Spike Statistics

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Computational Neuroscience (Lecture 6, 2024/2025)

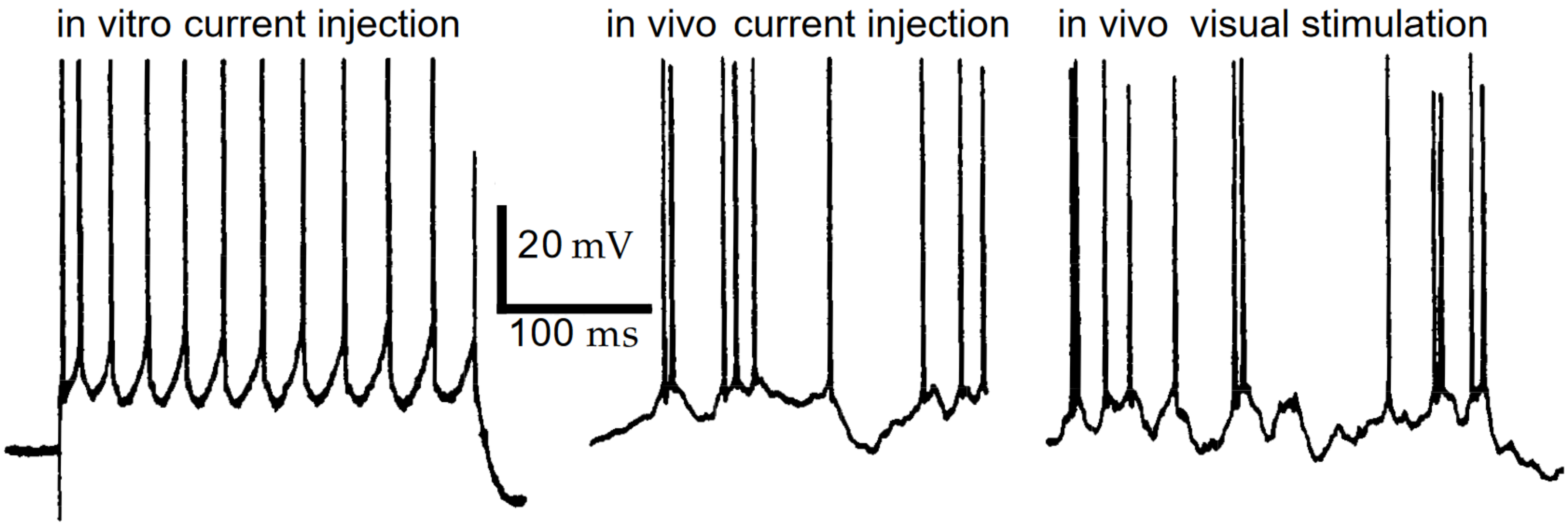
Overview of Lecture

- Neuronal spiking patterns
- Poisson statistics
- Generating Poisson spike statistics in a leaky integrate and fire neuron

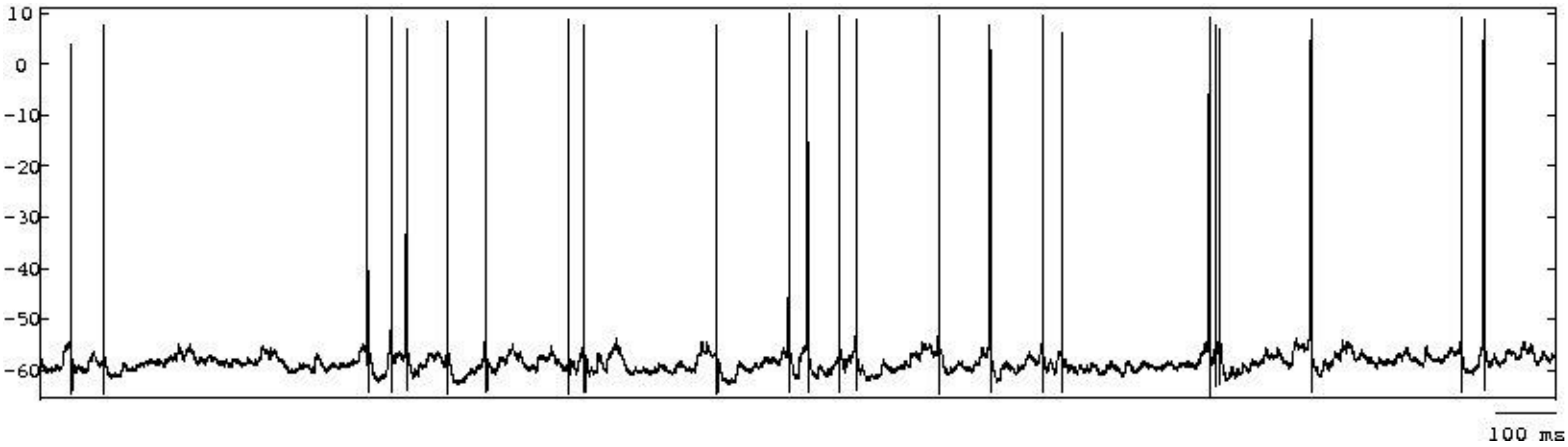
Spiking Statistics

What patterns of spiking activity do neurons produce? What causes neurons to produce these patterns? How do these spike patterns change in different conditions?

Why do we care? 1) This is how neurons represent and transmit information 2) It gives insight into the operating regime of the brain 3) It's the only way we have to study the brain…



Spiking Statistics



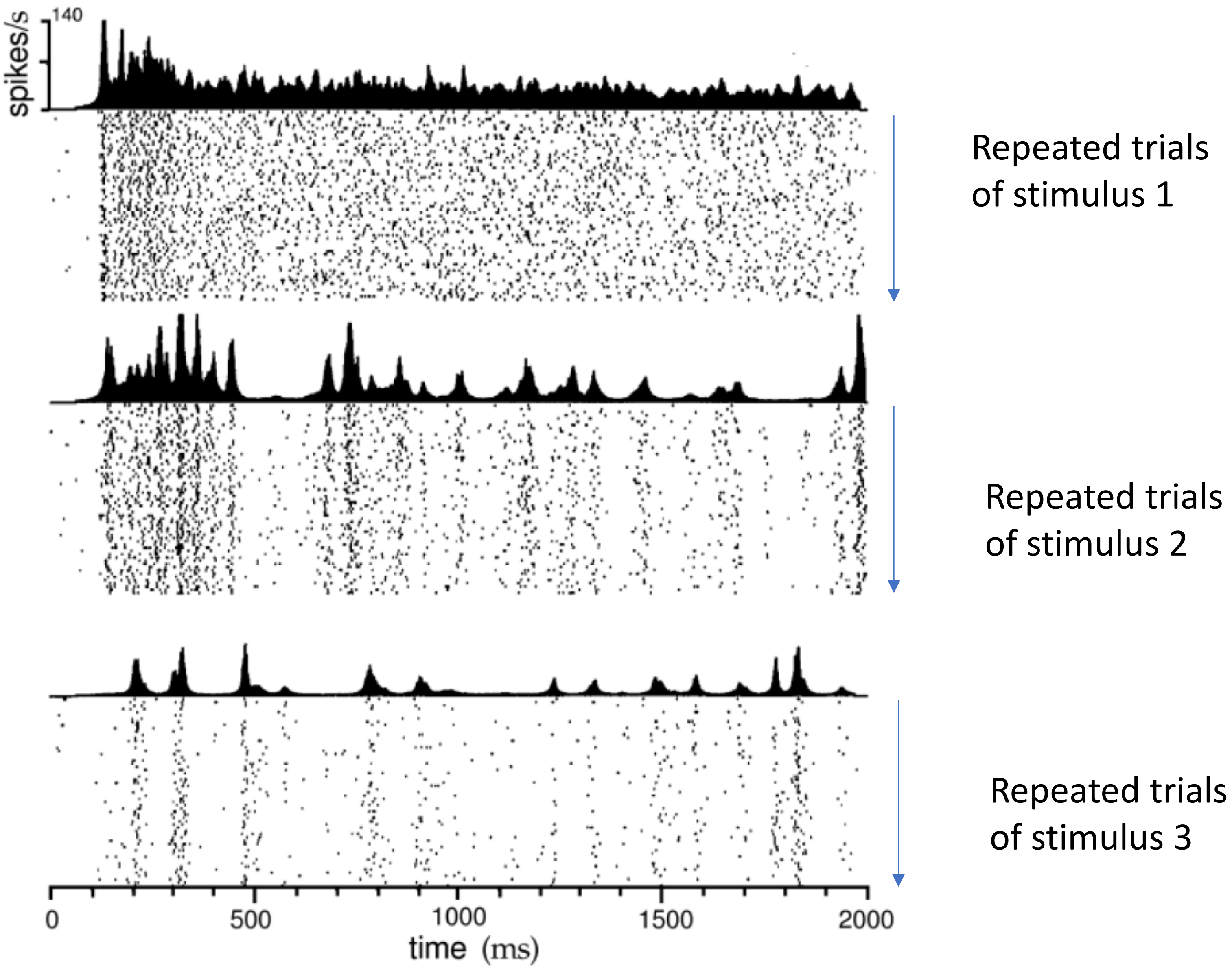
In cortex, and in vivo (i.e. natural conditions), spiking is typically:

1) Asynchronous/irregular
2) Highly variable/random (as far as we can tell…)
3) Sparse/low firing rates (~1-10 Hz)

Spiking Statistics – Trial to Trial Variability

Spiking of neurons is modulated by external factors (e.g., a visual stimulus), but is also variable across repeated trials of the same stimulus.

The meaning of this variability is mysterious – is it just noise, or are the precise spike patterns on each trial meaningful?

