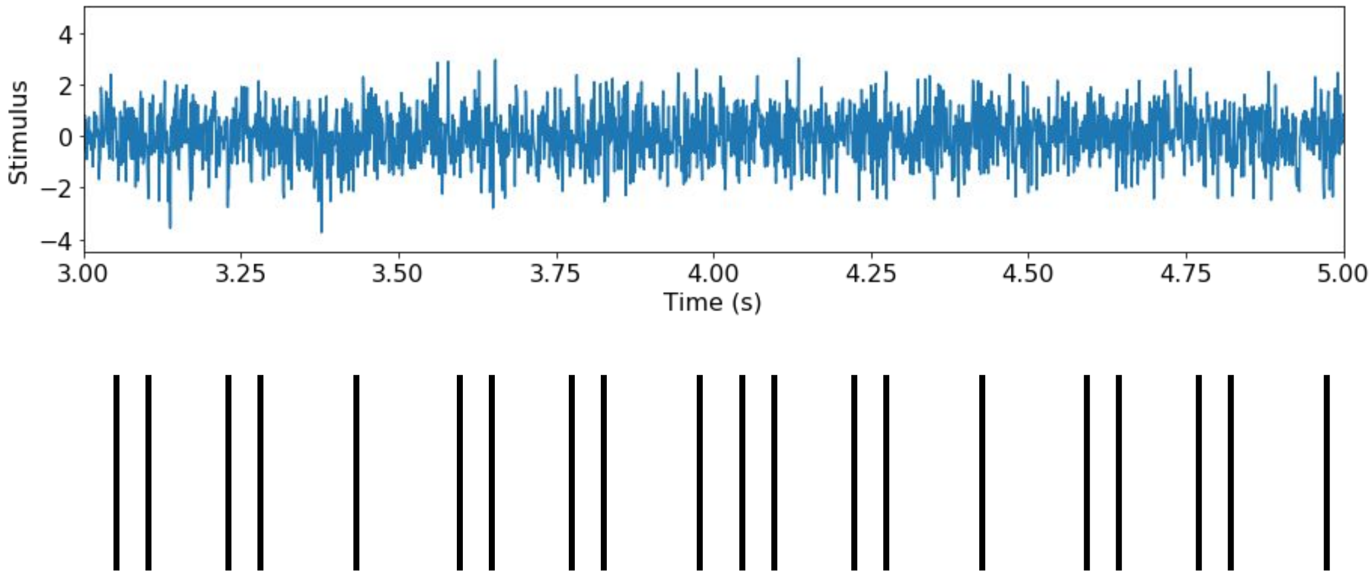
$$s_{sta}(\tau) = \frac{1}{N_{spk}} \sum_{t_{spk}} s(t_{spk} - \tau)$$

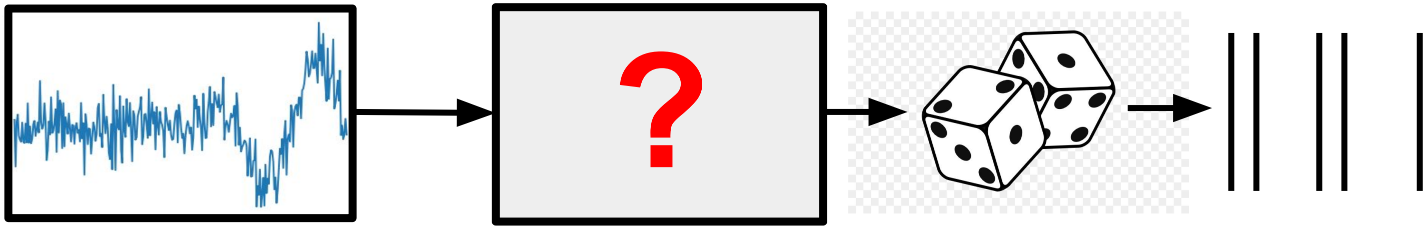
Spike-triggered average

Spike-triggered average (STA)

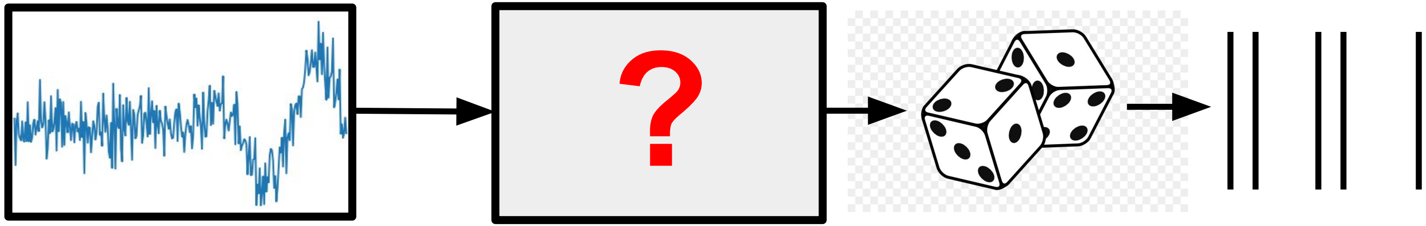


Spike train analysis: the spike-triggered average

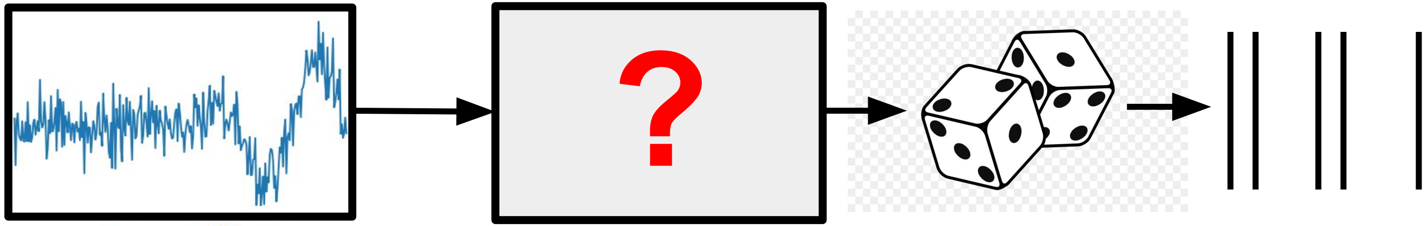




Spike train analysis: the spike-triggered average



Spike train analysis: the spike-triggered average



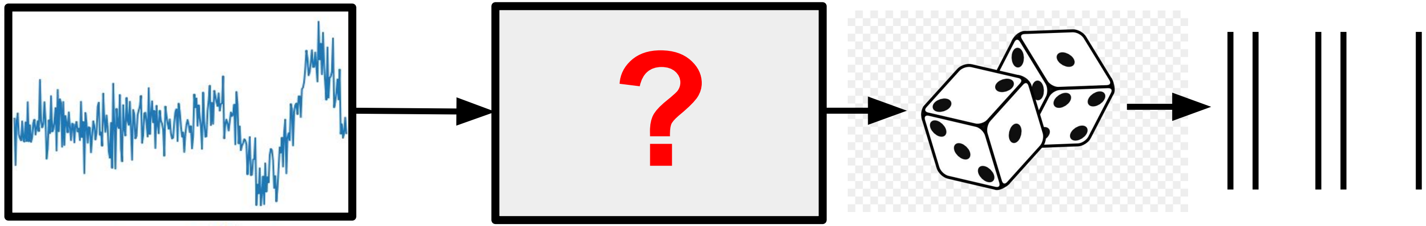
$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$

