

INTERSPIKE INTERVAL STATISTICS FOR QUADRATIC INTEGRATE-AND-FIRE NEURONS SUBJECT TO ALPHA-STABLE NOISE

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Abstract

The statistics of interspike intervals is one of the principle characteristics of the synaptic activity of neurons. This statistics can be presented with the values of the moments of these intervals. For the integrate-and-fire type models, the formalism of first passage time provides partial differential equations for a rigorous calculation of these values for neurons subject to a white Gaussian noise. However, the procedure of derivation of these equations is quite sophisticated and the results for Gaussian noise are not as trivial as they can appear if one does not look at the rigorous derivation procedure. The derivation of analogous partial differential equations for the case of alpha-stable (Lévy) noise is even more involved. In this paper, the equations providing moments of interspike intervals are derived for quadratic integrate-and-fire neurons subject to symmetric alpha-stable noise. The results are presumably generalizable to other integrate-and-fire type models (e.g., leakage ones).

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Key words

Lévy flights, alpha-stable noise, first passage time, interspike intervals, integrate-and-fire neurons

1 Introduction

The development of the first passage time formalism on the basis of the Fokker–Planck equation for systems subject to white Gaussian noise provided a partial dif-

ferential equation formulation delivering rigorous results on the first passage time and its moments [Gardiner, 1997]. In particular, this formalism gives the mean interspike interval and its variance for integrate-and-fire type models in mathematical neuroscience [Brunel et al., 2003; Lindner et al., 2003] (where other approaches can deliver approximate results [Goryunov et al., 2024] with their utility for one or another specific tasks, this framework is exact as long as the conditions are time-independent).

The case of non-Gaussian white noises, which must be α -stable ones with $\alpha < 2$ [Zolotarev, 1986], the generalization ought to be constructed carefully as one has to properly handle a non-Fickian diffusion term (fractional derivative) [Klyatskin, 1980; Klyatskin, 2005; Chechkin et al., 2003; Toenjes et al., 2013] instead of the normal diffusion one—the second order spatial derivative. Meanwhile the case of non-Gaussian fluctuations (Lévy flights) attracts attention in relation to the dynamics of neural networks [Roberts et al., 2015; Wang et al., 2021; Wang et al., 2022; Goldobin et al., 2024; Rybalova et al., 2024a; Rybalova et al., 2024b] and other systems where fractional-order derivatives emerge [Romero-Meléndez et al., 2022; Dolmatova et al., 2023; Rybalova et al., 2024c; Muhafzan et al., 2022].

2 Fractional backward Fokker–Planck equation

We consider a quadratic integrate-and-fire neuron (QIF) with additive noise [Izhikevich, 2007; Ermentrout et al., 1986],

$$\dot{V} = V^2 + \eta + \sigma\xi(t),$$

where V is the membrane voltage, the term η contains both the intrinsic properties of a QIF and its synaptic input current, which includes the contributions from the synaptic activity of other neurons in the population; σ is the noise scale (“amplitude”), $\xi(t)$ is the normalized δ -correlated α -stable noise [Zolotarev, 1986]. When the membrane voltage V reaches the threshold value $V_{\text{th}} \rightarrow +\infty$, it is reset to $V_{\text{res}} \rightarrow -\infty$ and emits a synaptic spike into network. The conditional probability density function $P(V, t|V_0, t_0)$ obeys a fractional Fokker–Planck equation [Klyatskin, 2005; Chechkin et al., 2003; Toenjes et al., 2013; Goldobin et al., 2024]:

$$\frac{\partial P(V, t|V_0, t_0)}{\partial t} + \frac{\partial}{\partial V} (f(V) P(V, t|V_0, t_0)) - \dot{\Phi}_t^{(\xi)}(i\widehat{Q})P(V, t|V_0, t_0) = 0, \quad (1)$$

where $f(V) \equiv \eta + V^2$ and $\widehat{Q} \equiv (\partial/\partial V)$, with initial conditions $P(V, t_0|V_0, t_0) = \delta(V - V_0)$. For the case of a symmetric α -stable noise (confer Eq. (3) in [Goldobin et al., 2024] with $\mu = \beta = 0$) of amplitude σ , function $\dot{\Phi}_t^{(\xi)}(k) = -\sigma^\alpha |k|^\alpha$. Here and hereafter, we consider only this symmetric case and use the form of operator $\dot{\Phi}_t^{(\xi)}(i\widehat{Q})$ in the Fourier space, where $\dot{\Phi}_t^{(\xi)}(i(\partial/\partial V)) e^{ikV} \equiv -\sigma^\alpha |k|^\alpha e^{ikV}$, $\alpha \in (0; 2]$.