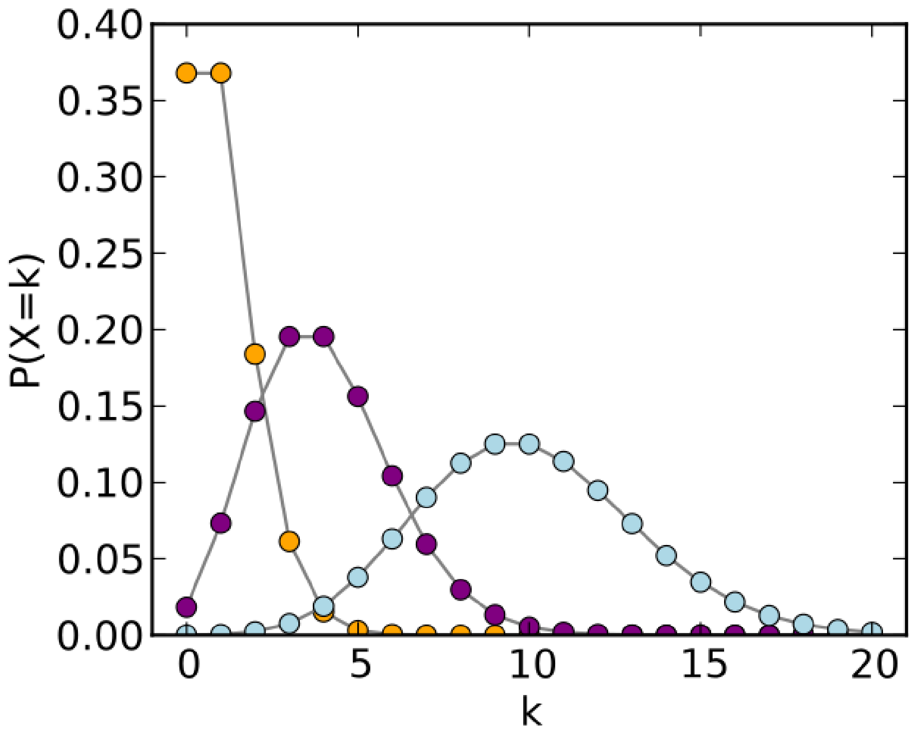


The Poisson Distribution – Spike Counts

- The Poisson distribution describes the number of events *N* that occur in a given time window *T*, assuming they occur randomly, independently and with constant rate *r:*

$$P(N = k) = \frac{(rT)^k e^{-rT}}{k!}$$

- Spike counts of neurons are often well-described by a Poisson distribution



Note: for large *rT the Poisson distribution becomes a normal distribution!*

$$k \sim N(\mu = rT, \sigma^2 = rT)$$

The Poisson Process – Spike Times

- The Poisson distribution describes the *number of events* in a fixed interval, the Poisson process describes the *event times* themselves (i.e., the spike times of a neuron)

- To simulate a Poisson process:

1) Divide time window *T* into short bins $\Delta t \ll 1/r$ (i.e., short enough that the chance of more than one event occurring in a bin is very small)

2) The probability that 1 event occurs during any given bin is:

$$P_T(N = k) = \frac{(rT)^k e^{-rT}}{k!} \implies P_{\Delta t}(N = 1) = r\Delta t e^{-r\Delta t} \approx r\Delta t$$

3) For each bin, randomly assign 0 or 1 spikes according to the above distribution [with P(N=0) = 1-P(N=1)]

Inhomogeneous Poisson Process

- In many cases, the spike rate of a neuron varies in time, so that the spikes cannot be described by a (homogeneous) Poisson process

- The inhomogeneous Poisson process allows for a time-varying rate, but assumes that spikes are conditionally independent of one another given this underlying rate

- For example, the rate might depend on a stimulus which varies in time (see figure)

- The method for simulating an inhomogeneous Poisson process is identical to that of the homogeneous one, but now with rate *r(t)*

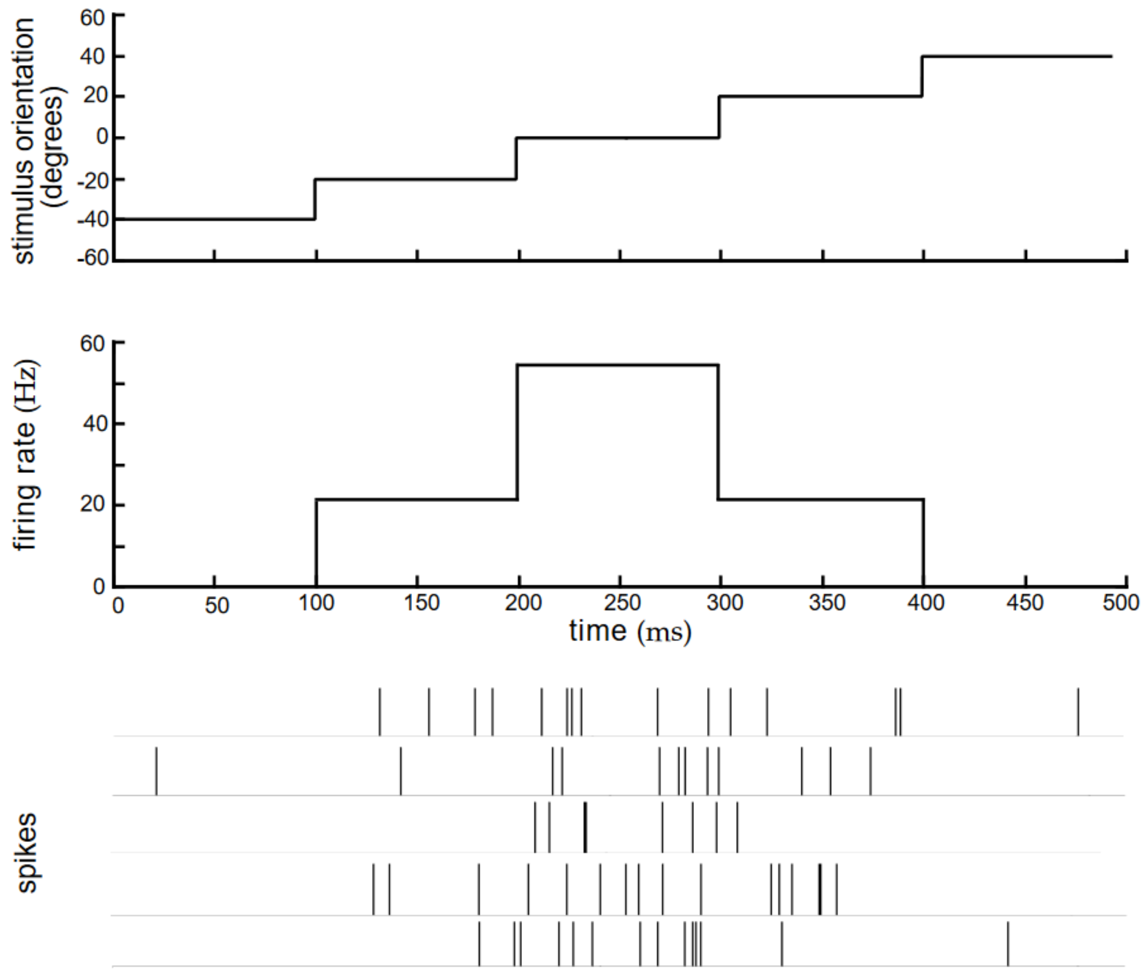


Figure 1.13 Model of an orientation-selective neuron. The orientation angle (top panel) was increased from an initial value of -40° by 20° every 100 ms. The firing rate (middle panel) was used to generate spikes (bottom panel) using a Poisson spike generator. The bottom panel shows spike sequences generated on five different trials.

The Fano Factor

- The Fano factor measures the variability of a process relative to it's mean. If we measure *N* spikes in a time window of duration *T*, the Fano factor is:

$$F(T) = \frac{\sigma_N^2(T)}{\mu_N(T)}$$

$$\mu_N(T) = \langle N(T) \rangle$$

$$\sigma_N^2(T) = \langle (N(T) - \mu_N(T))^2 \rangle$$

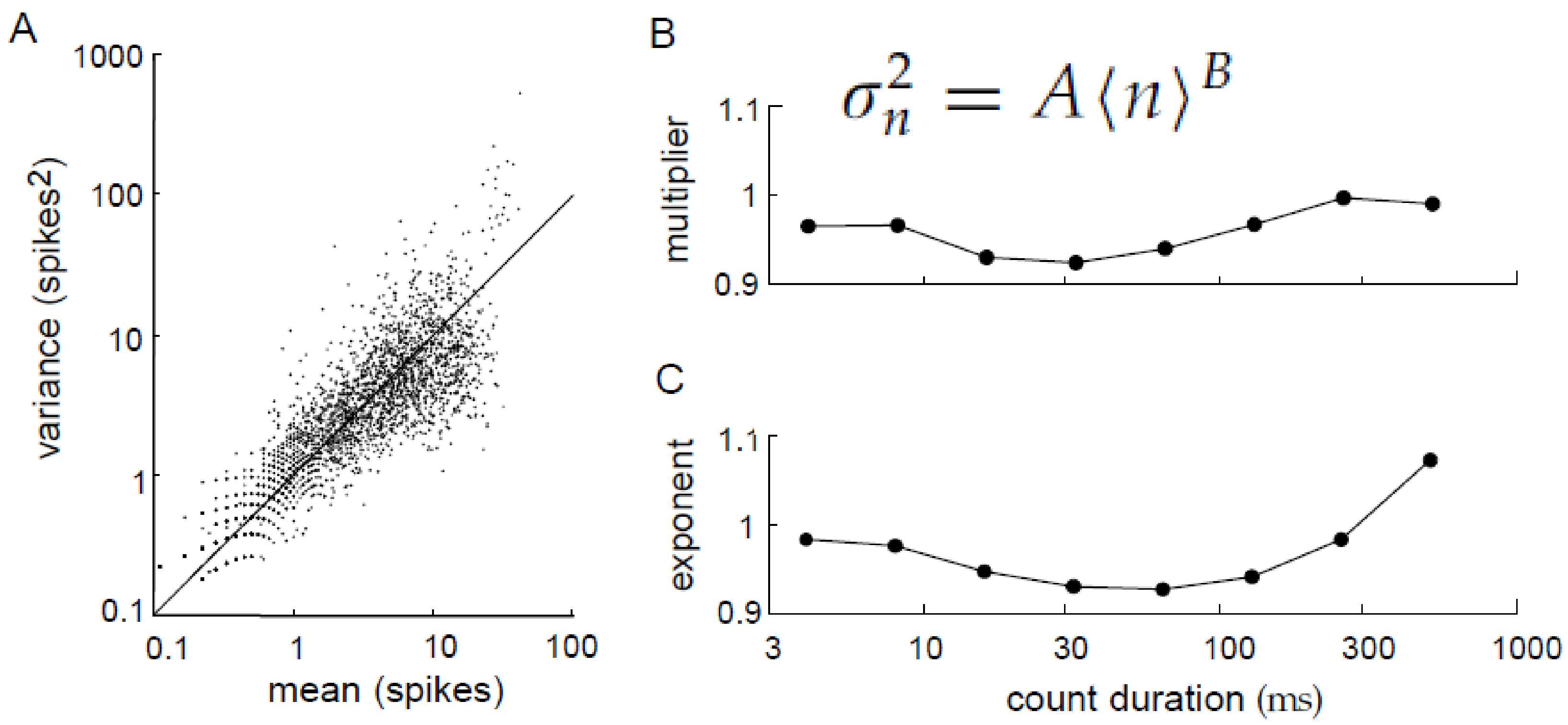
- The Poisson distribution has *F=1* (regardless of the rate *r* or time window *T*), because the mean and variance are both *rT.*

- This is why the Fano factor is useful – it gives a measure of the variance (or "dispersion") of a count process relative to a Poisson distribution. $F > 1$ implies over-dispersion, $F < 1$ implies under-dispersion.

- One can contrast the Fano factor with the coefficient of variation $CoV = \sigma/\mu$ - for most purposes the coefficient of variation is more natural (e.g., for interspike interval statistics), but for count models the Fano factor is a useful measure.