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

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

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

Spike train analysis: the spike-triggered average



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

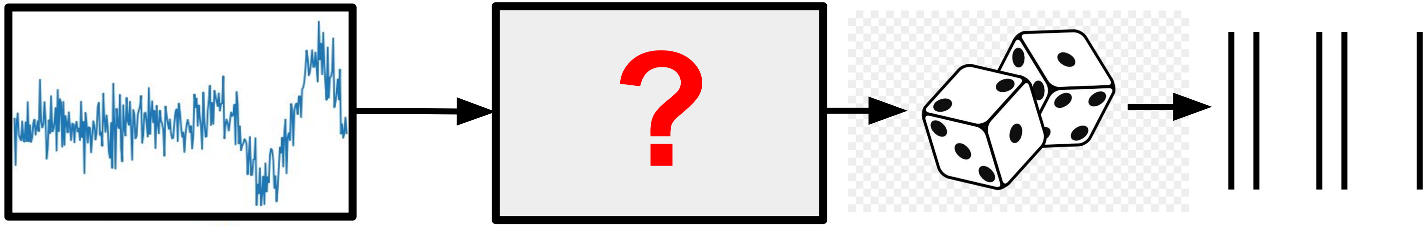
$r(t) = g(s_0(t))$

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

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

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

Spike train analysis: the spike-triggered average



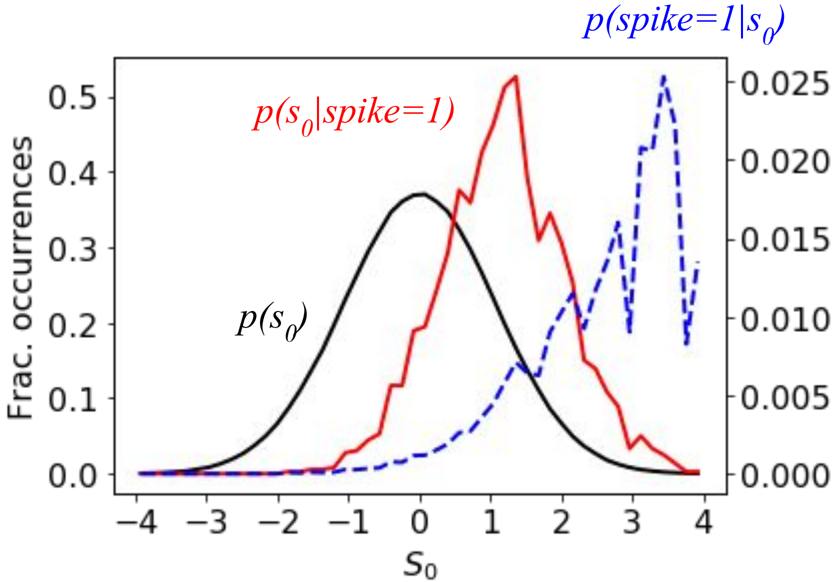
$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$

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

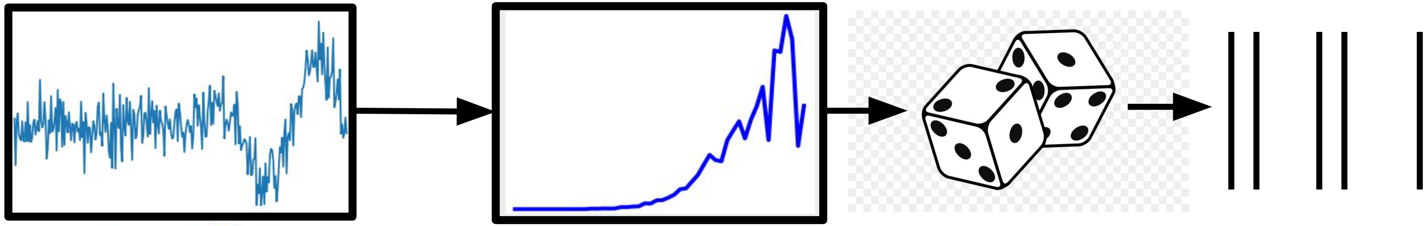
$p_{spk}(t) = r(t)\Delta t$

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

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



Spike train analysis: the spike-triggered average



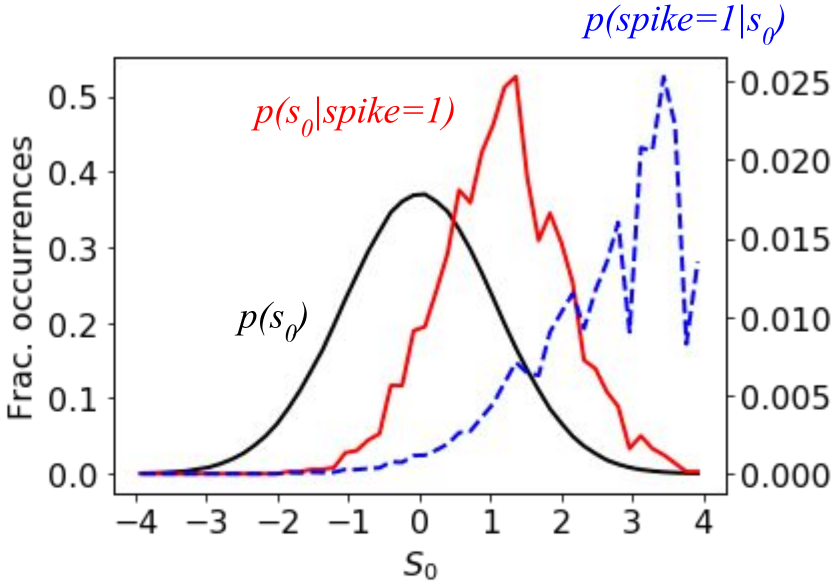
$$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$$

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

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

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

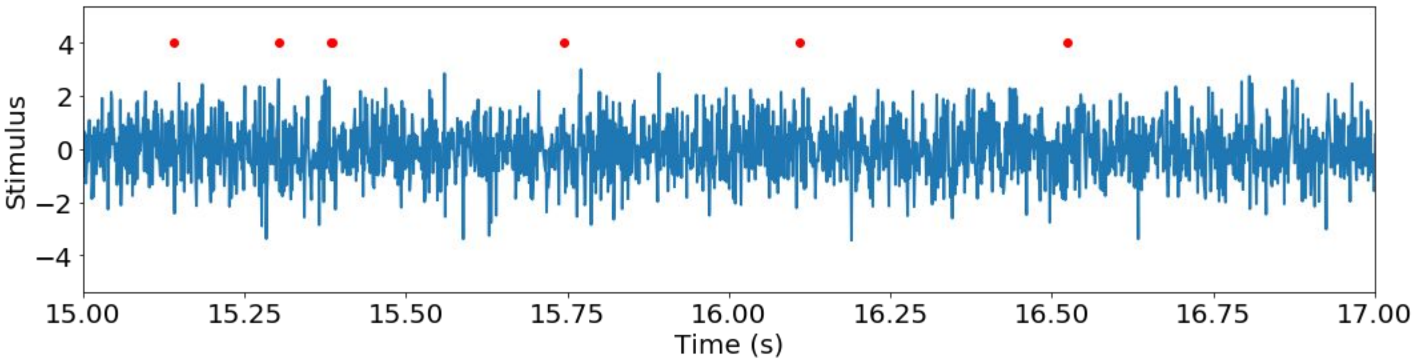
$$p(spike = 1|s_0) = \frac{p(s_0|spike = 1)p(spike = 1)}{p(s_0)}$$

