SAMSI Summer 2015: CCNS
Computational Neuroscience Summer School

Neural Spike Train Analysis 1: Introduction to Point Processes

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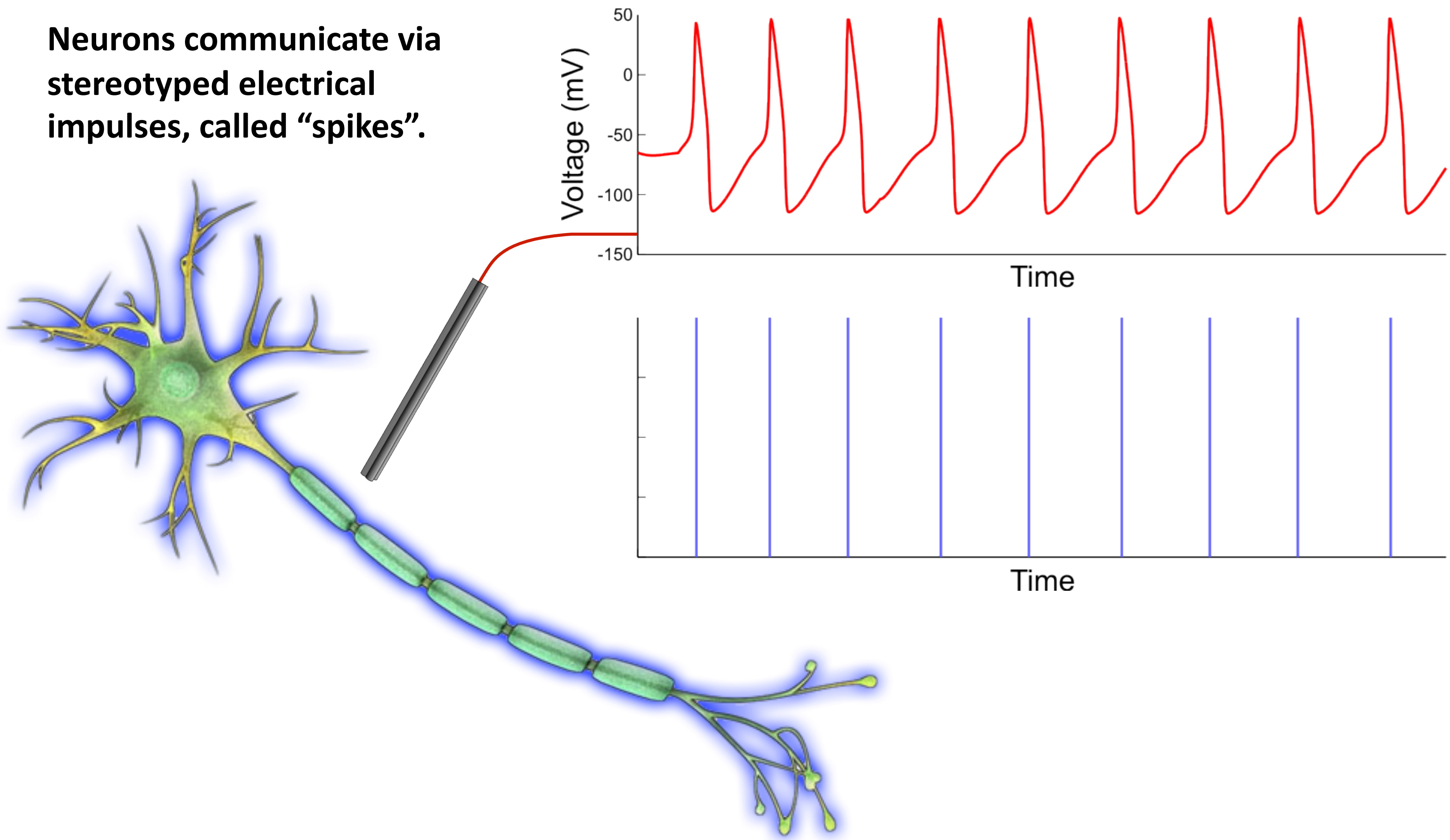
Spikes are the Language of the Brain

Neurons communicate via stereotyped electrical impulses, called "spikes".



Two distinct approaches to neural modeling

- Simplified statistical models
  - Capture the structure of, or predict the precise timing of spikes as a function of the biological/behavioral signals represented in the brain
  - Treat the neuron as a black box, looking for associations rather than mechanisms

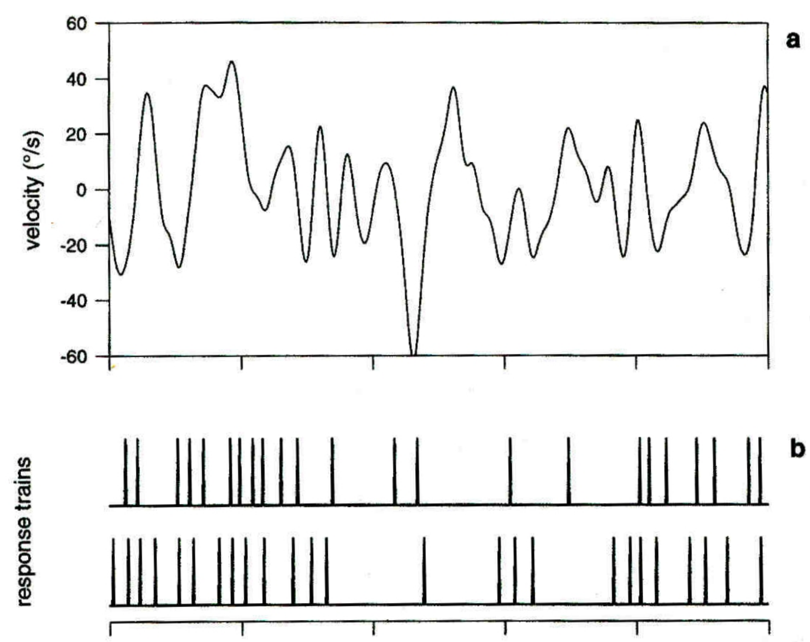
- Biophysical neural models
  - Mathematically describe interacting mechanisms that lead to qualitative patterns of neural spiking
  - Are complicated - coupled non-linear systems of differential equations with many unknown parameters