With the characteristic function

$$F_V(k, t) \equiv \langle e^{ikV} \rangle = \int_{-\infty}^{+\infty} P(V, t|V_0, t_0) e^{ikV} dV, \quad (2)$$

one can write the Fourier transform

$$P(V, t|V_0, t_0) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} F_V(k, t) e^{-ikV} dk, \quad (3)$$

and

$$\begin{aligned} \dot{\Phi}_t^{(\xi)}(i\widehat{Q})P(V, t|V_0, t_0) \\ = \frac{-\sigma^\alpha}{2\pi} \int_{-\infty}^{+\infty} |k|^\alpha F_V(k, t) e^{-ikV} dk. \end{aligned} \quad (4)$$

Hence, the fractional Fokker–Planck equation (1) reads

$$\begin{aligned} \frac{\partial P(V, t|V_0, t_0)}{\partial t} + \frac{\partial}{\partial V} (f(V) P(V, t|V_0, t_0)) \\ + \frac{\sigma^\alpha}{2\pi} \int_{-\infty}^{+\infty} dk |k|^\alpha e^{-ikV} \\ \times \int_{-\infty}^{+\infty} dV_1 e^{ikV_1} P(V_1, t|V_0, t_0) = 0. \end{aligned} \quad (5)$$

Further, one can derive the backward fractional Fokker–Planck equation (fractional Kolmogorov equation) for (5), which governs the conditional probability density of the QIF to be at V_0 at t_0 if it is at V at time instant $t \geq t_0$ —i.e. a version of partial differential equation (5) with respect to V_0, t_0 , instead of V, t . One can make use of the fact that the probability of a path trough point V_1 at t_1 is $P(V, t|V_1, t_1)P(V_1, t_1|V_0, t_0)$ integrated over V_1 is the total probability of the transition $(V_0, t_0) \rightarrow (V, t)$,

$$\int_{-\infty}^{+\infty} dV_1 P(V, t|V_1, t_1)P(V_1, t_1|V_0, t_0) = P(V, t|V_0, t_0),$$

and therefore is independent of t_1 . Namely,

$$\begin{aligned} 0 &= \frac{\partial}{\partial t_1} \int_{-\infty}^{+\infty} dV_1 P(V, t|V_1, t_1)P(V_1, t_1|V_0, t_0) \\ &= \int_{-\infty}^{+\infty} dV_1 \left(P(V, t|V_1, t_1) \frac{\partial P(V_1, t_1|V_0, t_0)}{\partial t_1} \right. \\ &\quad \left. + \frac{\partial P(V, t|V_1, t_1)}{\partial t_1} P(V_1, t_1|V_0, t_0) \right); \end{aligned}$$

substituting the first time-derivative term from (5), one obtains

$$\begin{aligned} \int_{-\infty}^{+\infty} dV_1 \left(-P(V, t|V_1, t_1) \frac{\partial (f(V_1) P(V_1, t_1|V_0, t_0))}{\partial V_1} \right. \\ \left. - P(V, t|V_1, t_1) \frac{\sigma^\alpha}{2\pi} \int_{-\infty}^{+\infty} dk |k|^\alpha e^{-ikV_1} \right. \\ \left. \times \int_{-\infty}^{+\infty} dV_2 e^{ikV_2} P(V_2, t_1|V_0, t_0) \right. \\ \left. + \frac{\partial P(V, t|V_1, t_1)}{\partial t_1} P(V_1, t_1|V_0, t_0) \right) = 0. \end{aligned} \quad (6)$$