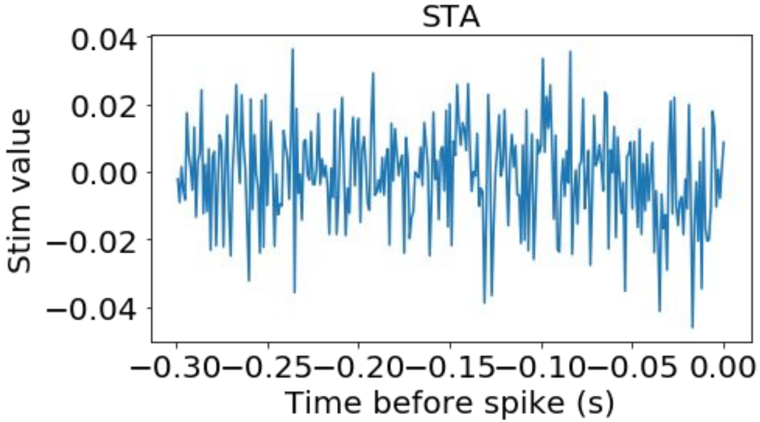


Spike train analysis: the spike-triggered average

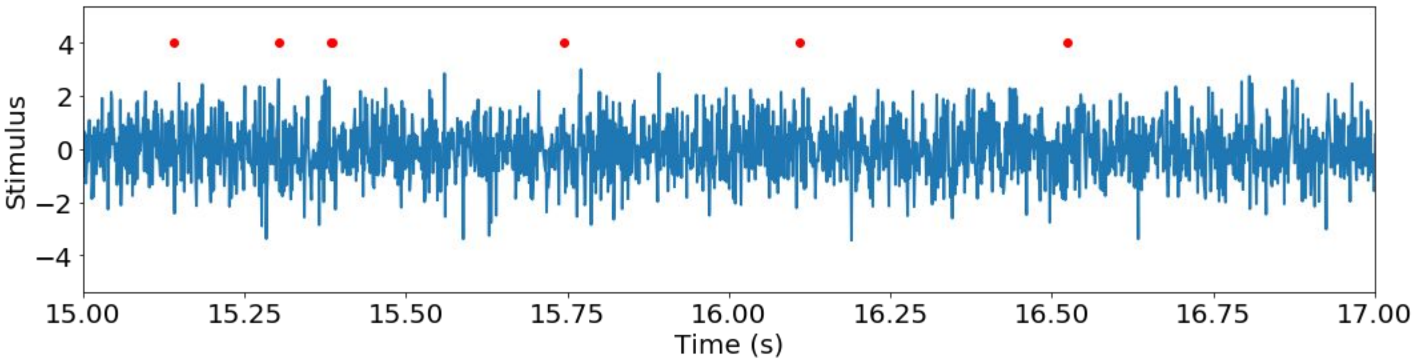
Will spike-triggered average always be informative?

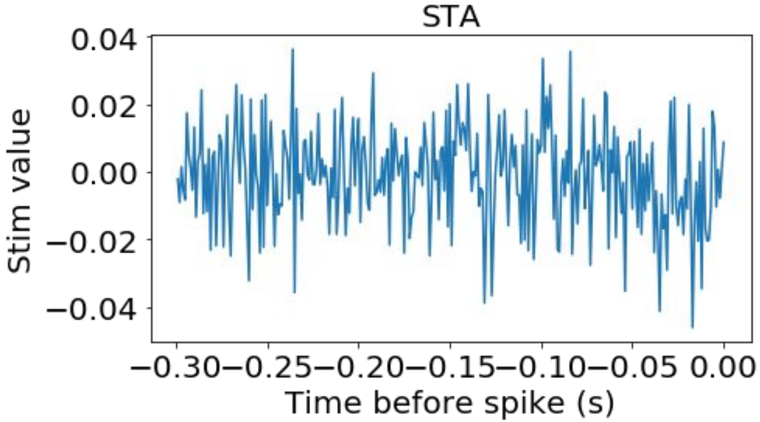
Spike train analysis: spike-triggered covariance analysis





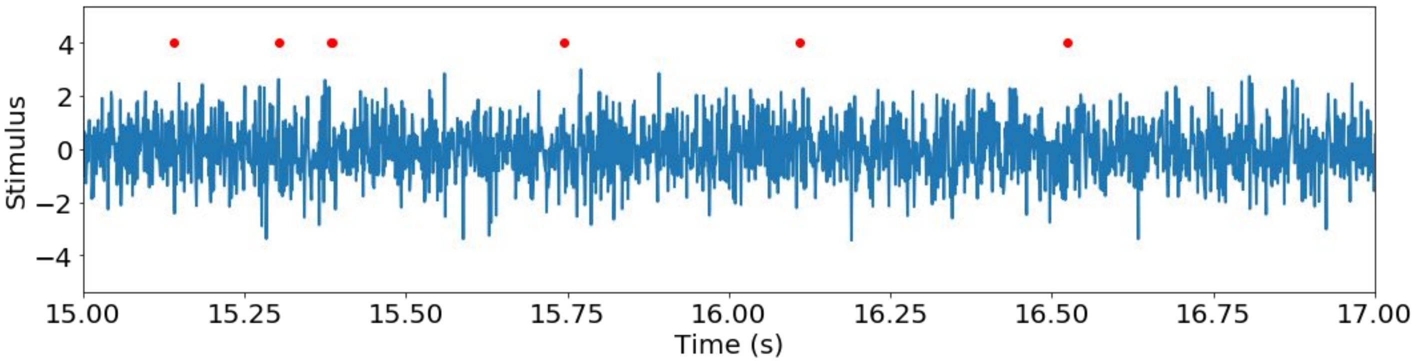
Spike train analysis: spike-triggered covariance analysis





STA not very interesting. What next?

Spike train analysis: spike-triggered covariance analysis



⋮

(.129, -.053, ..., -2.73, 1.353)

(-1.93, 1.22, ..., -1.88, 0.763)

⋮

Spike-triggered ensemble

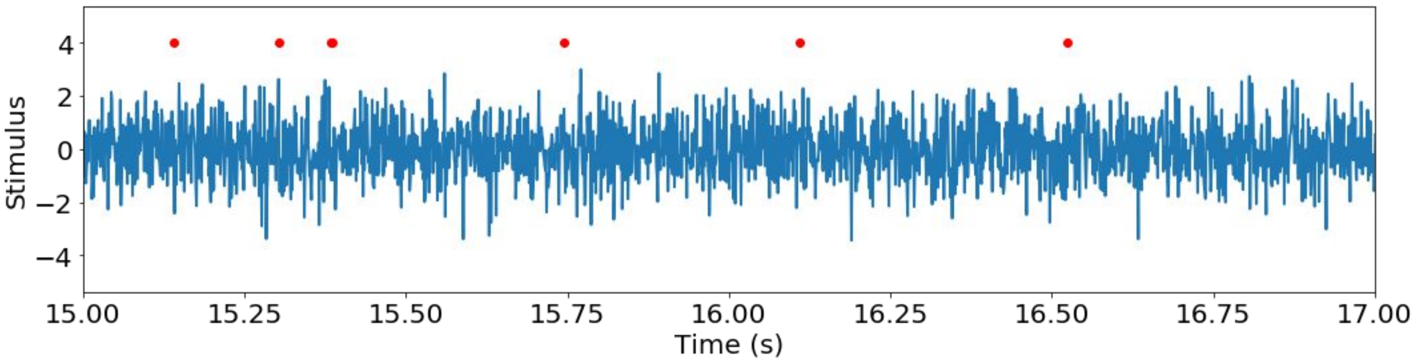
STA asks how ***first-order*** structure of spike-triggered ensemble differs from prior.

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



⋮

(.129, -.053, ..., -2.73, 1.353)

(-1.93, 1.22, ..., -1.88, 0.763)

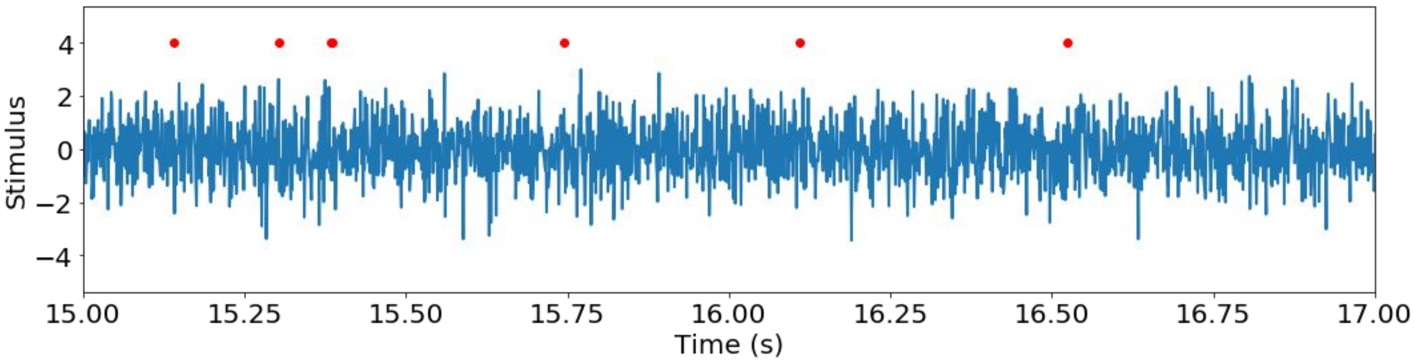
⋮

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, 1.353)