Day 1: Statistical Models of Neural Coding

Spiking Activity of the Fly H1 Neuron

Angular Velocity of Visual Stimulus

Spike Trains



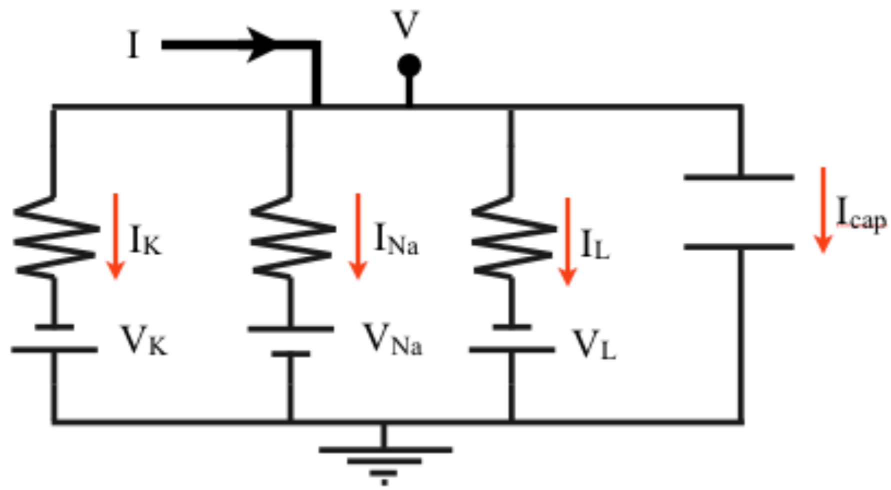
Rieke et al. (1997)

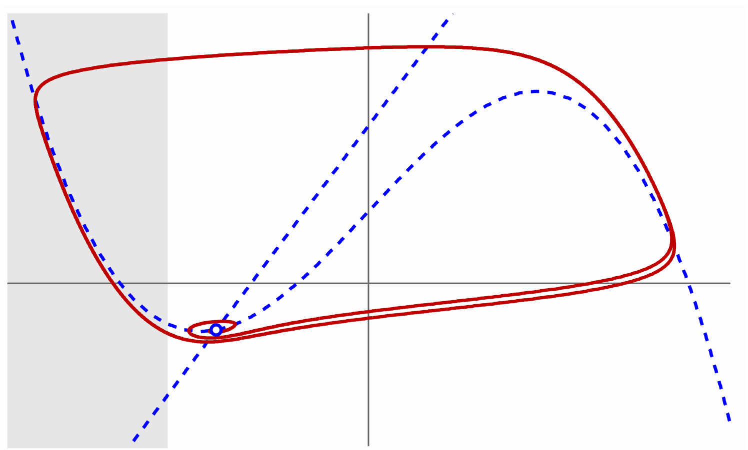
$$L\left(\text{Spikes at } \left\{s_i\right\}_{i=1}^{n} \middle| \left\{x_t\right\}_{t=0}^{T}, \theta\right)$$

Day 2: Computational Models

Another approach to analyze neural data: build mathematical models of “spikes”.

Biophysical models: integrate and fire, Hodgkin Huxley





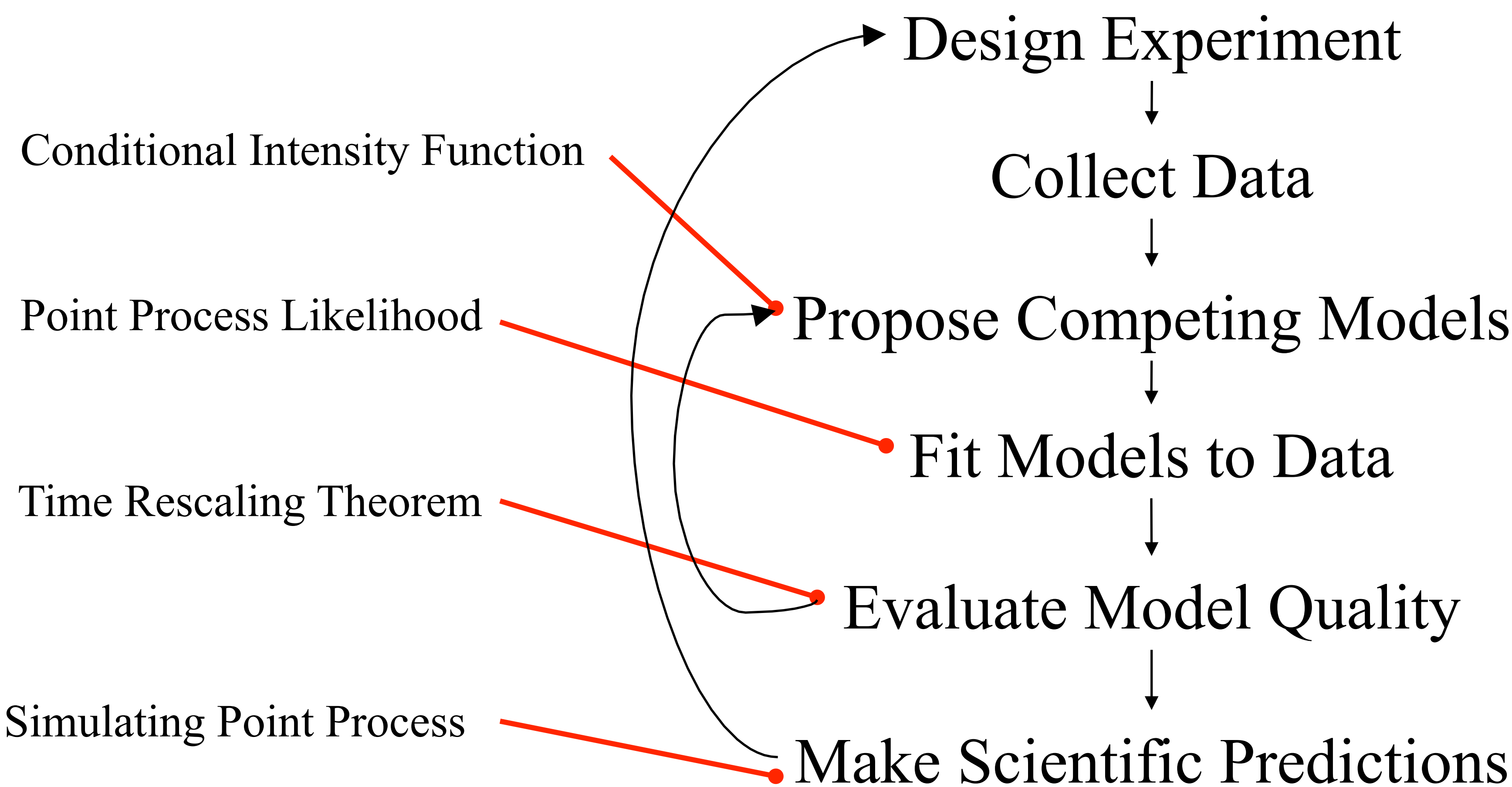
Dynamical model: FitzHugh-Nagumo

We’ll briefly introduce concept of data assimilation …

Part 1 - Point process theory

1. Definition of a Point Process
2. Poisson Processes
3. Conditional Intensity Functions
4. Point Process Likelihoods
5. Time Rescaling Theorem
6. Simulating Point Process