The Fano Factor – Real Neurons

- Neurons are often fairly close to Poisson as measured by Fano factor:



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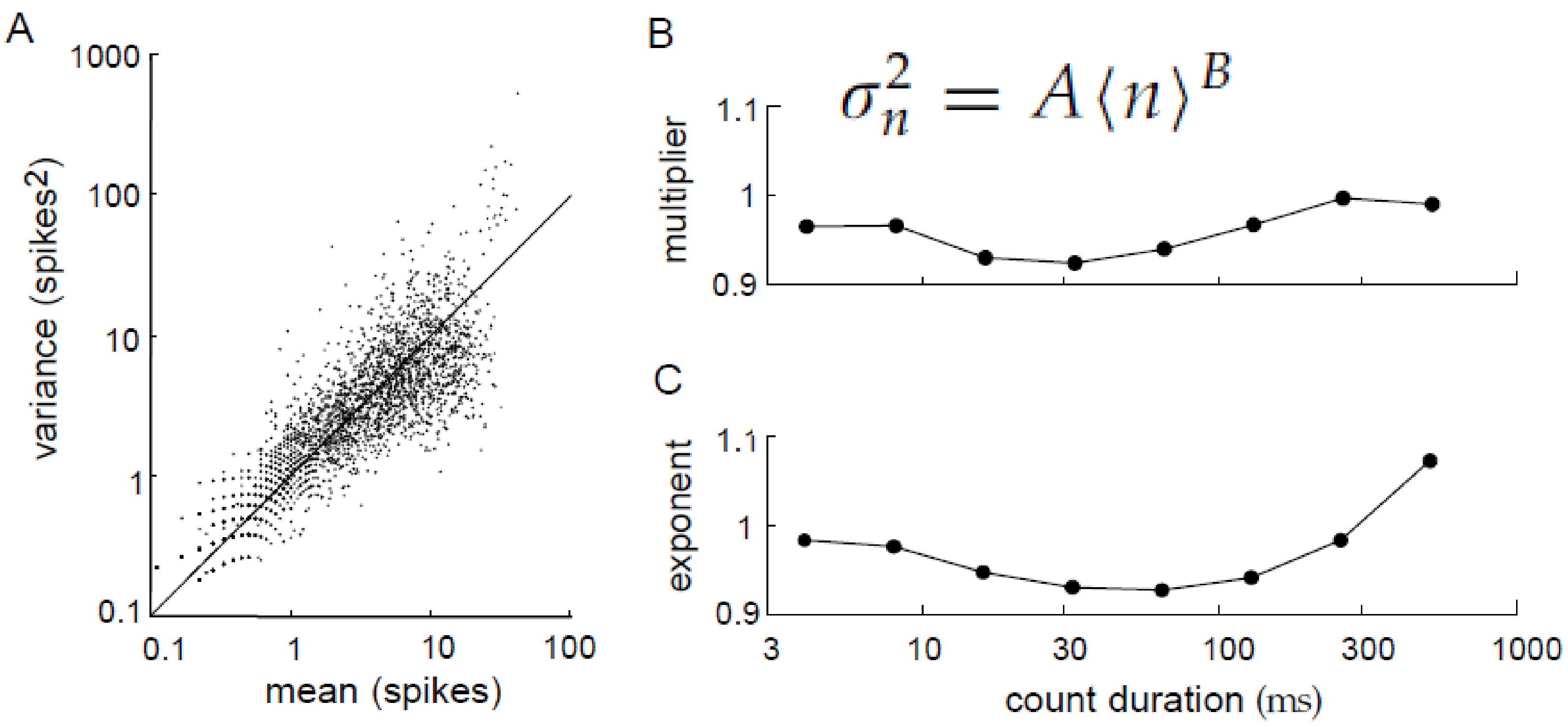

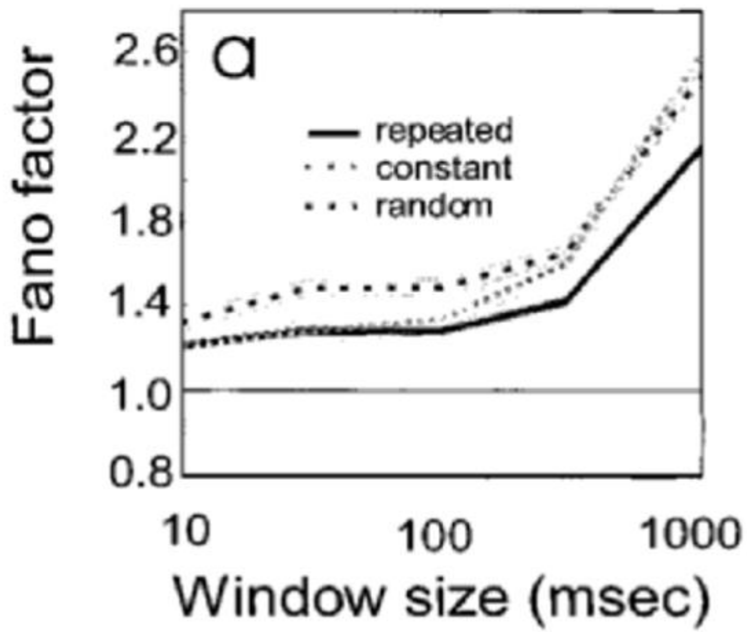

- However, neurons often have Fano factor > 1 (excess variability), which increases with time window. Perhaps due to inhomogeneous Poisson statistics? Or due to non-Poisson statistics?

The Exponential Distribution – Interspike Intervals

- The interspike interval is the time from one spike to the next $t_{isi}^{(i)} = t^{(i+1)} - t^{(i)}$

- What is its distribution if the spike times follow a Poisson process?

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  The probability that spike occurs after *n* bins is:

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Taylor expansion of log

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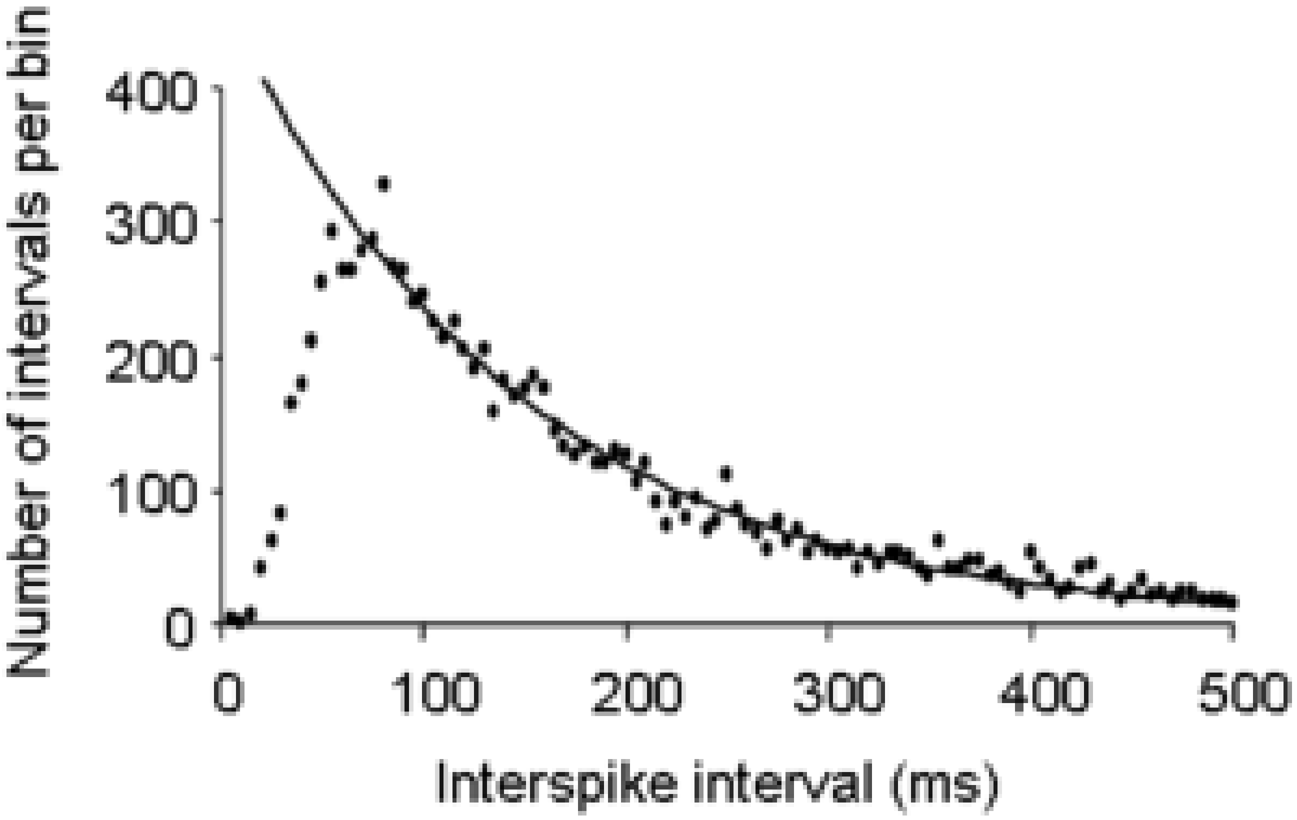
Taylor expansion of log

- To get continuous distribution ($\Delta t \to 0$), use $\int_0^\infty P(t_{isi}) dt_{isi} = 1 \implies P(t_{isi}) = re^{-rt_{isi}}$

- Thus, if spike times follow a Poisson process, interspike intervals follow an exponential distribution

Do Interspike Intervals Follow an Exponential Distribution

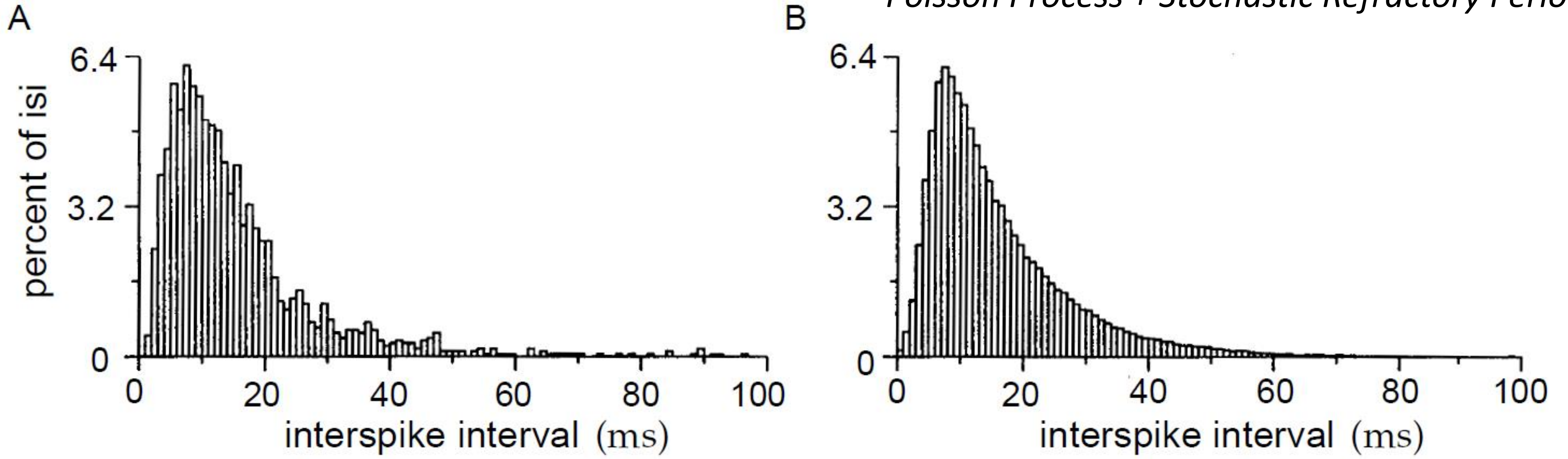


Interspike interval distribution recorded from a real neuron – note that the exponential distribution is a reasonable approximation for longer intervals, but not for short intervals