(-1.93, 1.22, ..., -1.88, 0.763)

⋮

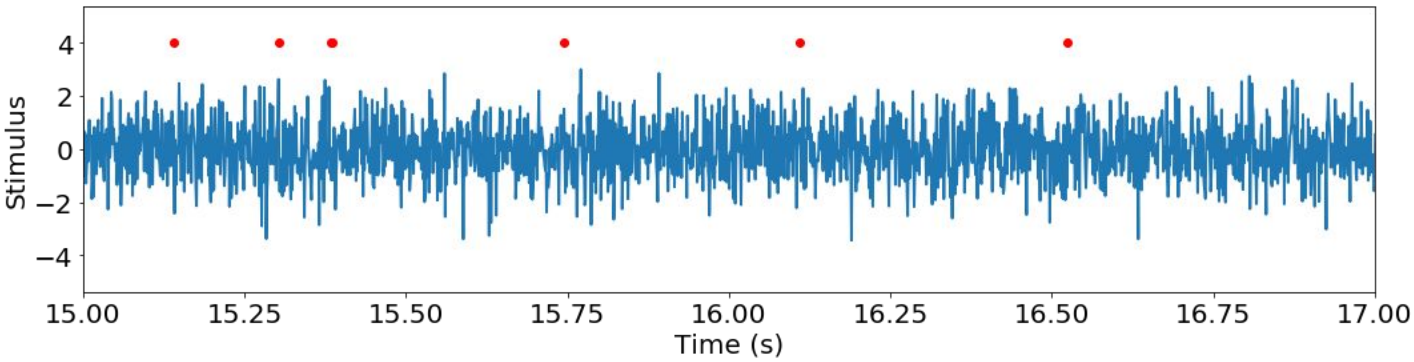
Spike-triggered ensemble

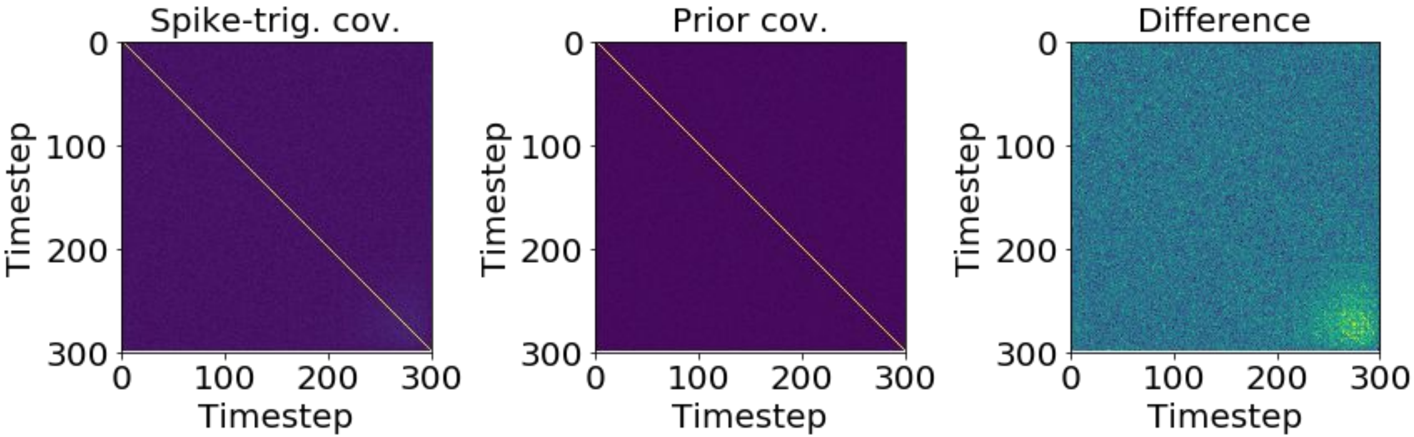
$$K^{spk}_{\tau,\tau'} = \mathrm{COV}(s(\tau), s(\tau'))$$
$$= \mathrm{E}_{t_{spk}}[(s(t_{spk}-\tau) - \mathrm{E}[s(t_{spk}-\tau)])(s(t_{spk}-\tau') - \mathrm{E}[s(t_{spk}-\tau)])]$$