For the first term one employs partial integration to find

$$\begin{aligned} - \int_{-\infty}^{+\infty} dV_1 P(V, t|V_1, t_1) \frac{\partial (f(V_1) P(V_1, t_1|V_0, t_0))}{\partial V_1} \\ = -P(V, t|V_1, t_1) f(V_1) P(V_1, t_1|V_0, t_0) \Big|_{V_1=-\infty}^{V_1=+\infty} \\ + \int_{-\infty}^{+\infty} dV_1 P(V_1, t_1|V_0, t_0) f(V_1) \frac{\partial P(V, t|V_1, t_1)}{\partial V_1} \\ = \int_{-\infty}^{+\infty} dV_1 P(V_1, t_1|V_0, t_0) f(V_1) \frac{\partial P(V, t|V_1, t_1)}{\partial V_1}, \end{aligned} \quad (7)$$

where the term $(\dots)|_{V_1=-\infty}^{V_1=+\infty}$ is zero since the voltage resetting of a QIF effectively creates the periodic boundary condition at $V = \pm\infty$. For the second term in the integrand of (6), one changes the notation of integration variables $V_1 \leftrightarrow V_2$ and $k \rightarrow -k$ to obtain

$$\begin{aligned} & - \int_{-\infty}^{+\infty} dV_2 P(V, t|V_2, t_1) \frac{\sigma^\alpha}{2\pi} \int_{-\infty}^{+\infty} dk |k|^\alpha e^{ikV_2} \\ & \quad \times \int_{-\infty}^{+\infty} dV_1 e^{-ikV_1} P(V_1, t_1|V_0, t_0) \\ & = - \int_{-\infty}^{+\infty} dV_1 P(V_1, t_1|V_0, t_0) \frac{\sigma^\alpha}{2\pi} \int_{-\infty}^{+\infty} dk |k|^\alpha e^{-ikV_1} \\ & \quad \times \int_{-\infty}^{+\infty} dV_2 e^{ikV_2} P(V, t|V_2, t_1), \quad (8) \end{aligned}$$

where we used the commutativity of the integrations over V_1 and V_2 for the rearrangements in (8). Substituting (7) and (8) into (6), one finds

$$\begin{aligned} & \int_{-\infty}^{+\infty} dV_1 P(V_1, t_1|V_0, t_0) \left(f(V_1) \frac{\partial P(V, t|V_1, t_1)}{\partial V_1} \right. \\ & - \frac{\sigma^\alpha}{2\pi} \int_{-\infty}^{+\infty} dk |k|^\alpha e^{-ikV_1} \int_{-\infty}^{+\infty} dV_2 e^{ikV_2} P(V, t|V_2, t_1) \\ & \quad \left. + \frac{\partial P(V, t|V_1, t_1)}{\partial t_1} \right) = 0. \quad (9) \end{aligned}$$

The latter equality is satisfied for all t_1 if the expression in the brackets is zero. This is the *fractional backward Fokker–Planck equation* (or *fractional Kolmogorov equation*):

$$\begin{aligned} & - \frac{\partial P(V, t|V_0, t_0)}{\partial t_0} - f(V_0) \frac{\partial}{\partial V_0} P(V, t|V_0, t_0) \\ & \quad + \sigma^\alpha \left| \frac{\partial}{\partial V_0} \right|^\alpha P(V, t|V_0, t_0) = 0. \quad (10) \end{aligned}$$

3 First passage time problem

The conditional probability of staying in $a < V < b$ at time instant t for the system starting from V_0 at t_0 is

$$p(a < V < b, t|V_0, t_0) = \int_a^b P(V, t|V_0, t_0) dV$$

and obeys the same Kolmogorov equation (10), which can be integrated with respect to V over the open interval $V \in (a, b)$:

$$\begin{aligned} & - \frac{\partial p(a < V < b, t|V_0, t_0)}{\partial t_0} - f(V_0) \frac{\partial p(a < V < b, t|V_0, t_0)}{\partial V_0} \\ & \quad + \sigma^\alpha \left| \frac{\partial}{\partial V_0} \right|^\alpha p(a < V < b, t|V_0, t_0) = 0. \quad (11) \end{aligned}$$