Adding a Refractory Period

Real Neuron

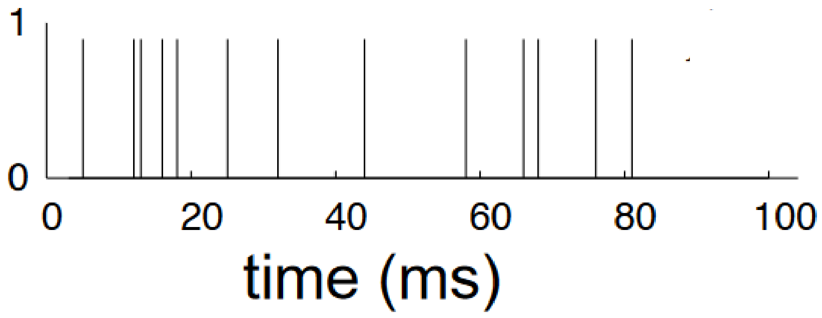
Poisson Process + Stochastic Refractory Period



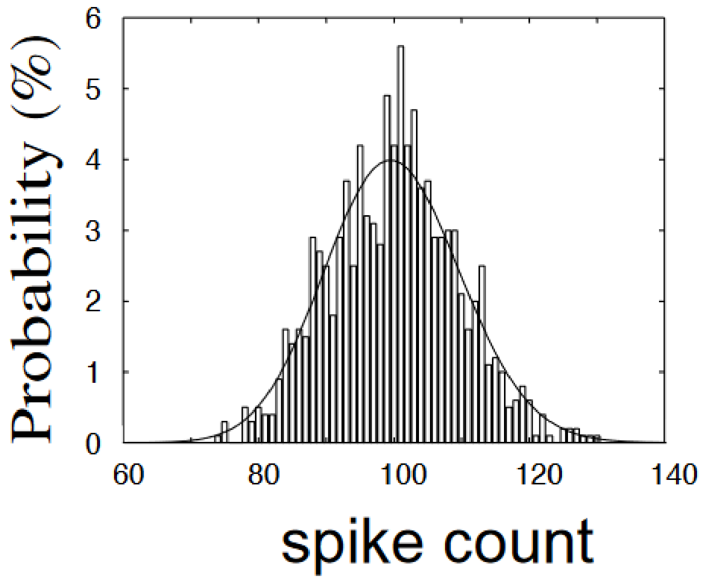
Putting it all together….

- Neurons often have approximately Poisson spike statistics
- This means that their spikes occur independently of each other in time
- Spike times follows a Poisson process, spike counts in a window of duration *T* follow a Poisson distribution, and inter-spike intervals follow an exponential distribution
- Poisson distribution has Fano factor = 1, exponential distribution has CoV = 1

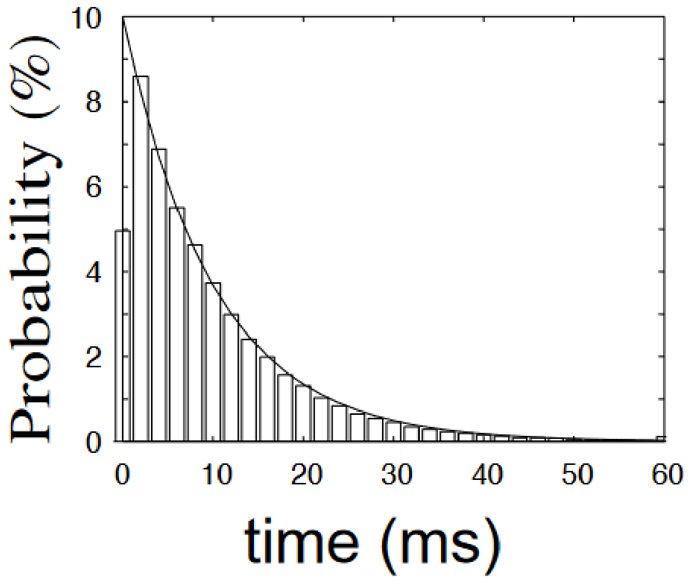
Poisson process



Poisson distribution



Exponential distribution



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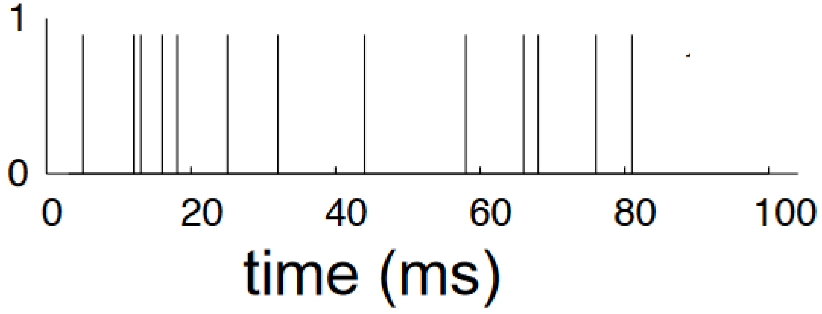

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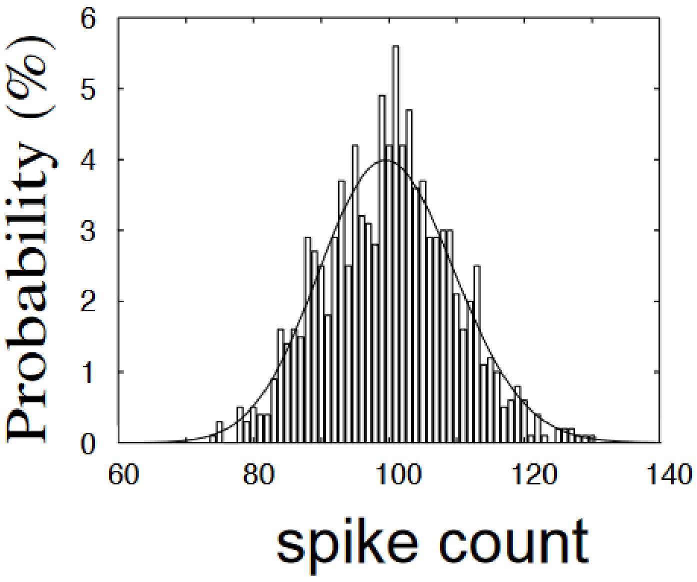

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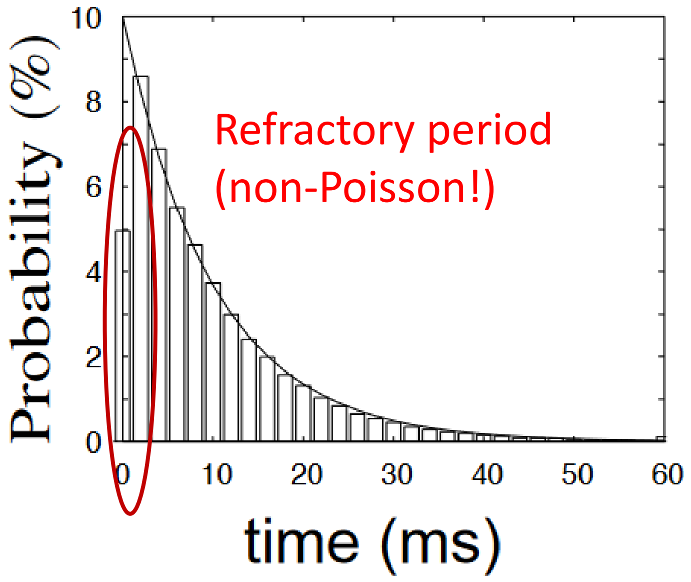


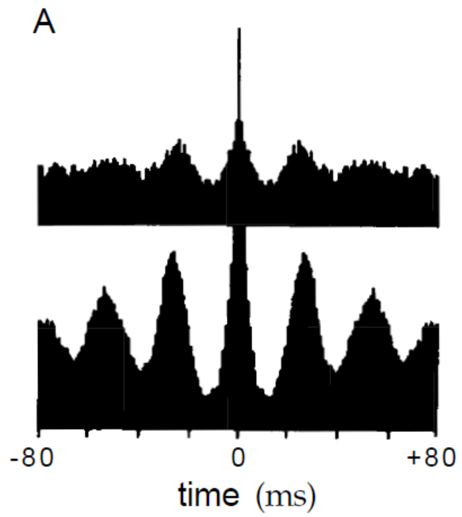
Evidence for Non-Poisson Spike Statistics

- Many forms of non-Poisson spike statistics have been observed, including:

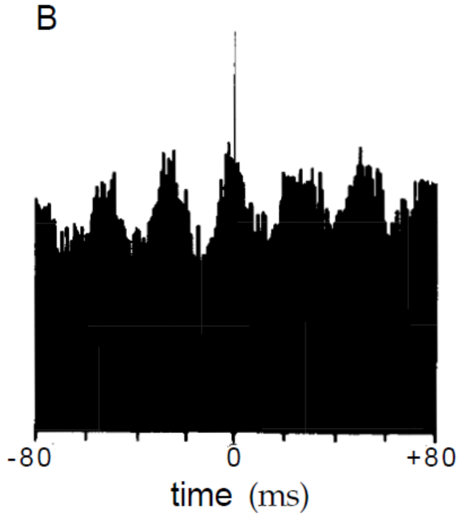
- Refractory period
- Synchrony, oscillations, etc.
- Burstiness of spikes
- Spike rate adaptation
- Over-dispersion and under-dispersion ($F > 1$, $F < 1$)

- Many of these can be modelled with an inhomogeneous Poisson process, or modifications to the Poisson process (e.g., “renewal processes”)