Part 1 - Point process theory

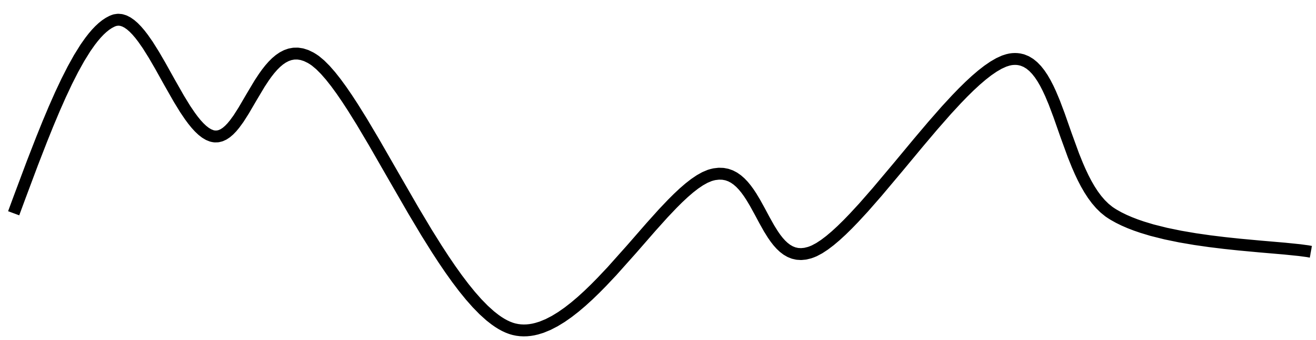


1. Definition of a Point Process

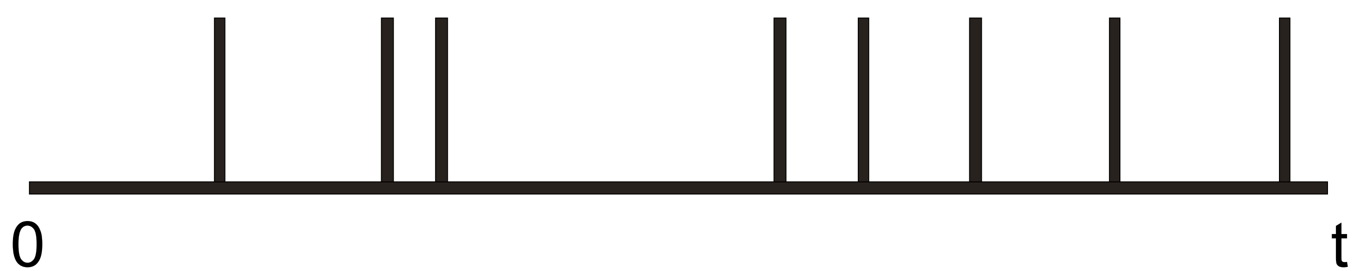
- What it is:
  - Point processes are used to mathematically model physical systems that produce a stochastic set of localized events in time or space.
- When to use:
  - If your data are more aptly described as events than as a continuous series.
- Examples:
  - Spike Trains
  - Heart Beats
  - Earthquake sites and times

Continuous vs Point Processes in Time

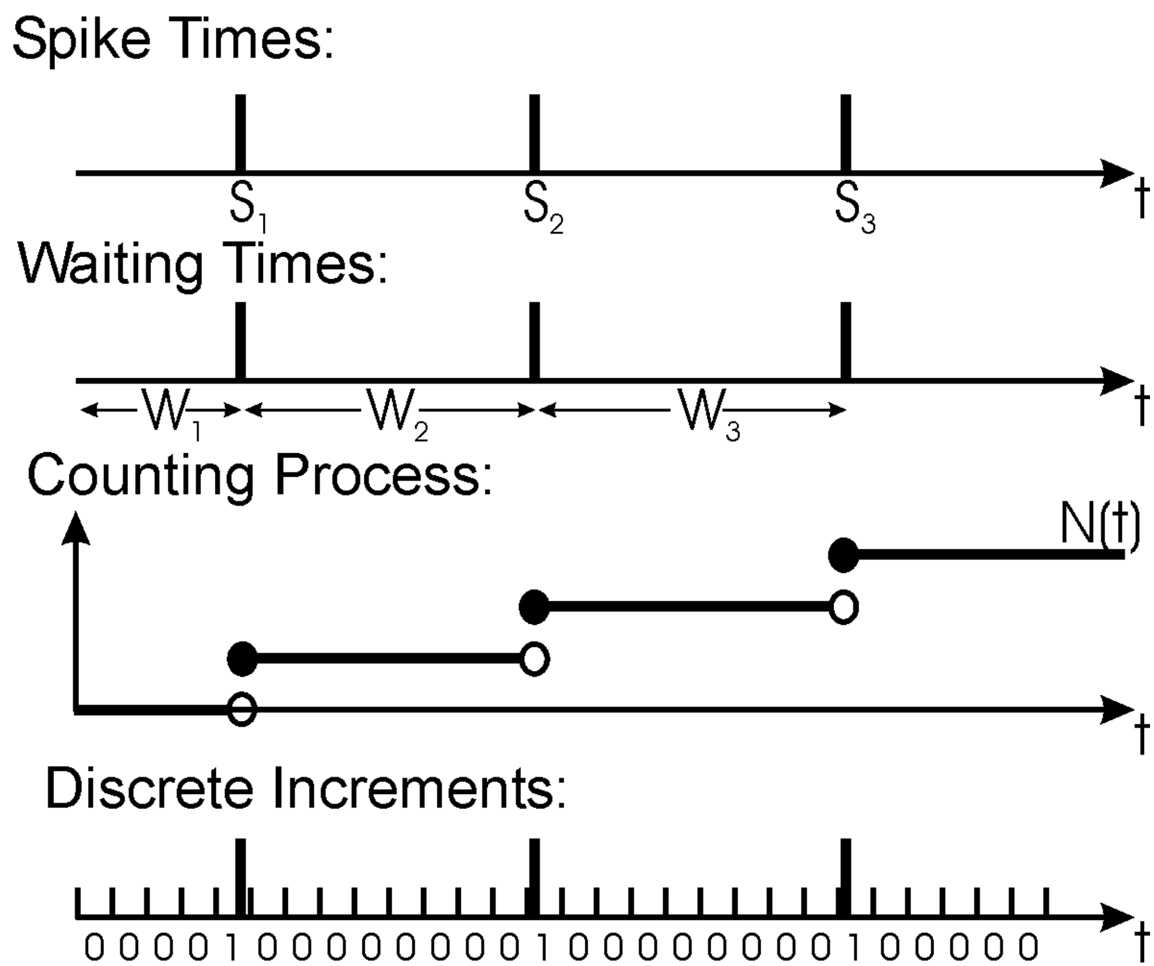
Continuous Process:



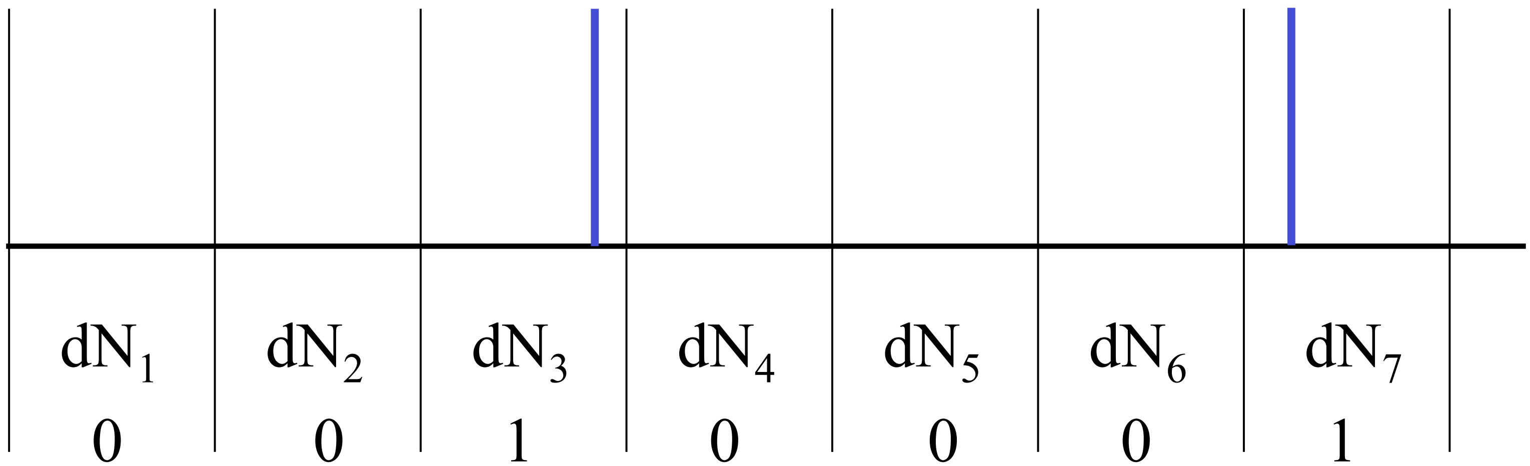
Point Process:



Descriptions of a Point Process



Discrete Time Spike Train Data



dN_k is the spike indicator function in interval k

λ_k is the intensity of spiking at time k. For a Poisson process, this is called the Poisson rate function.

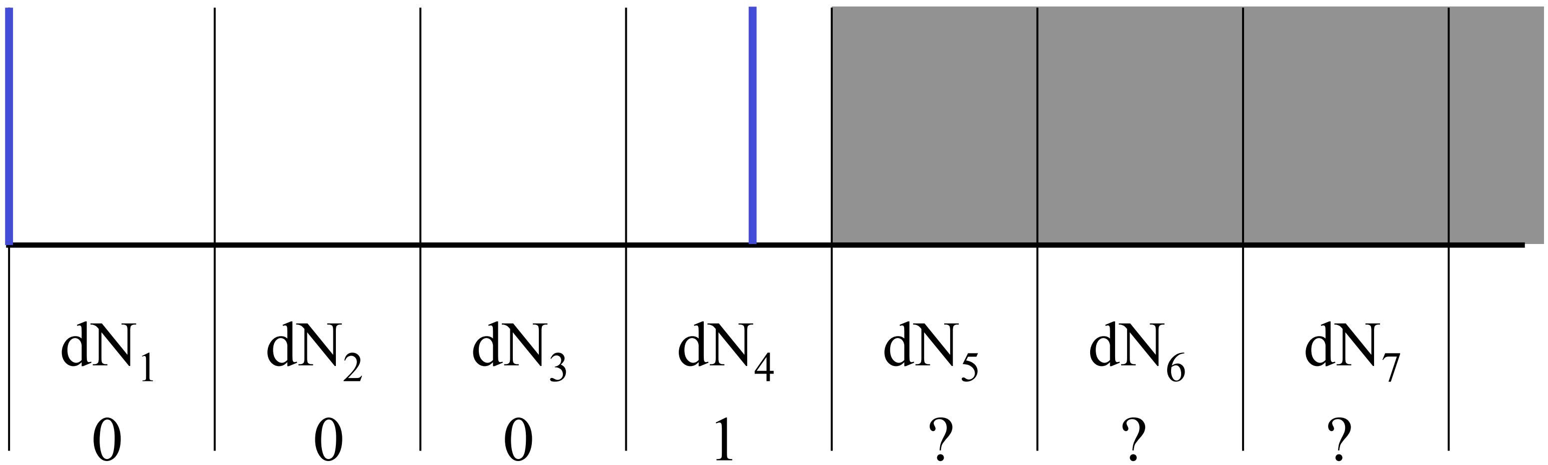
2. Poisson Process Factoids

- The probability distribution for the number of events in an interval is given by:

$$\Pr[n \text{ events in } (t_i, t_i + \Delta t]] = \frac{(\lambda_i \Delta t)^n \cdot e^{-\lambda_i \Delta t}}{n!}$$

- The distributions for the number of events in non-overlapping intervals is independent.
- If λ is constant, i.e. $\lambda_i = \lambda$, the waiting time between events is exponentially distributed with parameter λ.

