Integrate and Fire like models with stable distributions for the Interspike Intervals.

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Brain Dynamics and Statistics: Simulation versus Data

Outline

- Stable distributions
  - Definition and main properties
  - Why stable distributions look interesting for neuronal modelling
- Integrate and Fire models
  - Gerstein and Mandelbrot pioneering paper
  - Further models
- New models
  - A very simple IF model with stable ISIs distribution
  - A continuos time random walk with stable distributed inter-times
  - Advantages and gaps of the model
  - A further model
- Future developments

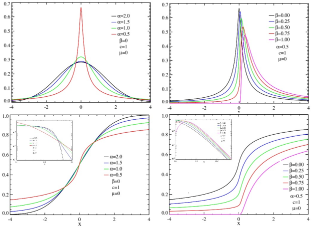
Stable distributions

What are stable distributions?

Definition

Let X_1 and X_2 be independent copies of a random variable X. Then X is said to be stable if

- it is not degenerate;
- for any constants $a > 0$ and $b > 0$ the random variable $aX_1 + bX_2$ has the same distribution as $cX + d$ for some constants $c > 0$ and d.

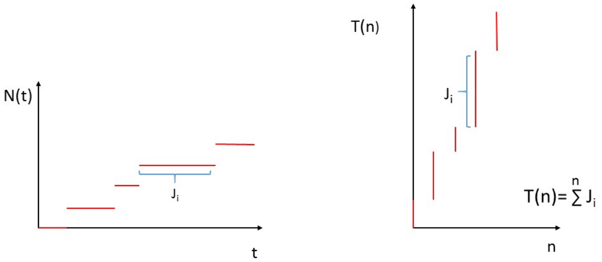


Why univariate Stable Distributions are interesting?

- heavy tails: the tail probabilities (and densities) are asymptotically power laws:
$$P(X > x) \approx c_{\alpha,\beta} x^{-\alpha} \quad (1)$$
- there are no closed form expression for general stable distributions (except the cases of Normal, Cauchy or Inverse Gaussian distribution). However, the Laplace/Fourier transforms are known;
- their distributions form a four-parameter family of continuous probability distributions;
- Not all the moments exist (this may give problems for estimation tasks)
- Sums of $\alpha-$stable random variables are $\alpha-$stable. This result can be extended to the case of dependent summands, under suitable hypotheses;
- Suitable limit theorems hold.

Stochastic Processes related with Sums of i.i.d. r.v.s

- Let $J_i, i = 1, 2, \ldots$ be a sequence of positive independent identically distributed random variables; we interpret J_i as waiting times between successive jumps of a stochastic process;
- Let $T(n) = \sum_{i=1}^{n} J_i$;
- Let $N(t) = \max\{n \geq 0 : T(n) \leq t\}$ be the number of jumps of the process up to time t



{N(t)≥n}={T(n)≤ t}

Limit Process

Theorem

Let $J_i, i = 1, 2, \ldots$ be distributed as $J \in DOA(D)$, where D is $\beta-$stable, with $0 < \beta < 1$ (example $P(J > t) = Bt^{-\beta}, B > 0$). Then $c_n T(\lfloor nt \rfloor) \to D(t)$ and the increasing process $D(t)$ is called a $\beta-$stable subordinator.

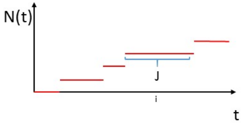
Definition

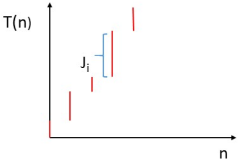
The process $E(t) = \inf\{u > 0 : D(t) > t\}$ is said *Inverse Stable Subordinator, it is the first passage time of the process $D(t)$.*

Remarks

- *The processes D, E are inverses: $\{E(t) \leq u\} = \{D(u) \geq t\}$*
- *If we chose $c_n = n^{-1/\beta}$ one has $c^{-\beta} N(ct) \Rightarrow E(t)$.*

Links between the considered processes

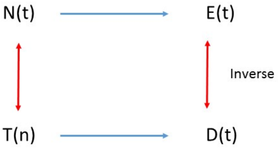




$T(n)=\sum^{n} J_i$

$\{N(t)\geq n\}=\{T(n)\leq t\}$

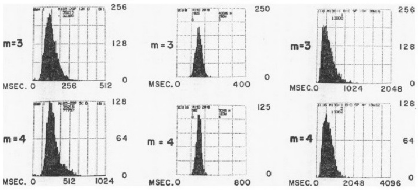
Inverse



$$E[\, e^{-i\lambda D(u)} \,] = e^{-u(i\lambda)^{\beta}}$$

Gerstein and Mandelbrot data

In 1964 Gerstein and Mandelbrot studied the joint distributions of ISIs, observing the stable property on their data

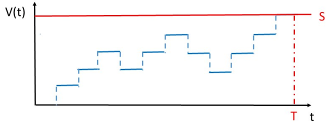


With suitable changes in time scale, the shape of each of the first few successive orders of scaled interval histogram remains approximately the same. This means that a sum of successive interspike intervals has the same probability density-to within a scale factor-as the basic interspike intervals

Gerstein and Mandelbrot: the integrate and Fire model

Remarks

1. Mathematical knowledge of stable distributions in 1964 *was limited; Gerstein and Mandelbrot knew three candidates to fit the data: Gaussian, Cauchy and Inverse Gaussian (IG) distributions.*
2. IG is the distribution of the First Passage Time of a Brownian Motion through a constant boundary: model the membrane potential as a random walk, take its limit and identify the interspike times with the first passage times of the random walk through a boundary.