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

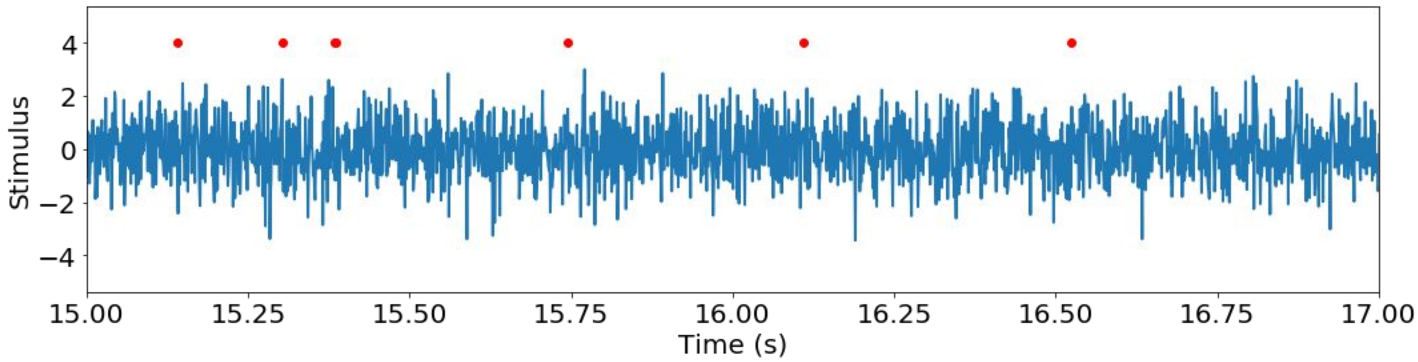
$$K^{diff} = K^{spk} - K^{pr}$$

Spike train analysis: spike-triggered covariance analysis

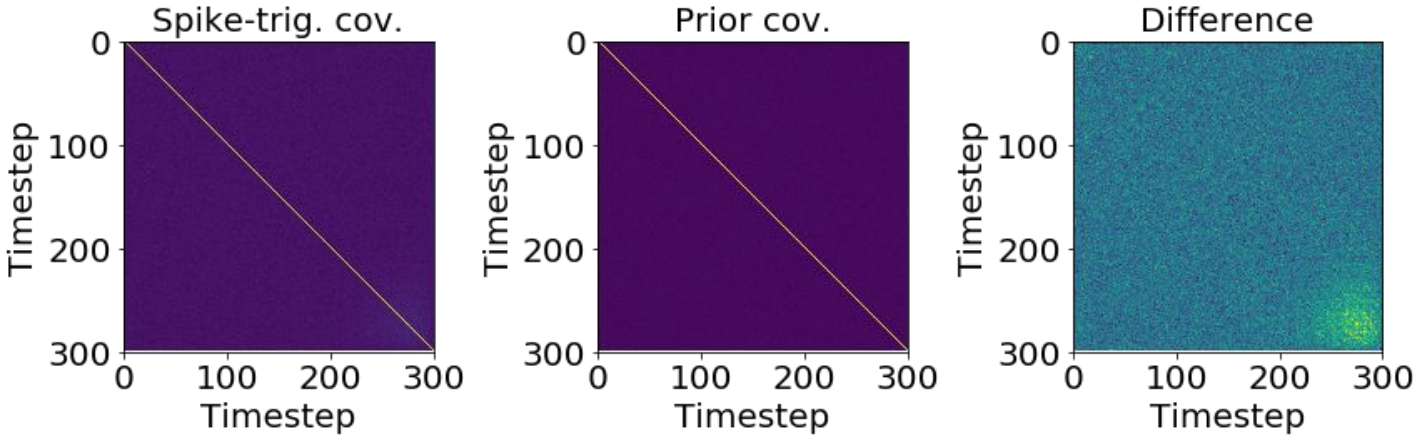




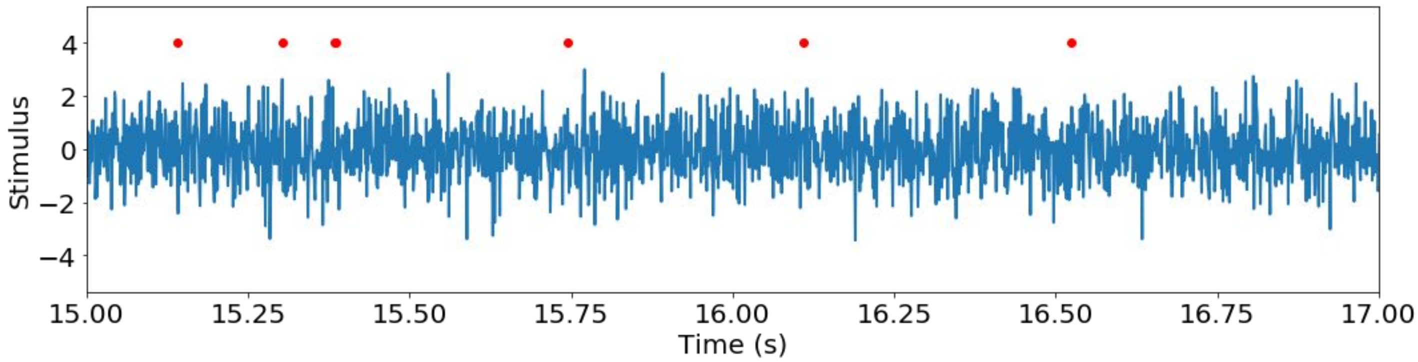
Spike train analysis: spike-triggered covariance analysis



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

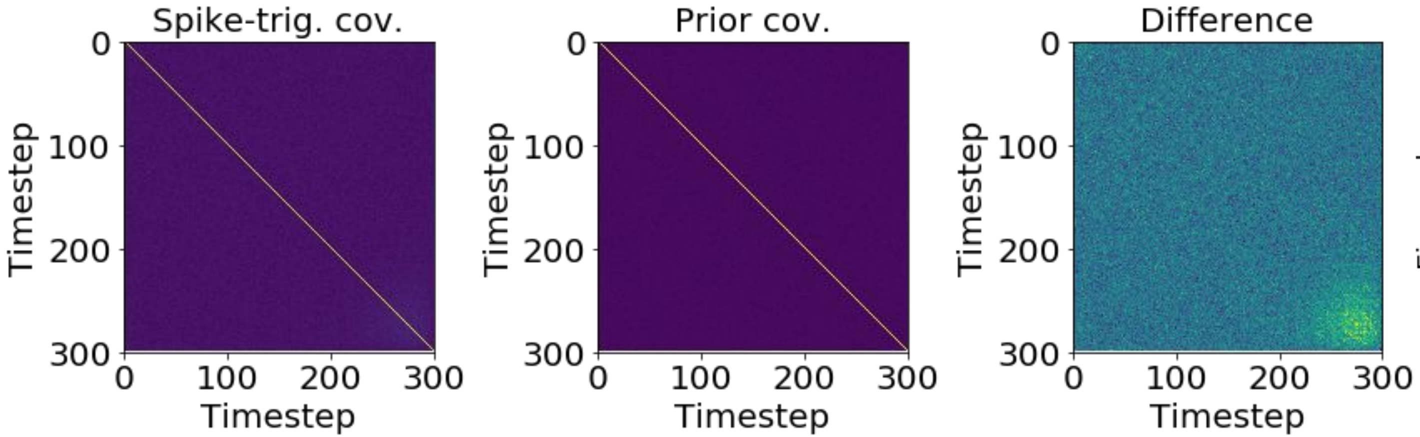


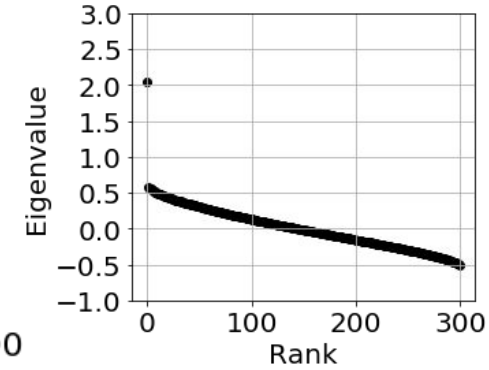
Spike train analysis: spike-triggered covariance analysis



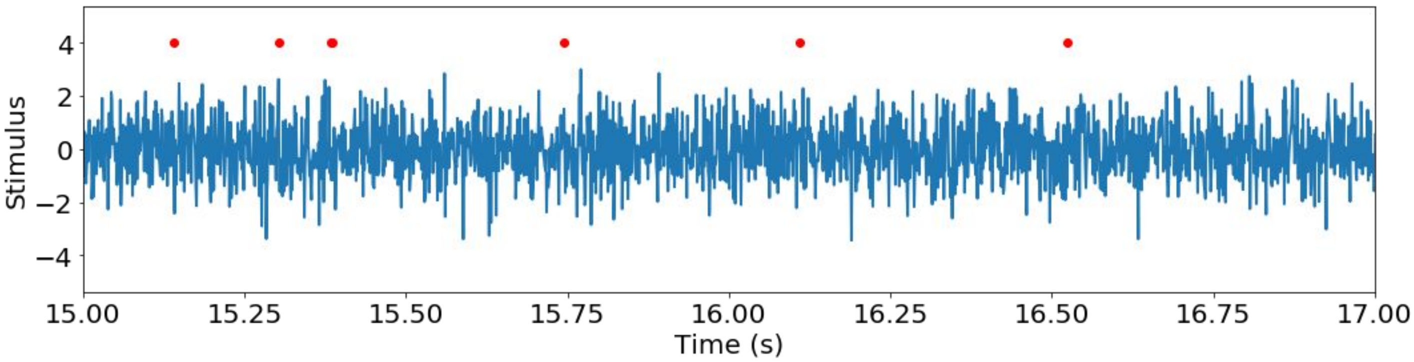
How should we quantify structure of K^{diff}?

Eigenvectors!





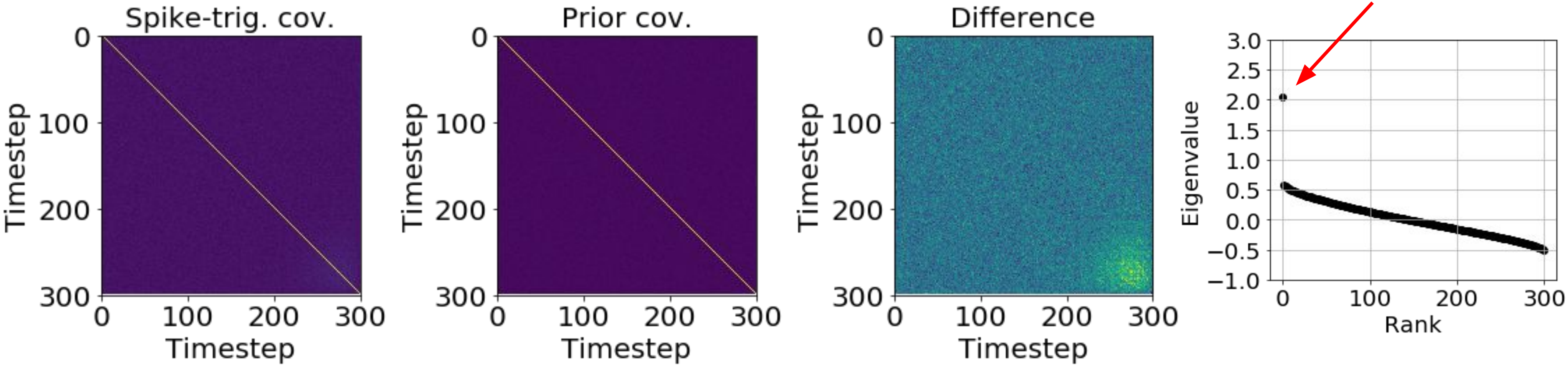
Spike train analysis: spike-triggered covariance analysis