ISI Density vs. Poisson Rate



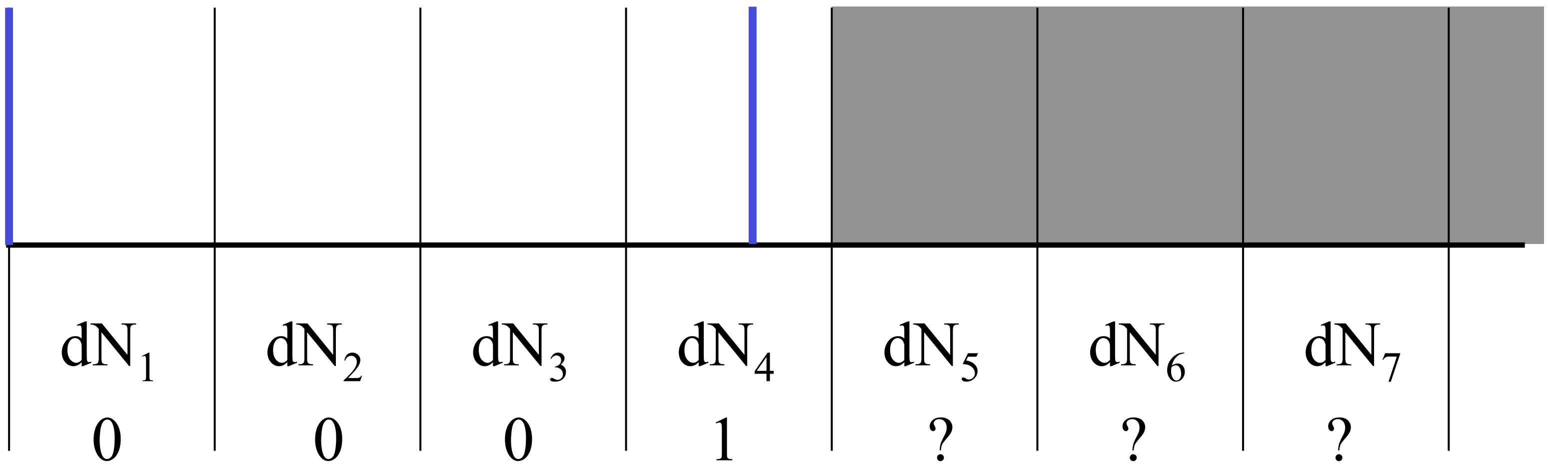
Poisson Case (Independent intervals):

$$p(ISI \text{ is in } (3,4]) = p(dN_1 = 0)\,p(dN_2 = 0)\,p(dN_3 = 0)\,p(dN_4 = 1)$$

$$= \left(e^{-\lambda_1 \Delta t}\right)\left(e^{-\lambda_2 \Delta t}\right)\left(e^{-\lambda_3 \Delta t}\right)\left(\lambda_4 \Delta t \cdot e^{-\lambda_4 \Delta t}\right)$$

$$= \lambda_4 \Delta t \cdot \exp\left(-\sum_{t=1}^{4} \lambda_t \Delta t\right)$$

Non-Poisson Case



$$p(dN_1, dN_2, dN_3) = \cancel{p(dN_1)p(dN_2)p(dN_3)}$$

$$= p(dN_1)p(dN_2 \mid dN_1)p(dN_3 \mid dN_1, dN_2)$$

In order to construct general point process models, we need the models to describe these conditional probabilities.

3. Conditional Intensity Function

- The conditional intensity of a neuron, $\lambda(t \mid H_t)$, is defined by:

$$\lambda(t \mid H_t) = \lim_{\Delta t \to 0} \frac{\Pr(\text{Spike in } (t, t + \Delta t) \mid H_t)}{\Delta t}$$

  where, H_t is the history of the the spiking process up to time t.

- This generalizes the rate function for a Poisson process since we can now determine the probability of spiking in any interval, even if it is not independent of other intervals.

3. Conditional Intensity Function

- The conditional intensity provides the building blocks for computing probabilities and likelihoods.
- For small Δt ,

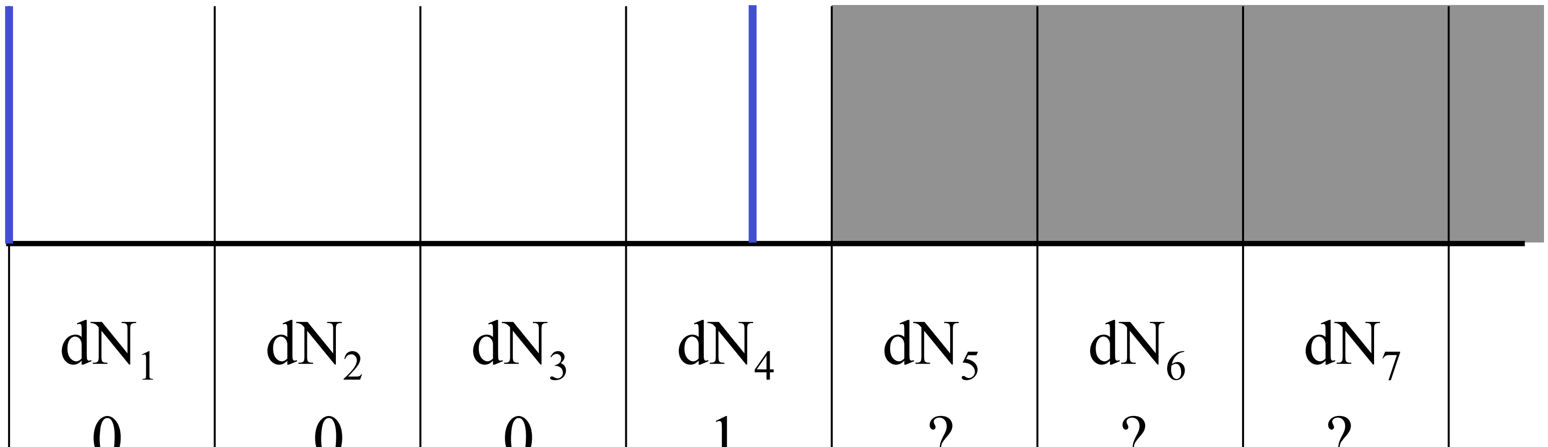
$$\Pr\left[dN_i = 0 \mid H_i\right] = \left[1 - \lambda\left(t_i \mid H_i\right)\Delta t\right] + o\left(\Delta t\right) = e^{-\lambda(t_i \mid H_i)\Delta t} + o\left(\Delta t\right)$$

$$\Pr\left[dN_i = 1 \mid H_i\right] = \lambda\left(t_i \mid H_i\right)\Delta t + o\left(\Delta t\right)$$

$$= \lambda(t_i \mid H_i)\Delta t e^{-\lambda(t_i \mid H_i)\Delta t} + o\left(\Delta t\right)$$

$$\Pr\left[dN_i = 2 \mid H_i\right] = o\left(\Delta t\right)$$

ISI Density vs. Conditional Intensity



Non-Poisson Case:

$$p(ISI \text{ is in } (3,4]) = p(dN_1)\,p(dN_2 \mid H_2)\,p(dN_3 \mid H_3)\,p(dN_4 \mid H_4)$$

$$= \left(e^{-\lambda(t_1|H_1)\Delta t}\right)\left(e^{-\lambda(t_2|H_2)\Delta t}\right)\left(e^{-\lambda(t_3|H_3)\Delta t}\right)\left(\lambda(t_4 \mid H_4)\Delta t \cdot e^{-\lambda(t_4|H_4)\Delta t}\right)$$

$$= \lambda(t_4 \mid H_4)\Delta t \cdot \exp(-\sum_{u=1}^{4} \lambda(t_u \mid H_u)\Delta t)$$