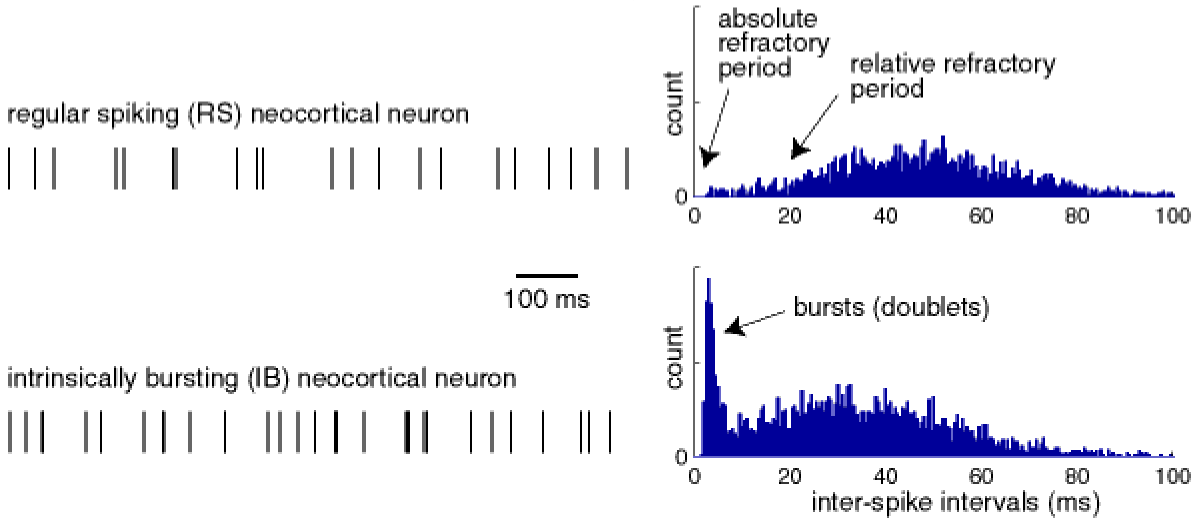
Spike autocorrelations



Spike cross-correlations



Bursting

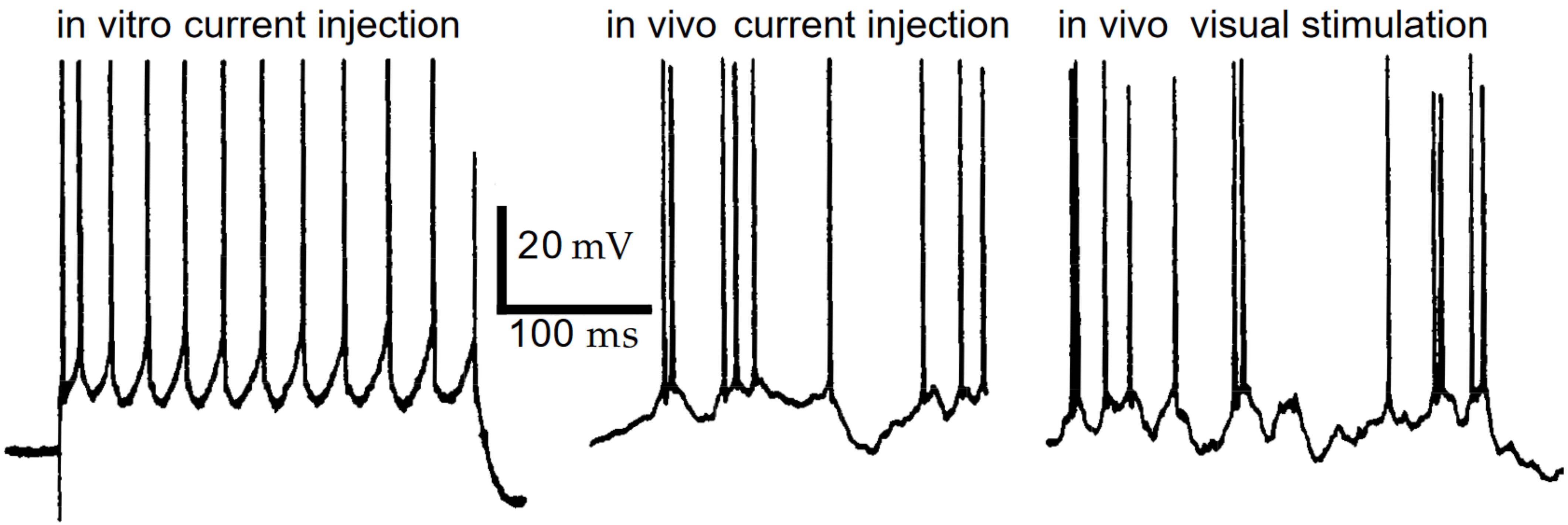


Summary: Poisson Statistics

- Spike patterns of neurons in the brain are often well-described by Poisson statistics
- Poisson distribution characterises counts, Poisson process characterises spike times, exponential distribution characterises interspike intervals
- Poisson rate can be modulated by various factors (stimulus, internal state, etc.) – can use inhomogeneous Poisson process to model that
- Fano factor is a useful measure of Poissonality (or CoV for ISIs)
- Real neurons exhibit various deviations from Poisson statistics (depends on brain state, stimulus etc.)

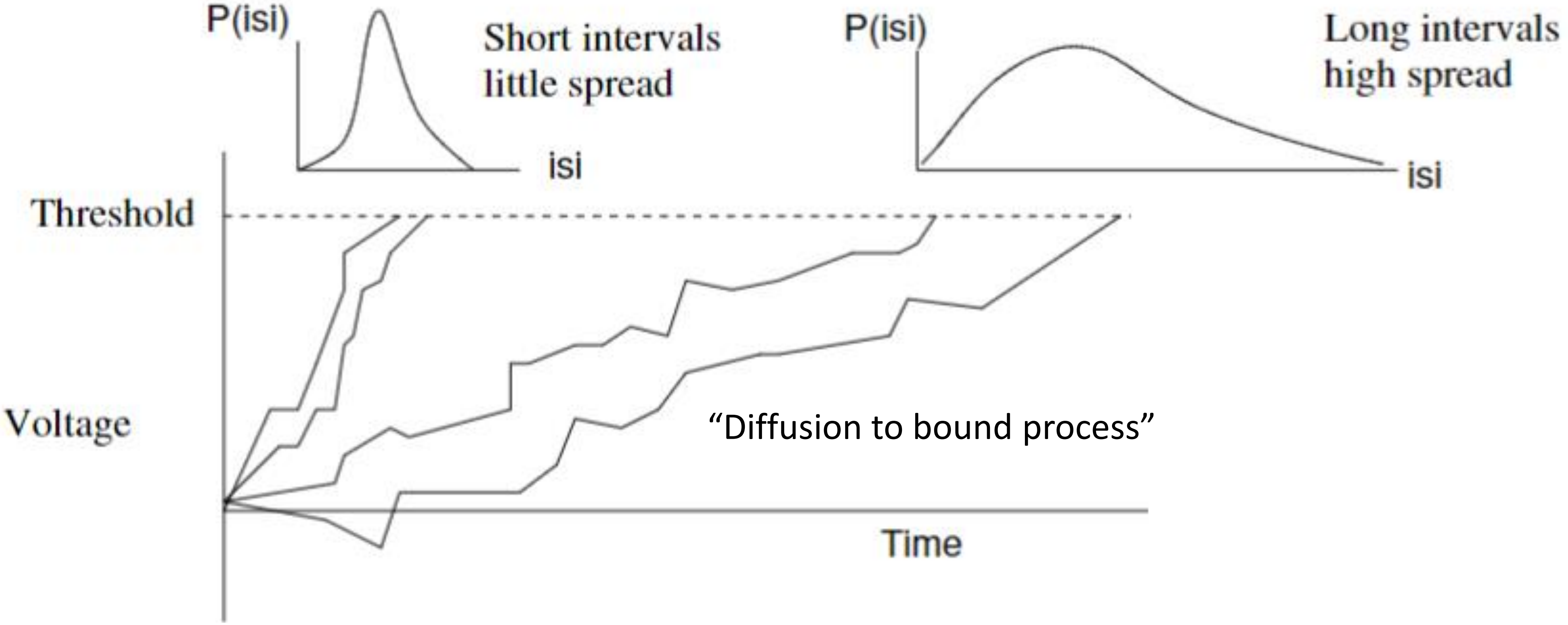
How Do Neurons Generate Poisson Variability

- Constant current injection (to LIF or HH or real neuron) generates reliable spike patterns
- But neurons in the brain have highly asynchronous/irregular/Poisson spike patterns
- Why? What are we missing?
- So far we have considered statistical models for irregular spike patterns, but what is the biophysical mechanism?



Noisy Integrate and Fire Neuron

- Can we capture neural spike statistics by injecting noisy current input into an integrate and fire neuron?
- If so, what does this noisy current input represent?



Modelling Many Synaptic Inputs

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total synaptic input → $g_{syn}(t)$

sum over synapses → $\sum_{j=1}^{N_s}$

$$g_{syn}(t) = \sum_{j=1}^{N_s} g_{syn}^{(j)}(t)$$

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total synaptic input — sum over synapses — Delta synapses

$$g_{syn}(t) = \sum_{j=1}^{N_s} g_{syn}^{(j)}(t) = \sum_{j=1}^{N_s} \sum_{i=1}^{N(j)} \bar{g}_{syn}^{(j)} \delta(t - t_j^{(i)})$$

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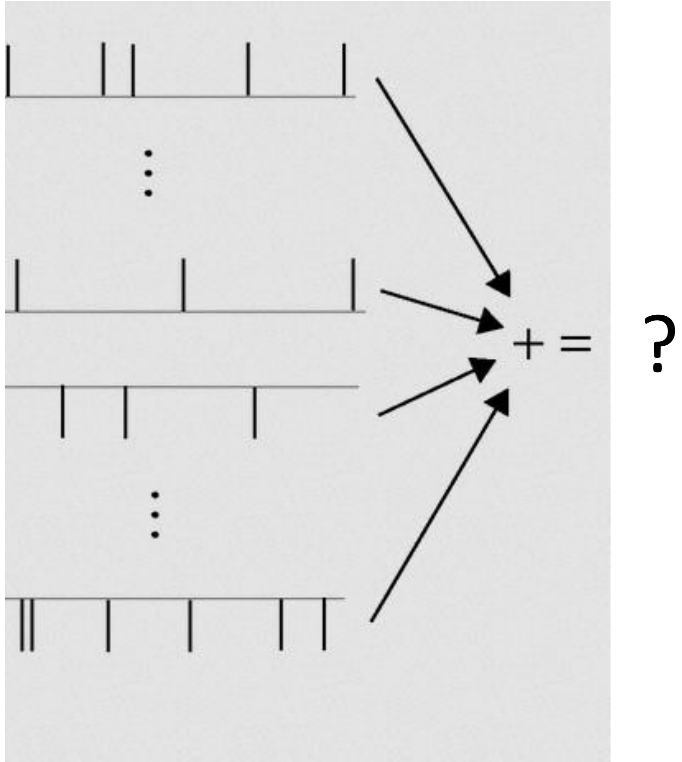

- Can we simplify/approximate this? Assume each synapse is independent and follows Poisson process… What happens when $N_s \to \infty$ and $\bar{g}_{syn} \to 0$?