For the first passage problem, where the states are adsorbed as soon as they arrive at the boundary, Eq. (11) must be supplemented with the conditions:

$$p(a < V < b, t|V_0, t_0) = 0 \quad \text{for } V_0 \leq a \text{ and } V_0 \geq b,$$

which serve as boundary conditions for this equation, and obvious initial condition

$$p(a < V < b, t_0|V_0, t_0) = \begin{cases} 1, & \text{for } a < V_0 < b; \\ 0, & \text{otherwise.} \end{cases}$$

The system state escapes the domain (a, b) during infinitesimal period dt with likelihood $(-\frac{\partial p}{\partial t} dt)$; therefore, for the first passage time T , one finds

$$\begin{aligned} \langle T^m \rangle & = \int_{t_0}^{+\infty} t^m \left(-\frac{\partial p}{\partial t} dt \right) \\ & = -t^m p(a < V < b, t|V_0, t_0) \Big|_{t_0}^{+\infty} \\ & \quad + m \int_{t_0}^{+\infty} t^{m-1} p(a < V < b, t|V_0, t_0) dt \\ & = t_0^m + m \int_{t_0}^{+\infty} t^{m-1} p(a < V < b, t|V_0, t_0) dt, \quad (12) \end{aligned}$$

where we assumed no trapped states with infinite residence time and set

$$\lim_{t \rightarrow +\infty} t^m p(a < V < b, t|V_0, t_0) = 0. \quad (13)$$

Multiplying Eq. (11) by t^{m-1} and integrating over t from t_0 to $+\infty$ one finds

$$\begin{aligned} & - \int_{t_0}^{+\infty} dt \frac{\partial p(a < V < b, t|V_0, t_0)}{\partial t_0} t^{m-1} \\ & \quad - f(V_0) \frac{\partial}{\partial V_0} \frac{\langle T^m \rangle}{m} + \sigma^\alpha \left| \frac{\partial}{\partial V_0} \right|^\alpha \frac{\langle T^m \rangle}{m} = 0, \end{aligned}$$

where we employed $\frac{\partial}{\partial V_0} t_0^m = 0$. For autonomous systems, $p(a < V < b, t|V_0, t_0)$ depends on the time difference $(t - t_0)$, but not times t and t_0 individually; hence,

$$\frac{\partial p(a < V < b, t|V_0, t_0)}{\partial t_0} = - \frac{\partial p(a < V < b, t|V_0, t_0)}{\partial t}$$

and

$$-f(V_0) \frac{\partial}{\partial V_0} \langle T^m \rangle + \sigma^\alpha \left| \frac{\partial}{\partial V_0} \right|^\alpha \langle T^m \rangle = m \langle T^{m-1} \rangle, \quad (14)$$

with $\langle T^m \rangle = 0$ at adsorbing boundaries ($V_0 = a$ and $V_0 = b$).

4 Other boundary conditions and the case of QIF

Some physical set-ups (systems with the mirror-symmetry of V , physically inadmissible domains of V , etc.) can correspond to different boundary conditions, not adsorbing ones. Specifically, in the case of the problem of the interspike interval statistics of QIF, for the system state travel from $-\infty$ to $+\infty$, one must set boundaries at $a = -\infty$, $b = +\infty$, where b is an adsorbing boundary:

$$\langle T^m \rangle|_{V_0=b \rightarrow +\infty} = 0. \quad (15)$$

But no states can escape from $(a; b)$ through a if $a \rightarrow -\infty$, as there is an infinite deterministic state flow $f(V) = \eta + V^2$ towards positive V [inwards the domain $(a; b)$], which dominates any negative fluctuative displacements. On the other hand, the system instantly leaves the $(-\infty)$ -state; therefore, the escape times from initial states with large negative V_0 must be nearly identical, i.e.,

$$\lim_{\substack{V_0 \rightarrow a+0 \\ a \rightarrow -\infty}} \frac{\partial \langle T^m \rangle}{\partial V_0} = 0. \quad (16)$$