ISI Density vs. Conditional Intensity

In discrete time, the ISI probability is:

$$p(t \mid H_t) = \lambda(t \mid H_t)\Delta t \cdot \exp(-\sum_{u=1}^{t} \lambda(u \mid H_u)\Delta t)$$

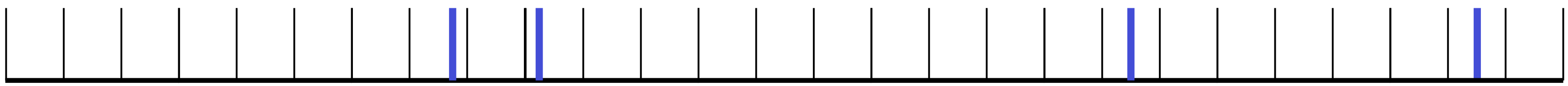
In continuous time, the ISI density becomes:

$$p(t \mid H_t) = \lambda(t \mid H_t) \cdot \exp(-\int_0^t \lambda(u \mid H_u)du)$$

We can also invert this function to obtain the conditional intensity from the ISI density:

$$\lambda(t \mid H_t) = \frac{p(t \mid H_t)}{1 - \int_0^t p(u \mid H_u)du}$$

4. Point Process Likelihood



$$p(\text{Spike Train}) = \prod_{u=1}^{T} p(dN_u \mid H_u)$$

$$= \prod_{t \in \text{Spikes}} \lambda(t \mid H_t)\Delta t \cdot \exp(-\lambda(t \mid H_t)\Delta t) \prod_{n \notin \text{Spikes}} \exp(-\lambda(n \mid H_n)\Delta t)$$

$$= \prod_{t \in \text{Spikes}} \left(\lambda(t \mid H_t)\Delta t\right) \cdot \exp(-\sum_{u=1}^{T} \lambda(u \mid H_u)\Delta t)$$

$$= \exp(\sum_{u=1}^{T} \log(\lambda(u \mid H_u)\Delta t) dN_u - \lambda(u \mid H_u)\Delta t)$$

Continuous Time Likelihood

$$L\left(\text{Spike Train} \mid \theta\right) = \exp\left(\sum_{u=1}^{T} \log(\lambda(u \mid H_u)\Delta t)\Delta N_u - \lambda(u \mid H_u)\Delta t\right)$$

$$\downarrow$$

$$L(\text{Spike Train} \mid \theta) = \exp(\int_0^T \log(\lambda(u \mid H_u))dN - \lambda(u \mid H_u)du)$$

Any point process describing neural spike train data can be modeled using a conditional intensity function, and has this likelihood form!

5. Time Rescaling

Let's return to the probability distribution for a single ISI:

$$p(t \mid H_t) = \lambda(t \mid H_t) \cdot \exp(-\int_0^t \lambda(u \mid H_u) du)$$

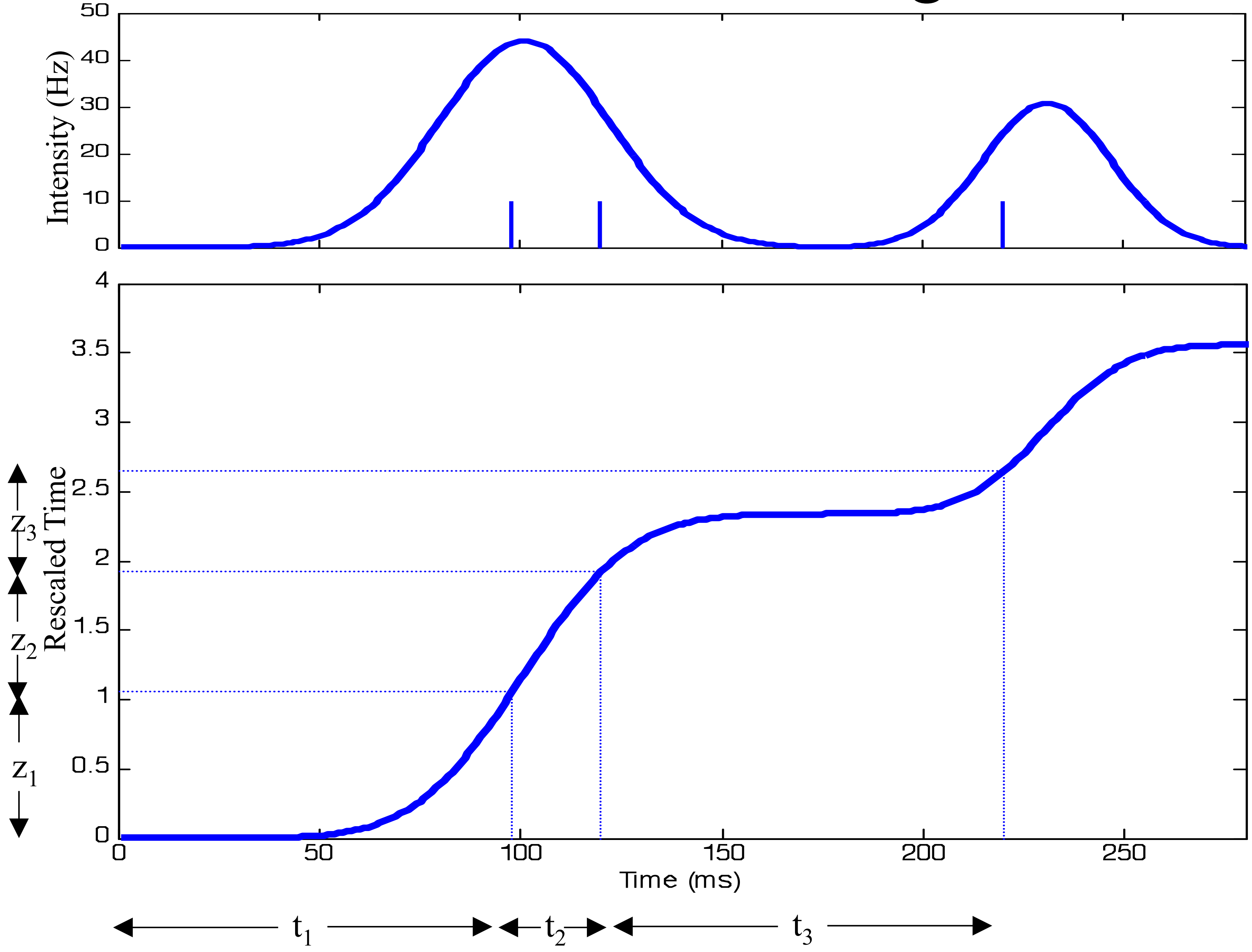
and make a change of variables,

$$z = \int_0^t \lambda(u \mid H_u) du$$

Then the distribution $p(z) = p(t \mid H_t) \left| \frac{dz}{dt} \right|^{-1} = \exp(-z)$