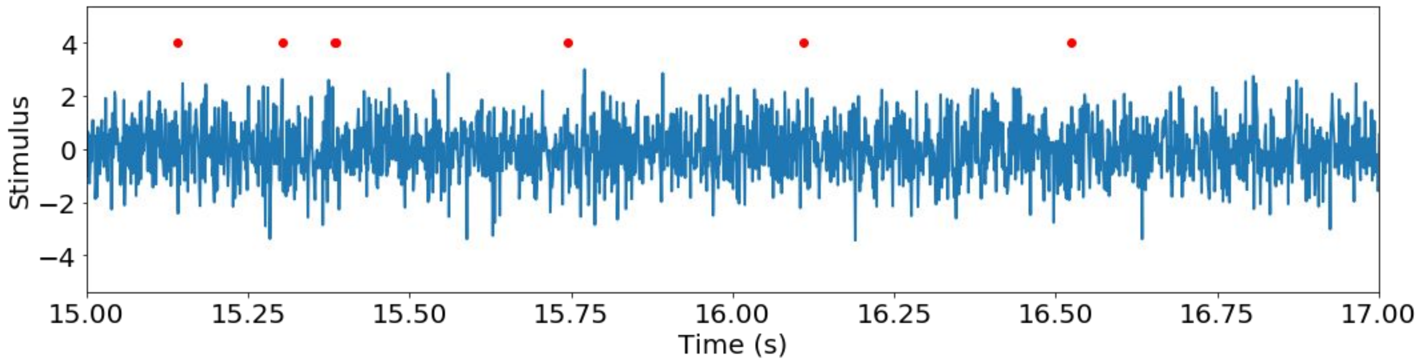
How should we quantify structure of K^{diff}?

Eigenvectors!

1 “mode” of interest



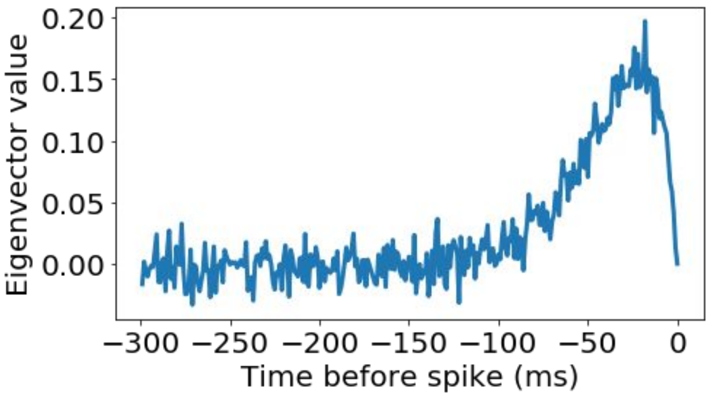
Spike train analysis: spike-triggered covariance analysis



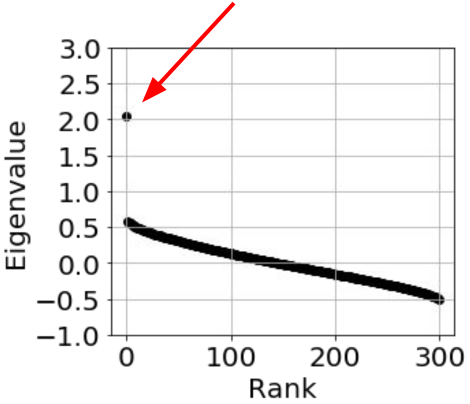
How should we quantify structure of K^{diff}?

Eigenvectors!

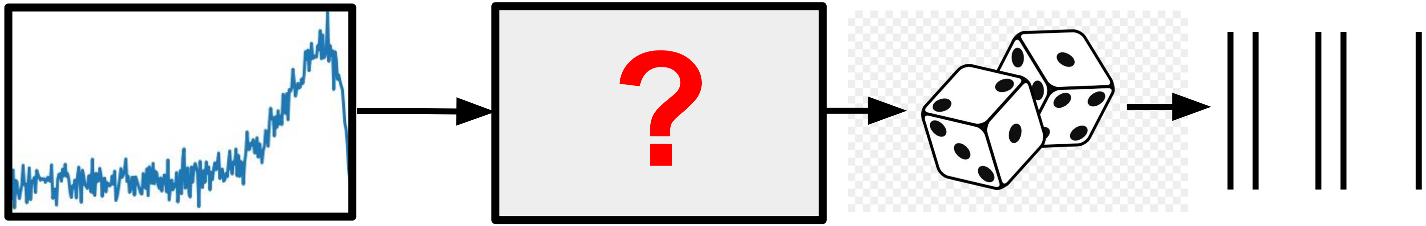
Top mode of K^{diff}



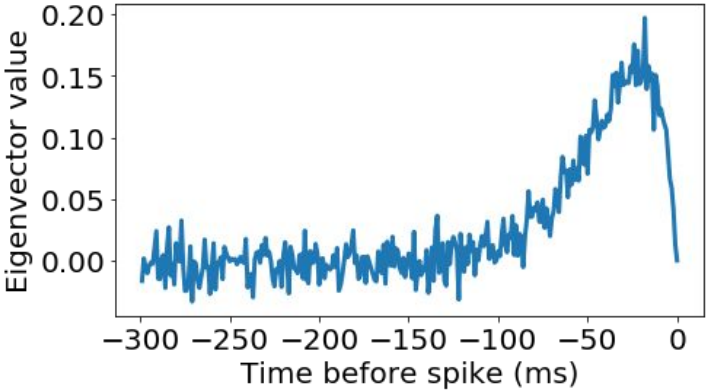
1 “mode” of interest



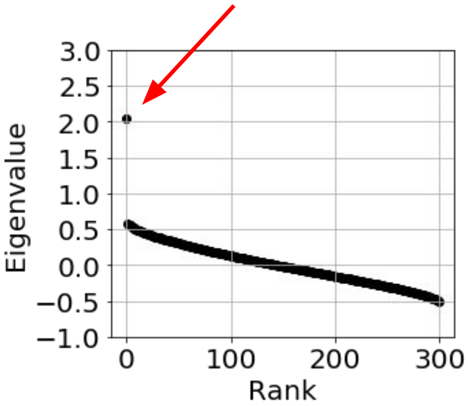
Spike train analysis: spike-triggered covariance analysis