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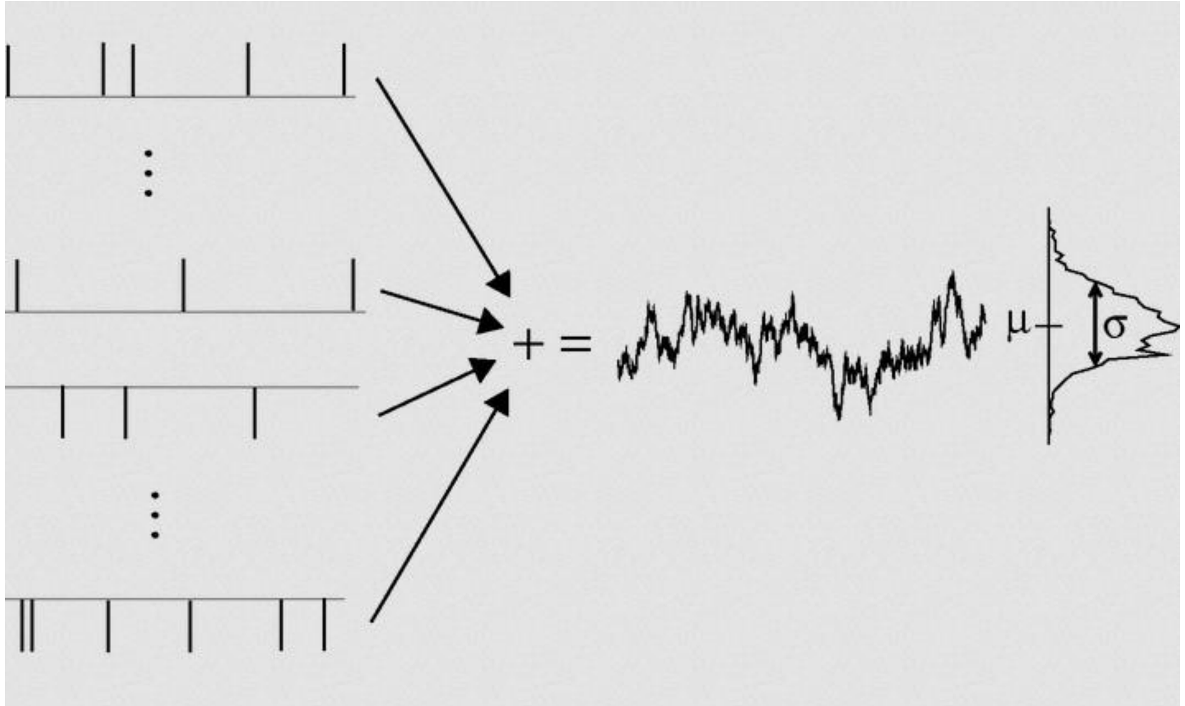
- Answer: Sum of many independent Poisson processes is approximately Gaussian white noise.



$$g_{syn}(t) \sim N(\mu, \sigma^2) \qquad \langle g_{syn}(t) \rangle = \mu$$

$$\langle (g_{syn}(t) - \mu)(g_{syn}(t') - \mu) \rangle = \sigma^2 \delta(t - t')$$

Modelling Many Synaptic Inputs

Sum of many Poisson synapses

total synaptic conductance

sum over synapses

Delta synapses

Poisson spike times

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Mean and variance of total synaptic conductance (in limit of many synapses):

$$\langle g_{syn} \rangle = \bar{g}_{syn} r N_s = \mu \qquad \langle (g_{syn} - \mu)^2 \rangle = \bar{g}_{syn}^2 r N_s = \sigma^2$$

Average strength of synapses ($\bar{g}_{syn}$)

Average presynaptic spike rate (r)

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Sum of many Poisson synapses

total synaptic conductance; sum over synapses; Delta synapses; Poisson spike times

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Mean and variance of total synaptic current:

$$\langle I_{syn} \rangle = \langle -g_{syn}(V - E_{syn}) \rangle$$

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Average strength of synapses ($\bar{g}_{syn}$)

Average presynaptic spike rate (r)

Mean and variance of total synaptic current:

$$\langle I_{syn} \rangle = \langle -g_{syn}(V - E_{syn}) \rangle = -\langle g_{syn} \rangle \langle V - E_{syn} \rangle = -\mu(\langle V \rangle - E_{syn}) = \mu_I$$

$$\langle (I_{syn} - \langle I_{syn} \rangle)^2 \rangle = \langle (-g_{syn}(V - E_{syn}) - \mu_I)^2 \rangle = \sigma^2 \langle (V - E_{syn})^2 \rangle = \sigma_I^2$$

Membrane Potential Dynamics with Noisy Inputs

- The passive membrane potential dynamics under many Poisson synaptic inputs is:

$$g_m \tau_m \frac{dV}{dt} = -g_m(V - E_m) - g_{syn}(t)(V - E_{syn}) \approx -g_m(V - E_m) + \mu_I + \sigma_I \eta(t)$$

- Where $\eta(t)$ is Gaussian white noise. This equation is known as an Ornstein-Uhlenbeck process

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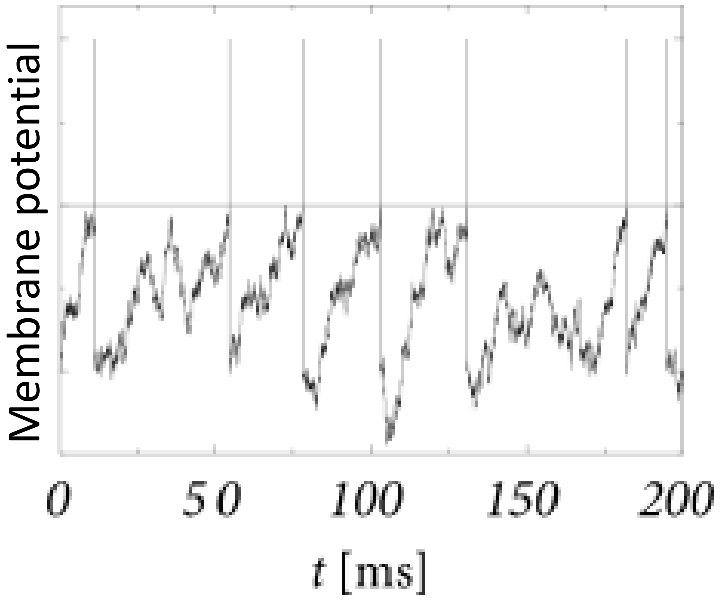

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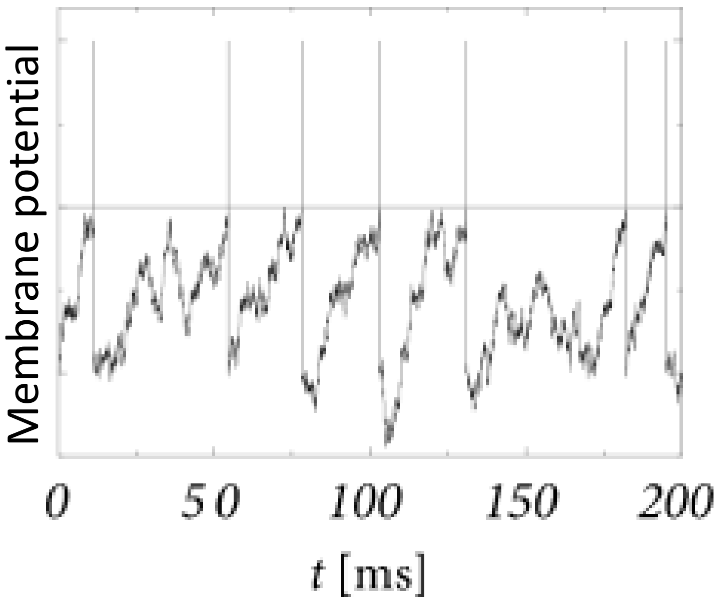
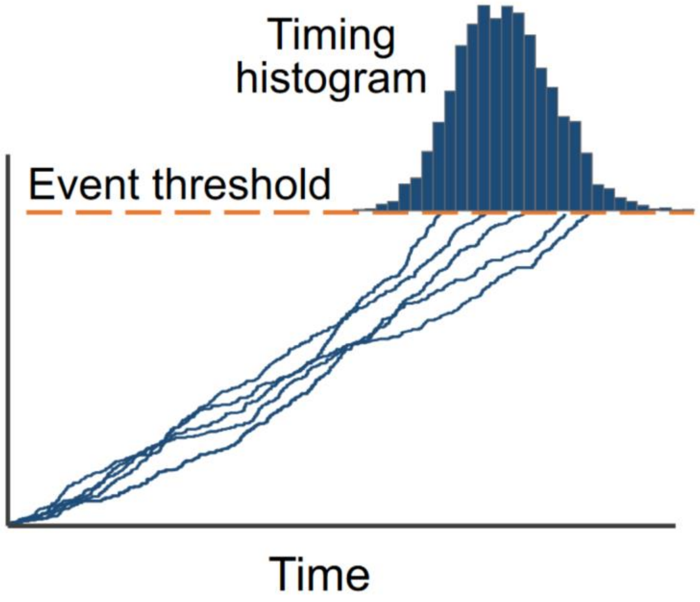
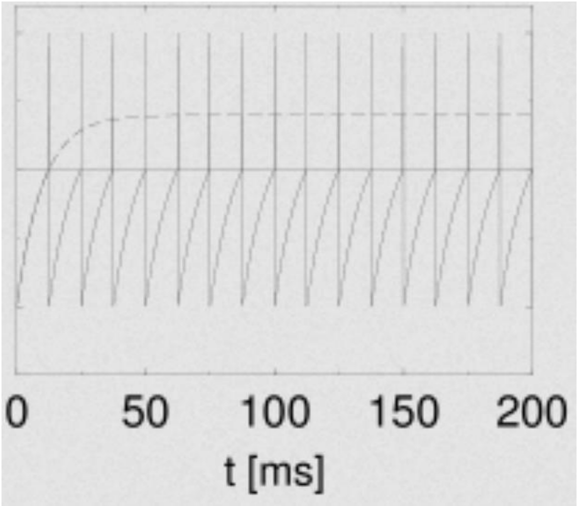
- This OU process generates temporally correlated Gaussian noise in the membrane potential V
- The above OU process describes only the passive membrane dynamics, but one can compute spiking statistics using "first passage times" (i.e., time from to reach threshold after a spike-reset)





Mean vs Fluctuation Driven Regimes

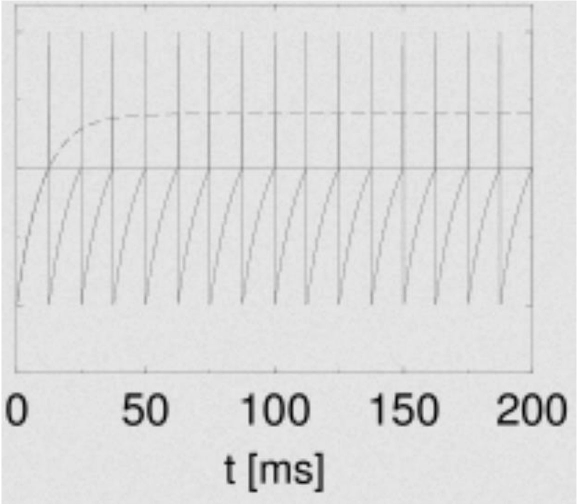
Mean Driven Regime

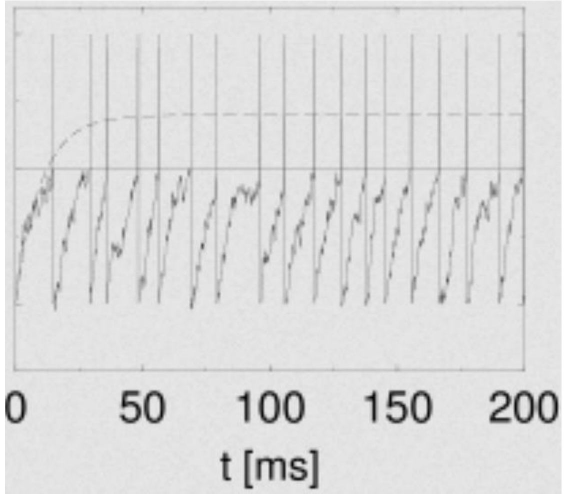


- Two regimes: 1) neurons would spike even without noise (mean-driven regime, regular spiking)