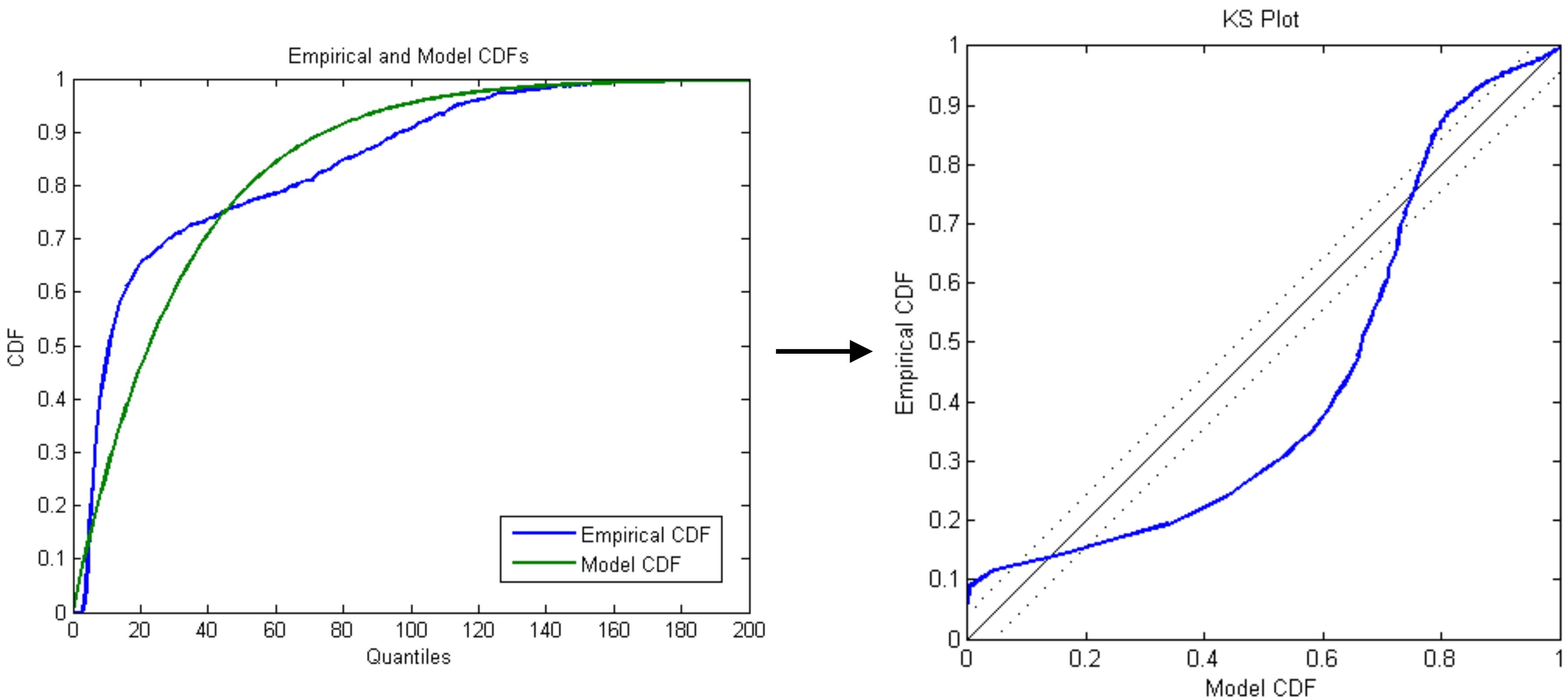
is exponential with parameter $\lambda = 1$.

Time Rescaling



KS Plots

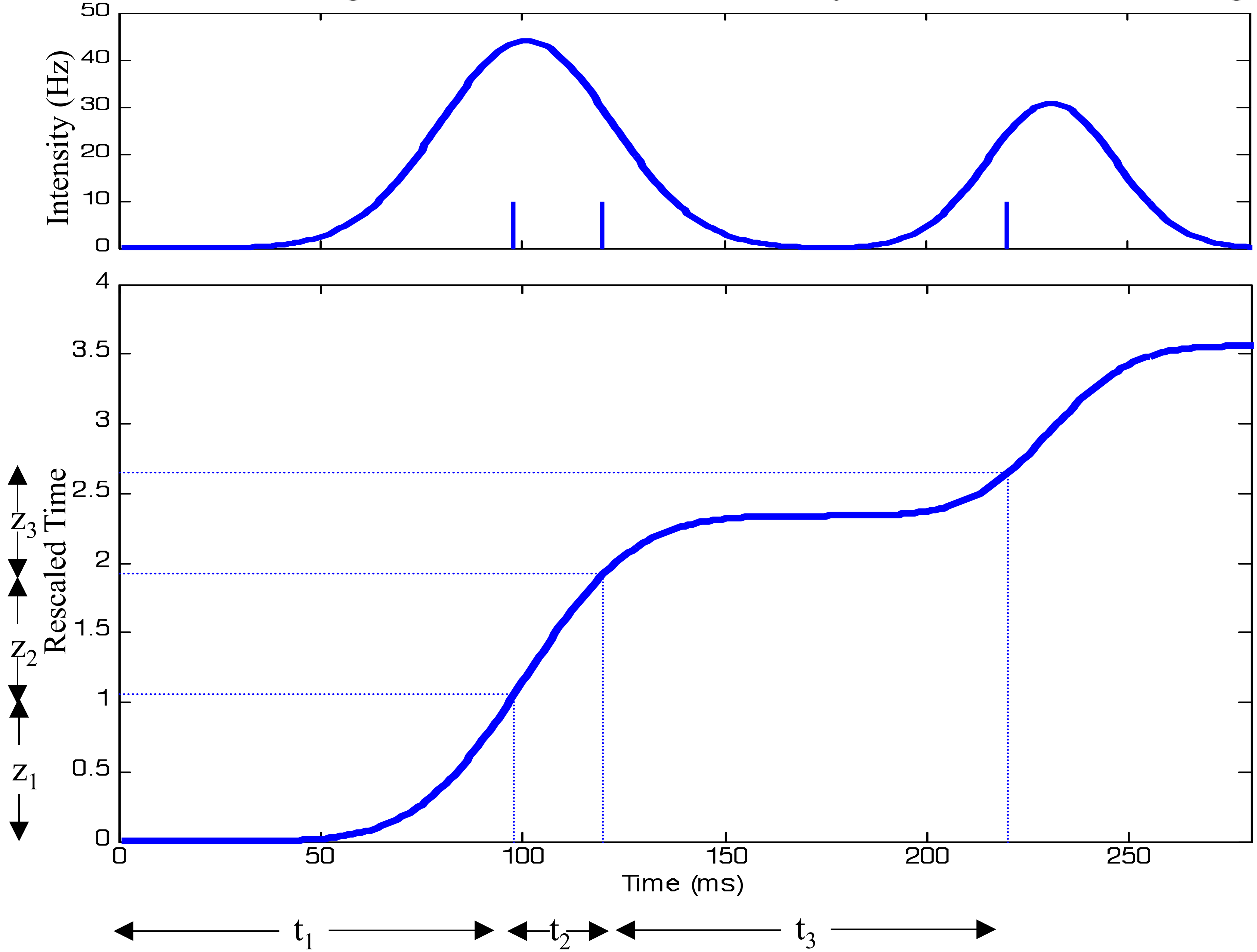
Graphical measure of goodness-of-fit, based on time rescaling, comparing an empirical and model cumulative distribution function. If the model is correct, then the rescaled ISIs are independent, identically distributed random variables whose KS plot should produce a 45° line [*Ogata, 1988*].