Stable distribution for neural code

Remark

In 1975 A. Holden observed: information in a spike train is preserved when the p.d.f. is stable under convolution with itself. A hypothesis is proposed that stable interspike interval distributions characterize a simple information transmission pathway, and that non-stable interval distributions suggest more complex information processing functions.

Remark

A code characterized by stable ISIs is more robust: the possible lost of some PSPs does not change the distribution of ISIs (in the case of many PSPs impinging on the neuron)

Improvements of Integrate and Fire model

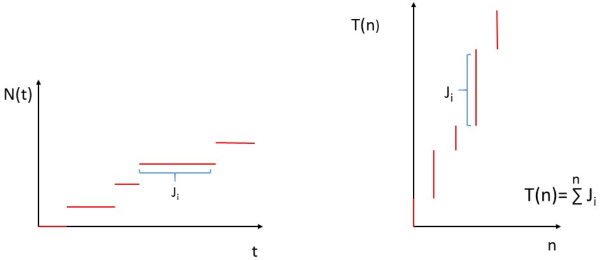
Many variants of the original Gerstein and Mandelbrot have appeared in the literature inspired by the Integrate and Fire paradigm:

- Including the spontaneous membrane potential decay (Leaky Integrate and Fire Models)
- Including reversal potentials
- Using time dependent thresholds
- Relaxing the renewal hypothesis (multi-compartment models)
- ...

Remark

Incredibly, all those models forgot the original motivation of Integrate and Fire paradigm: the ISI have stable distribution! Data show ISIs distributions with heavy tails (Segev, Benveniste et al., 2001)

A simplified model with stable ISIs distribution



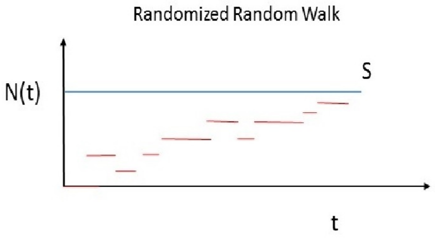
$$\{N(t) \geq n\} = \{T(n) \leq t\}$$

… But we want positive and negative jumps!

Let us rethink to integrate and fire models

Remark

Brownian motion is the continuous limit of a simple random walk, but it is also the limit of a randomized random walk: intertimes between jumps are exponential and the first passage time is Inverse Gaussian (stable)



Questions

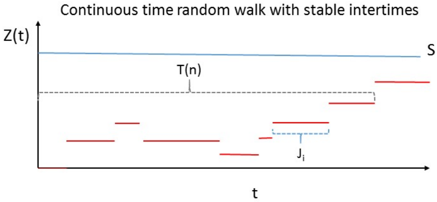
1. *Is it possible to model the membrane potential evolution by means of a process whose jumps happen according with a stable distribution, getting Interspike times characterized by stable distribution?*
2. *When the number of jumps diverges in a suitable way, can we study the limit process and its First Passage time distribution?*

A LIF model generating a stable ISIs distribution is proposed in Persi, Horn, Volman, Segev and Ben-Jacob (2004) to model bursting activity. They introduce a time non-homogeneous model characterized by frequency-dependent synapses, to generate stable distributions.

Continuous-Time Random Walk

Definition

We call continuous-time random walk (CTRW): $Z := \{Z(t), t \in \mathbb{R}\}$ such that $Z(t) = X_{N(t)}$, where X is a simple r.w. with symmetric jumps



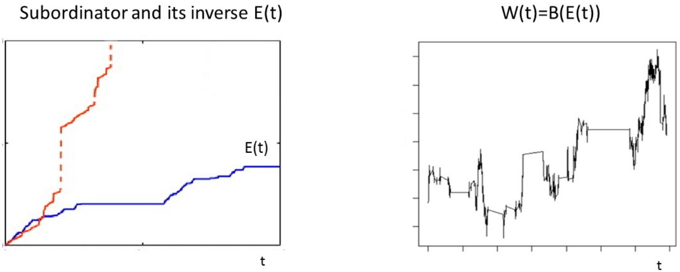
We model the membrane potential evolution through a Continuous Time Random Walk

Scaling limit

Remark

It is well-known (Meerschaert) that the CTRW Z possesses a scaling limit process, namely $W := \{W(t), t \in \mathbb{R}\}$ *such that* $W(t) = B(E(t))$*, where* $B(t)$ *is a standard Brownian motion with diffusion coefficient equal to* $a^2/2$ *and* $E(t)$ *is an inverse* β*-stable subordinator independent of* B*.*

Rescaled limit processes



ISIs distribution computation: Marginal distribution of $W(t)$

Remark

The process W is also called Grey Brownian Motion. It is associated with Sub-Diffusion Processes since it is slower then the corresponding Diffusion Process.