For the interspike interval τ , one must calculate $\langle T^m \rangle(V_0)$ with partial differential equations (14) and boundary conditions (15,16) and pick-up travels from $V_0 = -\infty$:

$$\langle \tau^m \rangle = \langle T^m \rangle|_{V_0=-\infty}. \quad (17)$$

Consistency with the mean firing rate

The mean firing rate

$$r(t) = \lim_{V=\pm\infty} V^2 P(V, t|V_0, t_0)$$

after a long transient period, at a statistically stationary state, r becomes constant and the asymptotic distribution $P_0(V) = \lim_{t \rightarrow +\infty} P(V, t|V_0, 0)$ obeys the integral of Eq. (1) [Goldobin et al., 2024]:

$$f(V)P_0(V) + \int_V^{+\infty} dV_1 \sigma^\alpha \left| \frac{\partial}{\partial V_1} \right|^\alpha P_0(V_1) = r, \quad (18)$$

which can be compared to Eq. (4) for $m = 1$:

$$-f(V_0) \frac{\partial}{\partial V_0} \langle T \rangle + \sigma^\alpha \left| \frac{\partial}{\partial V_0} \right|^\alpha \langle T \rangle = 1. \quad (19)$$

Consider a cumulative distribution

$$G(V) = \int_V^{+\infty} P_0(V_1) dV_1;$$

hence, $P(V) = -\partial G/\partial V$ and Eq. (18) takes form:

$$-f(V) \frac{\partial G}{\partial V} - \int_V^{+\infty} dV_1 \sigma^\alpha \left| \frac{\partial}{\partial V_1} \right|^\alpha \frac{\partial}{\partial V_1} G(V_1) = r. \quad (20)$$

In Fourier space, one can see that derivatives $|\partial/\partial V_1|^\alpha$ and $(\partial/\partial V_1)$ are commutative; therefore, one finds for the second term of (20): $\int_V^{+\infty} dV_1 \frac{\partial}{\partial V_1} \left| \frac{\partial}{\partial V_1} \right|^\alpha G(V_1) = - \left| \frac{\partial}{\partial V} \right|^\alpha G(V)$. Hence, Eq. (20) turns into

$$-f(V) \frac{\partial G}{\partial V} + \sigma^\alpha \left| \frac{\partial}{\partial V} \right|^\alpha G(V) = r. \quad (21)$$

Thus, we have identical partial differential equations (19) and (21) for

$$\langle T \rangle(V_0) \quad \text{and} \quad \frac{G(V)}{r}$$

with boundary conditions

$$\langle T \rangle|_{V_0=-\infty} = \langle \tau \rangle, \quad \langle T \rangle|_{V_0=+\infty} = 0$$

and

$$G(-\infty) = 1, \quad G(+\infty) = 0,$$

respectively, which means an obvious relation

$$\langle \tau \rangle = \frac{1}{r}.$$

The results for the first passage time (equivalent to the interspike interval) are consistent with the mean firing rate.

5 Conclusion

To conclude, the statistics of the interspike intervals is formally given by problem (14) with boundary conditions (15,16). It is consistent with the mean firing rate. However, the cases of $m > 1$ require an involved study with recurrent calculation of not just point values $\langle \tau^m \rangle = \langle T^m \rangle|_{V_0=-\infty}$, but the functions $\langle T^{m-1} \rangle(V_0)$ over the entire axis of V_0 . It is yet difficult to conclude whether one can conduct this study in the same way as for the calculation of r by means of the formalism of characteristic functions in [Goldobin et al., 2024].

The case of Gaussian noise was solved in quadratures in [Brunel et al., 2003; Lindner et al., 2003] and only much later an analytical solution was presented for firing rate r in [di Volo et al., 2022]. The latter solution allowed for a progress in understanding and characterization of the neural dynamics [di Volo et al., 2022; Goldobin et al., 2024]. The rigorous formulation in terms of the chain of partial differential equations (14) with corresponding boundary conditions can help the development of the statistical theoretical characterization of interspike intervals for integrate-and-fire models. For the leakage models and specific types of synaptic networks one has to modify the function $f(V)$ and the position of adsorbing states (i.g., in the case of leakage models).

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