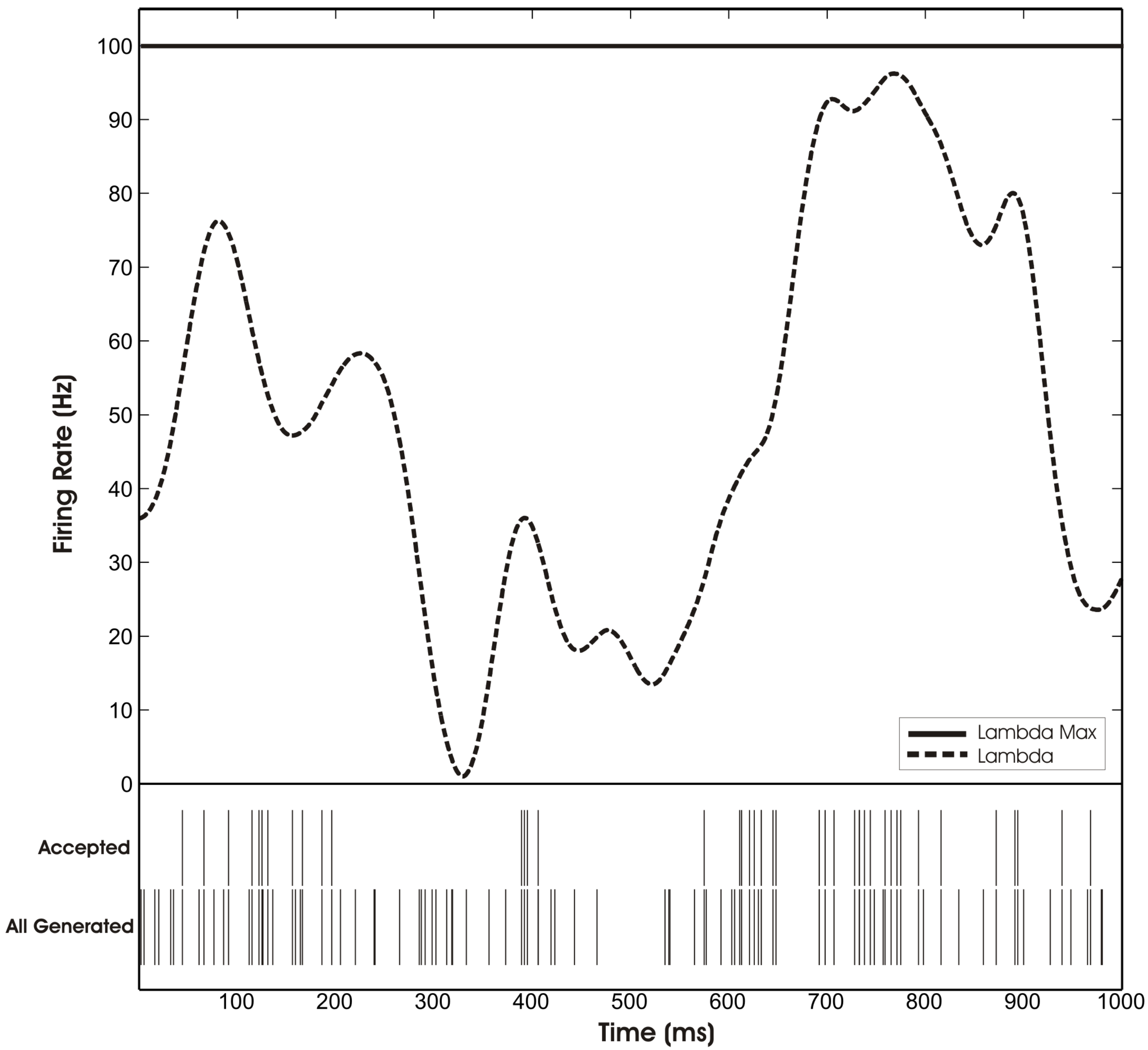
6. Simulating Point Processes

- Problem:
  - Given a conditional intensity function, $\lambda(t \mid H_t)$, generate a point process that has this as its conditional intensity.
- Methods:
  - Time-rescaling
  - Thinning

Simulating Point Processes by Time Rescaling



Simulating Point Processes by Thinning



Take Home Points

- The **conditional intensity function** generalizes the rate function of a Poisson process.
- Defining a conditional intensity function or **ISI density** fully characterizes the point process, and implicitly defines the other.
- The **likelihood function** for any point process can be expressed in a characteristic form, as a function of the conditional intensity.
- The **time rescaling theorem** allows us to map any point process into a Poisson process with unit rate.
- We can **simulate** point processes using either time-rescaling or thinning.

Question for neural coding analyses

- How do we relate neural spiking activity to biological and behavioral signals?

- A point process model expresses a conditional intensity function in terms of other relevant covariates.

$$\lambda(t \mid H_t) = f(t, x_t, H_t)$$

- Up next: Generalized linear Models (GLMs)