Mean vs Fluctuation Driven Regimes

Mean Driven Regime

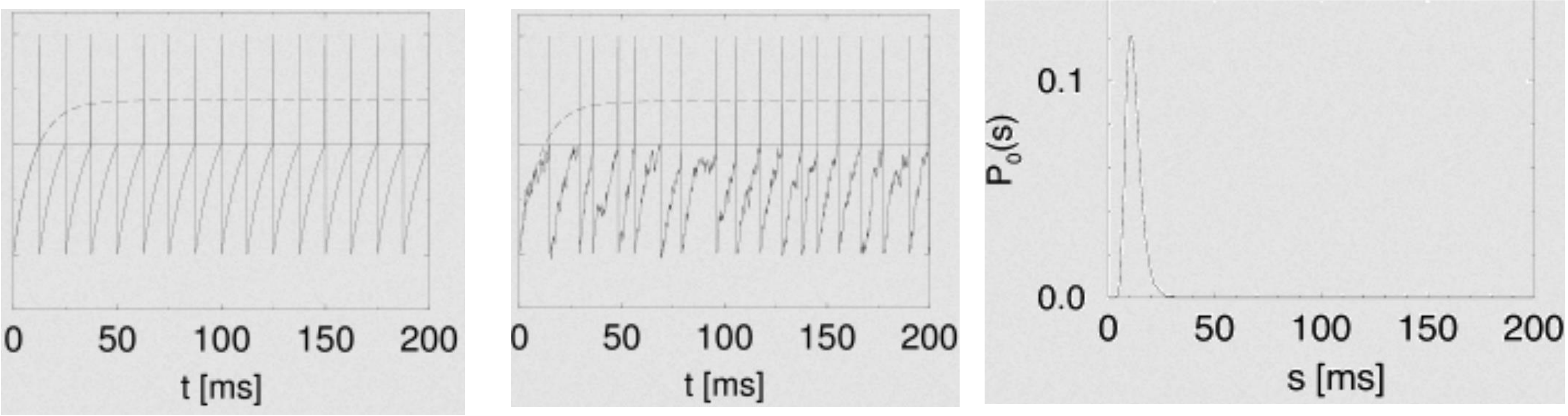




- Two regimes: 1) neurons would spike even without noise (mean-driven regime, regular spiking)

Mean vs Fluctuation Driven Regimes

Mean Driven Regime

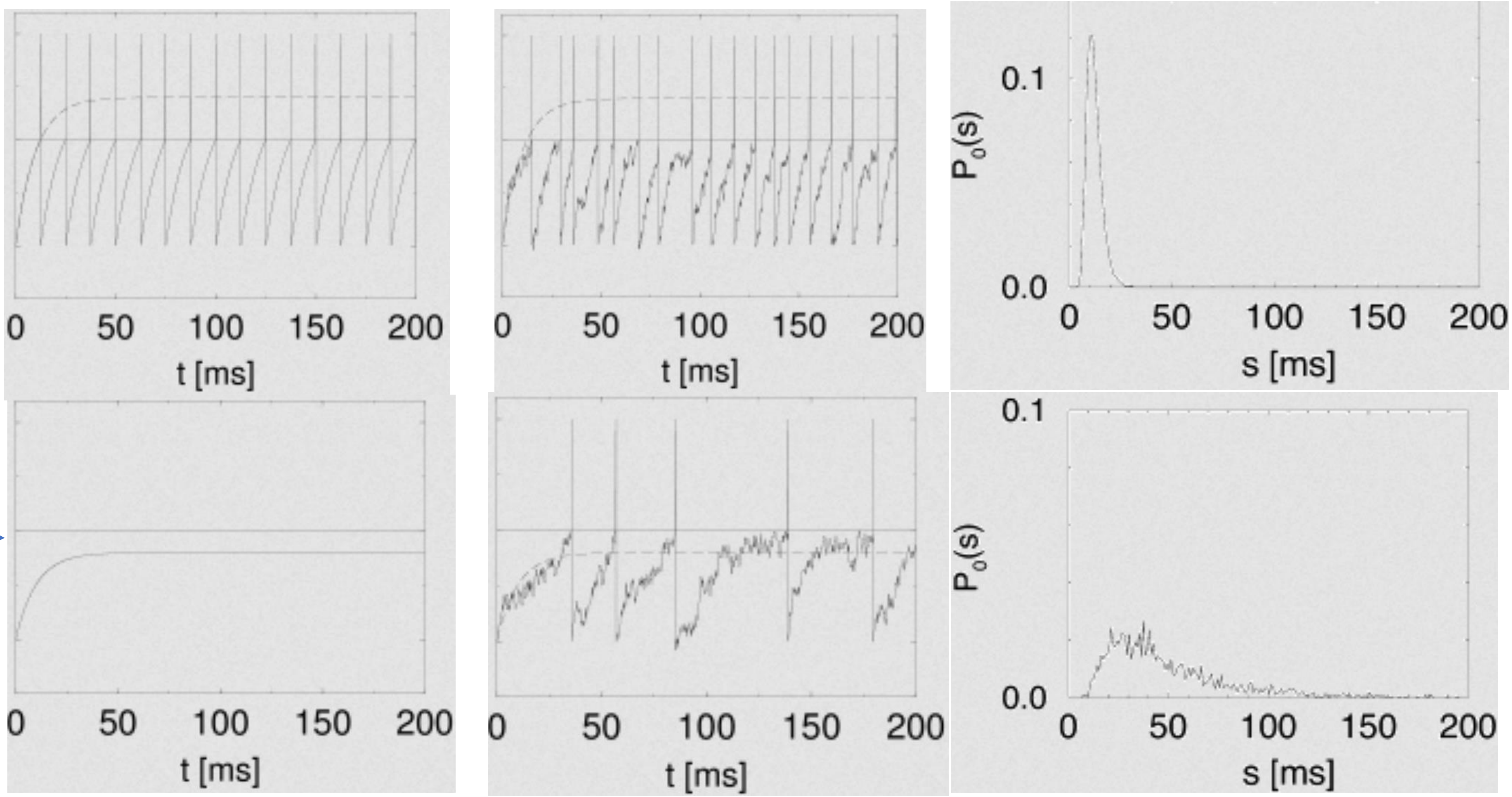


- Two regimes: 1) neurons would spike even without noise (mean-driven regime, regular spiking)

Mean vs Fluctuation Driven Regimes

Mean Driven Regime

Fluctuation Driven Regime



- Two regimes: 1) neurons would spike even without noise (mean-driven regime, regular spiking)

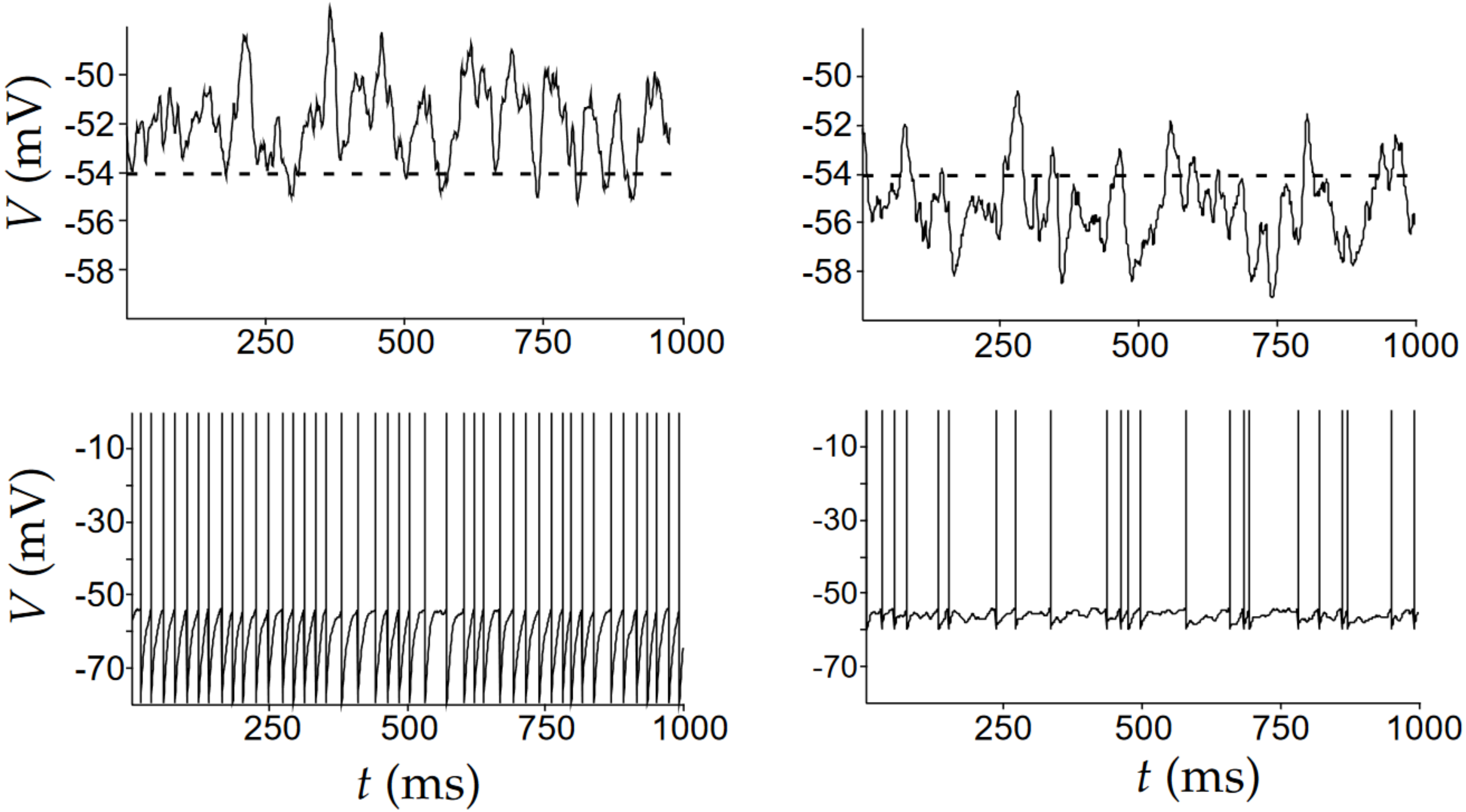
  2) neurons only spike due to noise (fluctuation-driven regime, irregular spiking)

Mean vs Fluctuation Driven Regimes

Mean Driven Regime *Fluctuation Driven Regime*

Spiking Turned Off

Spiking Kept In



Summary - Mean vs Fluctuation Driven Regimes

- The mean and fluctuation-driven regimes generate very different spike statistics
- The mean-driven regime has regular spiking (with minor jitter due to noise) and a narrow and sharply peaked interspike interval distribution
- The fluctuation-driven regime has irregular spiking, with spike times following approximately Poisson statistics and a broad and asymmetric interspike interval distribution

Mean vs Fluctuation Driven Regimes vs Data

- The fluctuation-driven regime provides a good explanation of the irregular spiking patterns of neurons recorded from cortex, such as the interspike interval distribution