Let $\lambda = a/\sqrt{2}$ and let $g(x,t)$ be the marginal density of W for each time t, it is solution of

$$D_t^{\beta} g(x,t) = \lambda^2 \frac{\partial^2}{\partial x^2} g(x,t), \qquad \beta \in (0,1), \tag{2}$$

where the differential operator is the Dzhrbashyan–Caputo derivative of order β whose solution is

$$g(x,t) = \frac{1}{2\lambda t^{\beta/2}} \sum_{r=0}^{\infty} \frac{1}{r!\Gamma(-r\beta/2 + 1 - \beta/2)} \left(-\frac{|x|}{\lambda t^{\beta/2}}\right)^r, \qquad t \in \mathbb{R}_+,\ x \in \mathbb{R}.$$

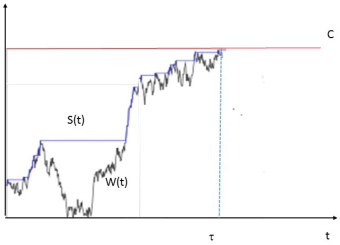
ISIs distribution: a trick to solve the problem

Problem

First Passage Time distribution of $W(t) = B(E(t))$ *through a boundary?*

Idea

The FPT of $W(t)$ *coincides with that of its running supremum* $S(t) = \sup_{0 \leq s \leq t}(W(s))$, $t \in \mathbb{R}_+$



The First Passage Time Problem

Remarks

1. *We can determine the one-dimensional distribution of $S(t)$:*

$$\mathbb{P}(S(t) \in dx)/dx = \frac{1}{\lambda t^{\beta/2}} \sum_{r=0}^{\infty} \frac{1}{r!\Gamma(-r\beta/2 + 1 - \beta/2)} \left(-\frac{x}{\lambda t^{\beta/2}}\right)^r.$$

2. *It holds:* $\mathbb{P}(T(C) < y) = \mathbb{P}(S(y) > C)$, *where*

$$T(C) = \inf\{t \colon S(t) > C\}, \qquad C > 0,$$

3. *The Laplace Transform of the First Passage Time is*

$$\begin{aligned}\mathbb{E}e^{-\vartheta T(C)} &= \int_0^\infty e^{-\vartheta y}\mathbb{P}(T(C) \in dy) \\ &= e^{-\frac{b}{\lambda}\vartheta^{\beta/2}}\end{aligned}$$

Strenghts and Gaps of the Model

Strenghts:

- The ISIs exhibit stable distributions, admitting density;
- The Laplace transform of the ISIs distribution is known

Gaps:

- The moments of the ISIs diverge (due to the heavy tails of the distributions);
- The present model is symmetric: no drift is included (but extensions to the case with drift are possible)
- Special distributions such as the Gamma distribution are not included in the model.

Remark

Data do not allow to observe the ISIs distribution tails for very large times. Models exhibiting ISIs with distributions similar to a stable distribution in some central region, but with lighter tails fit observed data.

Tempered stable distributions

Idea

To introduce distributions that are "stable-like" in the center but with lighter tails and to model the membrane potential evolution through Levy processes characterized by these distributions to as inter-times between jumps.

Remark

Recent works enlarge the class of stable distribution through the $\eta-$**tempered** $\alpha-$**stable distribution**.

Remark

This class includes stable distribution and other distributions such as the Gamma distribution. Its r.v.s may exhibit finite moments

Remark

Processes of sub-diffusion characterized by tempered power-law waiting times were proposed by Meeschaert, Sabzikar and Chen, 2015. These processes can be used to model the membrane potential evolution.

Following the same approach as in the case of stable distributions we are able to determine the Laplace transform of the ISIs distribution when the jumps have tempered stable distribution.

$$\mathbb{E}e^{-\vartheta T(C)} = \int_0^\infty e^{-\vartheta y}\mathbb{P}(T(C) \in dy) = \int_0^\infty dy e^{\vartheta y}\frac{\partial}{\partial y}\mathbb{P}(T(C) < y)$$
$$= e^{-\frac{C}{\lambda}[(\eta+\vartheta)^\beta - \eta^\beta]^{1/2}}.$$

Open Problems

- To introduce a drift term to avoid the symmetry of the model;
- To improve the model in order to have the same tempered stable distribution for the inter-arrival times and for the first passage times;
- To develop statistical methods to estimate the parameters of the tempered stable distribution.

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