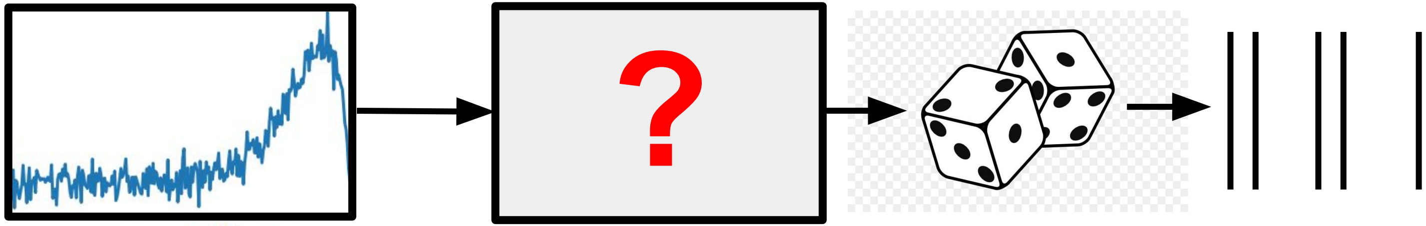
Top mode of K^{diff}



1 “mode” of interest



Spike train analysis: spike-triggered covariance analysis



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

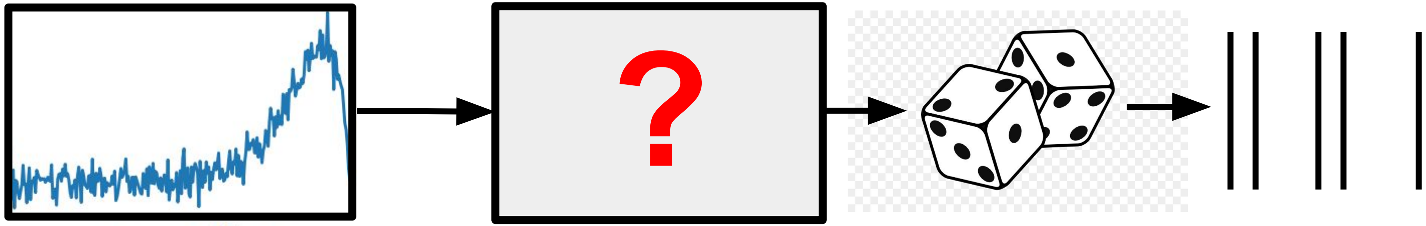
$r(t) = g(s_0(t))$

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

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

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

Spike train analysis: spike-triggered covariance analysis



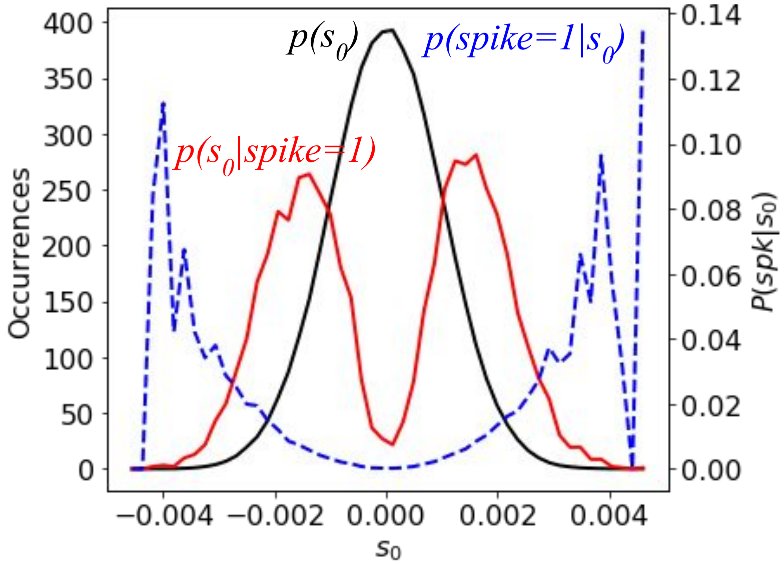
$s_0(t) = \mathbf{h}^T \mathbf{s}(t)$

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

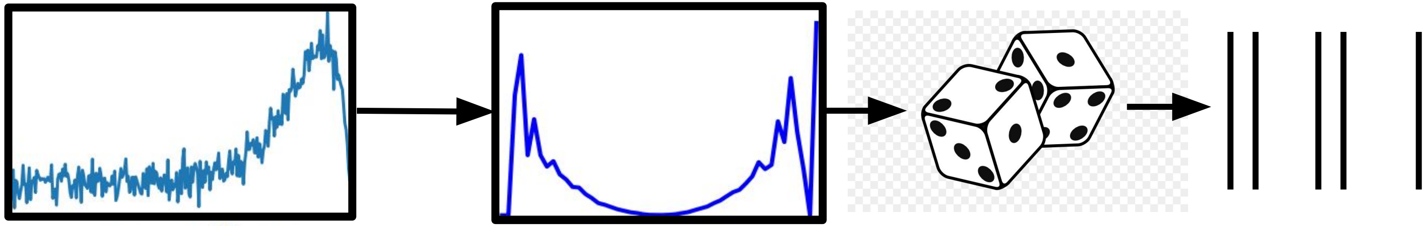
$p_{spk}(t) = r(t)\Delta t$

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

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



Spike train analysis: spike-triggered covariance analysis



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

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

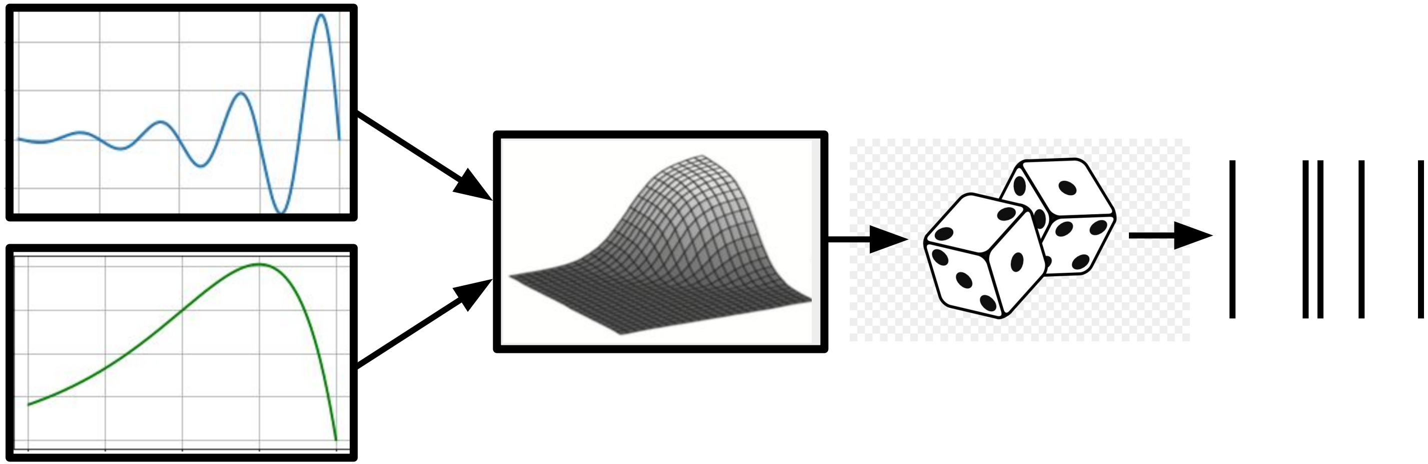
$$p_{spk}(t) = r(t)\Delta t$$

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

Spike train analysis: spike-triggered covariance analysis

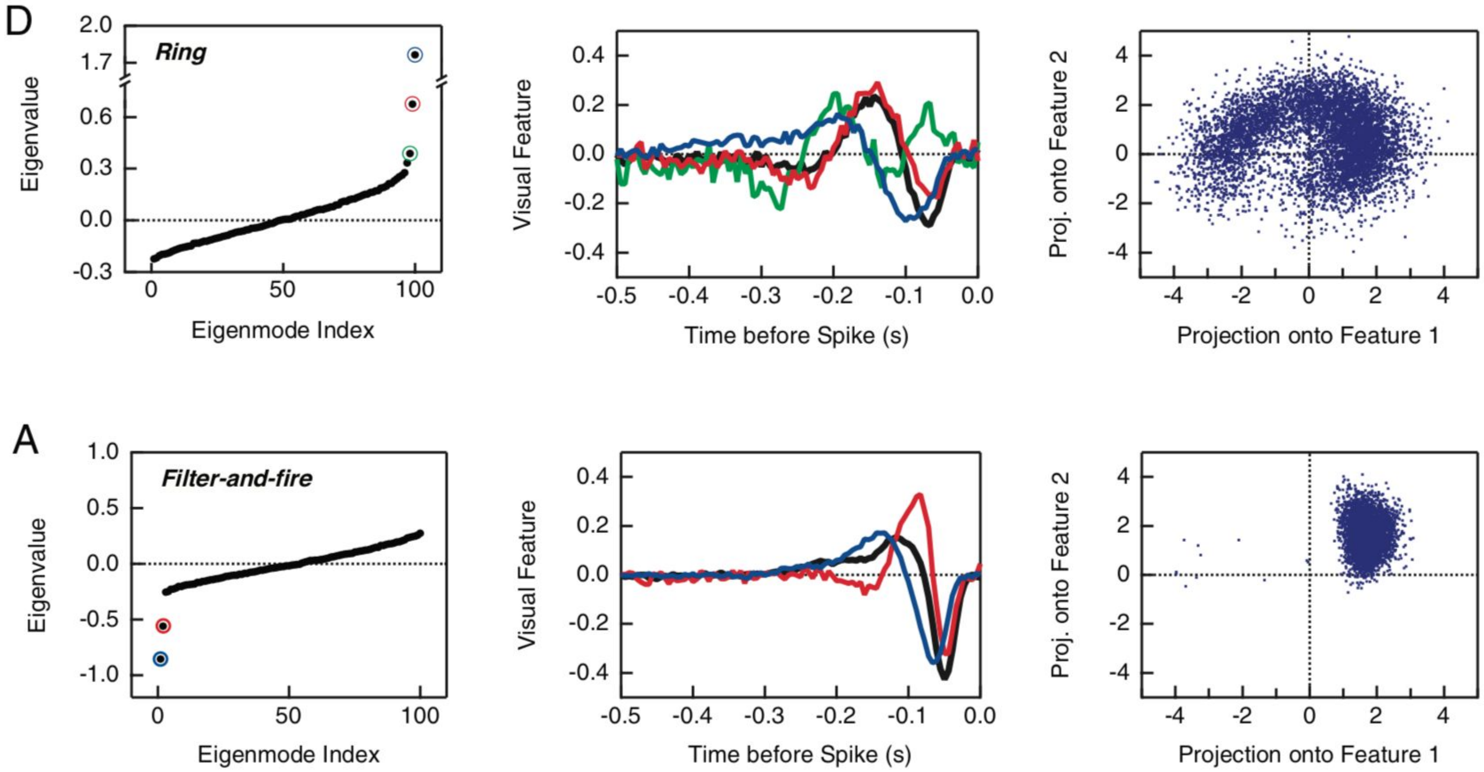
Can also have multiple top eigenmodes yielding multiple filters