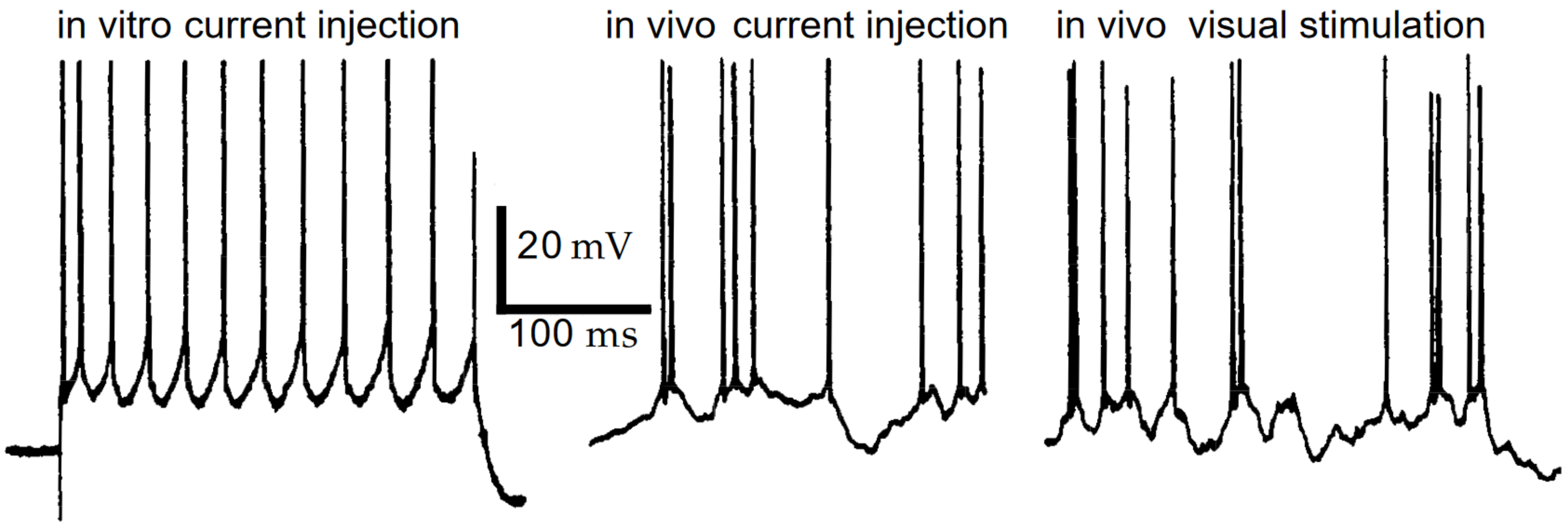
- The mean-driven regime can explain the spiking patterns of neurons in vitro (i.e. in a dish) in response to injected current

- This is the sign of a good model: we can explain quite different spike patterns by varying model parameters, and can go out and measure/test the predictions

Spiking Variability in Real Neurons

- Neurons *in vivo* (in an alive animal) have approximately Poisson spiking statistics

- Neurons *in vitro* (a neuron in a dish) tend to fire much more regularly



How Noisy Are Real Neurons?

- Neurons have intrinsic noise

  (due to stochastic ion channels, etc.)

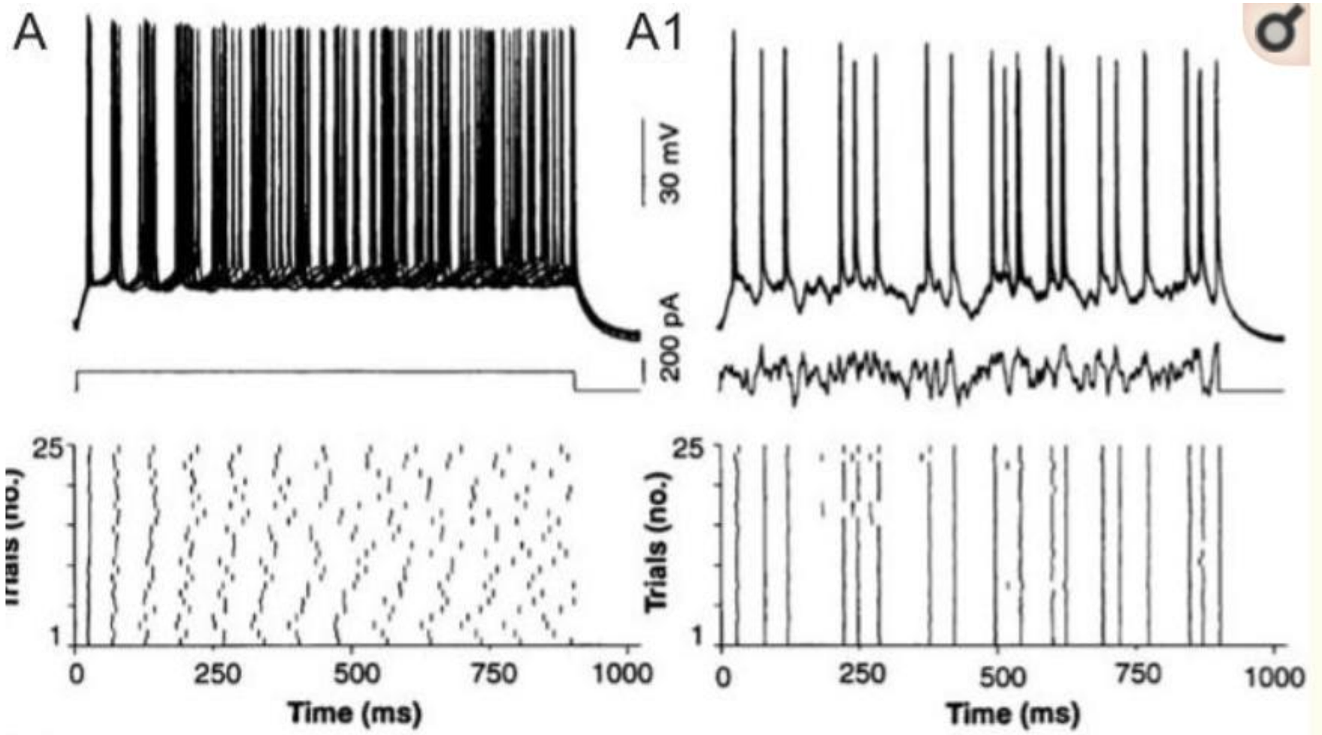
- They respond differently to identical repeats of a constant current step

- They respond regularly to identical repeats of irregular/fluctuating current inputs

- Input "noise" may actually make neurons more reliable in their spiking activity!

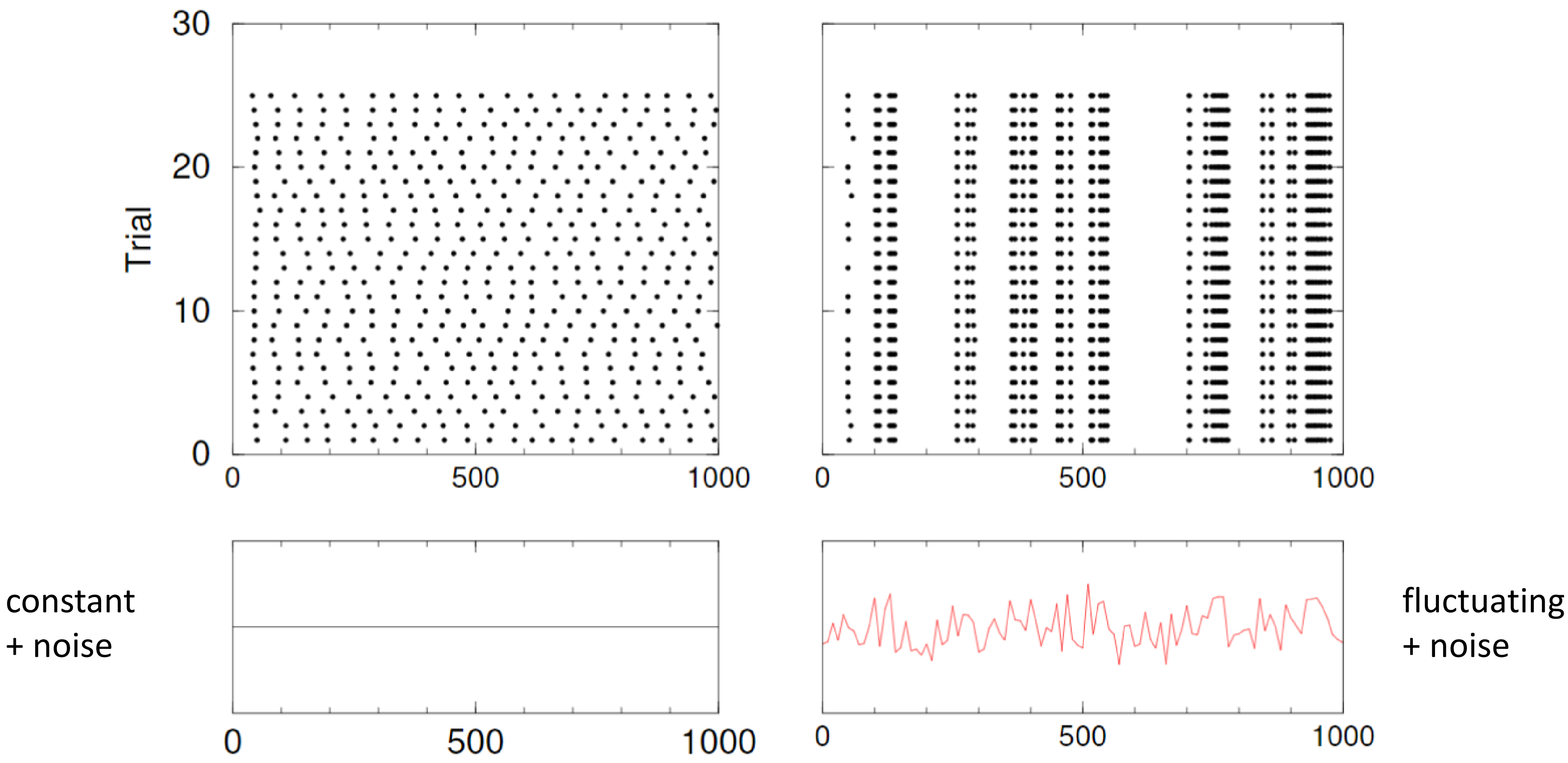
- There is considerable debate over how much noise there really is in the brain

Response of single neuron to multiple repeats of same current injection
Left: constant current. Right: fluctuating current



How Noisy Are Real Neurons?

- Spike locking in response to noisy but not constant input can be reproduced in an integrate and fire neuron



Summary: Neural Firing Statistics

- Spike patterns of neurons under natural conditions are typically highly irregular and variable
- Poisson models are typically a good first order approximation, but there are many non-Poisson effects to consider
- Spike patterns depend on brain region, cell type, brain state, stimulus, attentional state, and many other factors
- The highly irregular spike patterns observed in vivo can be recapitulated by a model assuming a barrage of Poisson synaptic input to a leaky integrate and fire neuron
- The model predicts two regimes (mean and fluctuation driven) which explain in vitro and in vivo firing statistics

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