Scalar or vector stim,
multiple filters



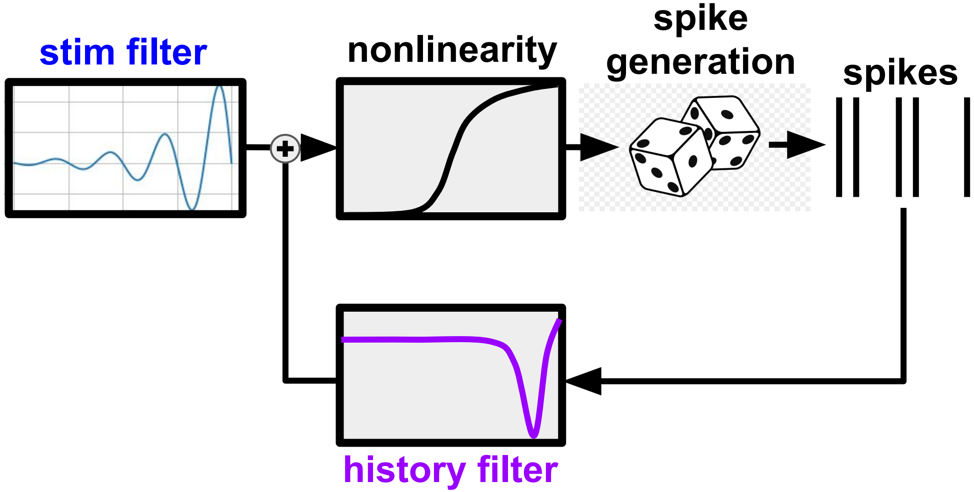
Spike train analysis: spike-triggered covariance analysis

Salamander retinal ganglion cells



Fairhall et al. 2006

Spike train analysis: generalized linear models



spike train generation

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

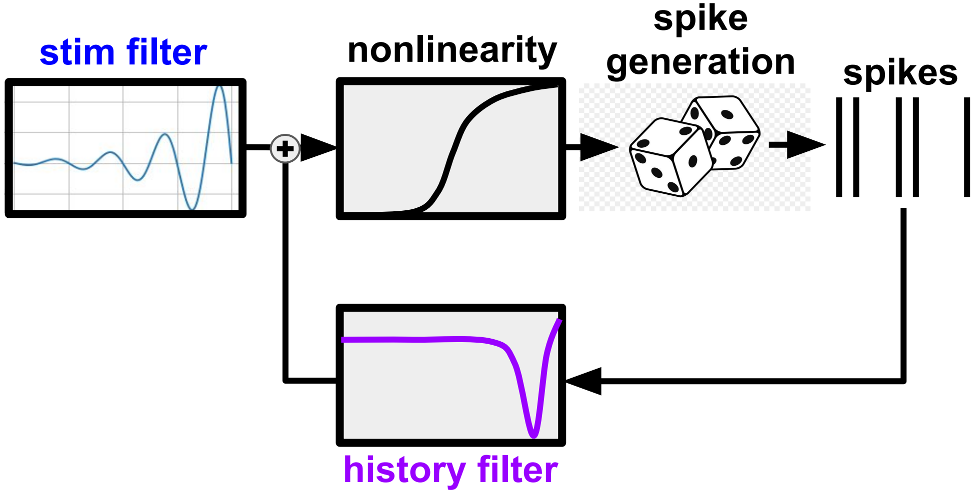
$$y_0(t) = \mathbf{h}_y^T \mathbf{y}(t)$$

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

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

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

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

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

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

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

Outline

- Crash course in 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: information in spikes

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

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.

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

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

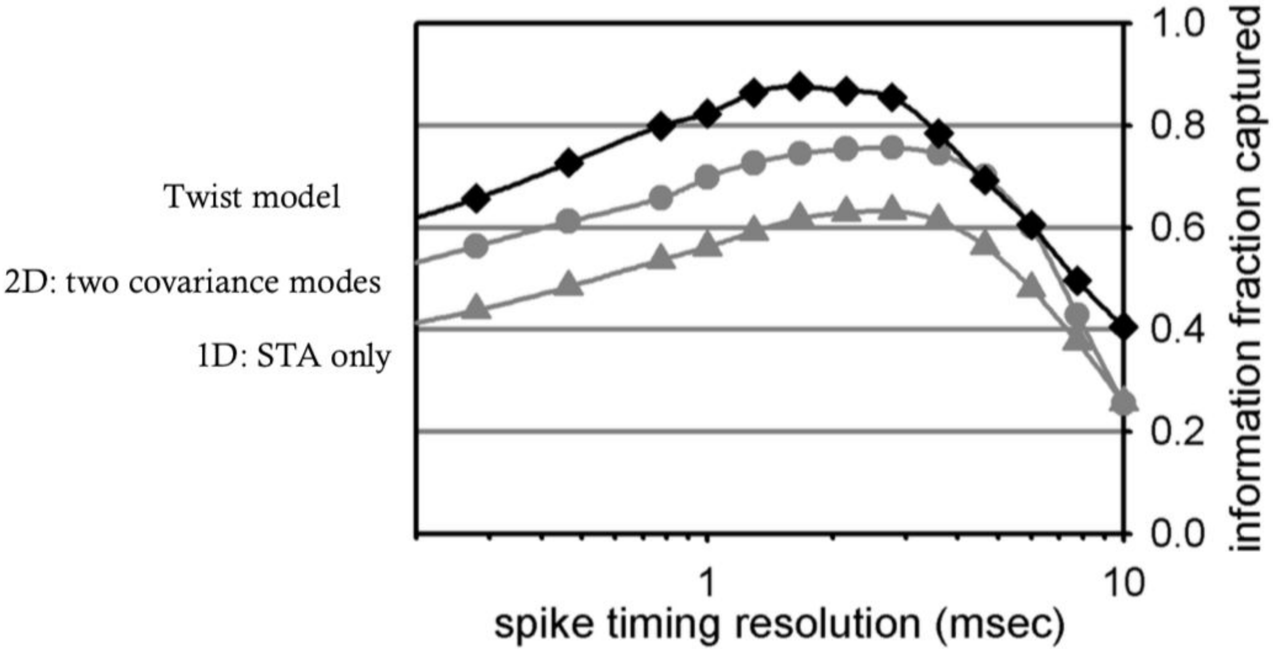
By definition Bayes' rule Dimensionality reduction

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

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-timing-dependent plasticity
- Inferring network structure from spikes
- Spike sequences

Problem set part 2

https://github.com/rkp8000/imbizo_2019_spikes_tutorial

problems_2.ipynb

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