

## Application of a generalised Levy residence time problem to neuronal dynamics

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**Abstract.** – The distribution of bursting lengths of neuron spikes, in a two-component integrate-and-fire model, is investigated. The stochastic process underlying this model corresponds to a generalisation of the Brownian motion underlying Levy’s arcsine law of residence times. The generalisation involves the inclusion of a quadratic potential of strength  $\gamma$  and  $\gamma = 0$  corresponds to Levy’s original problem. In the generalised problem, the distribution of the residence times,  $T$ , over a time window  $t$ , is related to spectral properties of a complex, non-relativistic Hamiltonian of quantum mechanics. The distribution of  $T$  depends on  $\gamma t$  and varies from a U-shaped distribution for small  $\gamma t$  to a bell-shaped distribution for large  $\gamma t$ . The first two moments of  $T$  of the generalised problem are explicitly calculated and the crossover point between the two forms of the distribution is calculated. The distribution of residence times is shown to be independent of the magnitude of the stochastic force. This corresponds, in the neuron model, to exactly balanced synaptic inputs and, in this case, the distribution of residence times contains no information on synaptic inputs.

*Introduction.* – After over a century of neurophysiological research [1], we still do not understand the principles by which a stimulus such as an odour, image or sound is represented within the nervous system by a distributed set of neural states. There is little doubt that much of the information processing power of the nervous system resides in the activities of neural spikes (electrical pulses in the temporal domain). While a large numbers of detailed analyses of completely deterministic or random spikes have been made, such results cannot address issues of the functional roles of various bursting patterns of neurons that have been widely observed in experiments [2]. If we can unlock the principles, by which information is encoded within these various patterns of spikes, we may actually be able to understand how the nervous system works.

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While substantial progress towards understanding, at a spike level, has been achieved over the past decades, there is virtually no rigorous result on analysing neuron bursting activity. The two main difficulties in achieving this have been firstly, the complexity of the model usually used to generate bursting activity and secondly, the lack of theoretical tools to tackle the model. In the letter, we aim to overcome some of these difficulties.

We shall derive results following from a generalisation of the stochastic process underlying Levy's arcsine law. This law [3] is a non-intuitive result for the distribution of time spent on the positive  $x$ -axis, during a bout of one-dimensional Brownian motion, and is a fundamental result of probability theory, as pointed out in [4]. To the best of our knowledge, a generalisation, of the type proposed here, has not been previously considered. Although we confine ourselves to a neuronal model, we expect that the method employed and results derived will be useful for the applications in other areas as well.

The neuronal model we consider is a two-compartment integrate-and-fire model which can naturally generate bursting activity and has been widely studied in the literature [5, 6]. We shall show that the total bursting-length distribution, within a given time window, is independent of synaptic inputs but depends on the time window, when the neuron receives an exactly balanced inhibitory and excitatory input. The critical value at which the distribution function changes from a convex function to a concave function is determined from a generalisation of the stochastic process underlying Levy's arcsine law.

*Calculation.* – To emphasise the general applicability of our results, we adopt the language of one-dimensional Brownian motion. To proceed, consider the stochastic differential equation governing the position of a particle that moves in one dimension along the  $x$ -axis. At time  $t$ , the particle has coordinate  $X(t)$  which obeys

$$dX(t)/dt = -\gamma X(t) + \alpha \xi(t). \quad (1)$$

Here,  $\gamma > 0$  and  $\xi(t)$  is a Gaussian distributed random function, with an expected value of zero,  $E[\xi(t)] = 0$ , and delta-function correlated covariances,  $E[\xi(t_1)\xi(t_2)] = \delta(t_1 - t_2)$ . Without loss of generality, the parameter  $\alpha$ , which is a measure of the magnitude of the random force, may be taken as positive. We shall consider statistical properties of  $X(t)$  when  $X(0) = 0$  in all realisations of the process. With  $\Theta(\bullet)$  denoting a Heaviside step function, the quantity

$$T = \int_0^t \Theta(X(s)) ds \quad (2)$$

is a random variable in the range  $[0, t]$  and corresponds to the time the particle spends in the region  $x \geq 0$ . The quantity  $T$  is often referred to as the residence or occupation time and the distribution (probability density) of residence times is

$$\phi(\tau) = E[\delta(\tau - T)] \quad (3)$$

(see, *e.g.*, [7] and references therein). The distribution  $\phi(\tau)$  does, implicitly, depend on the parameters  $t$  and  $\gamma$ . The distribution also, apparently, depends on the parameter  $\alpha$  which characterises the magnitude of the stochastic force; however as long as  $\alpha \neq 0$ , the distribution is independent of this parameter [8]. Accordingly, we set  $\alpha = 1$  in what follows.

It is well known that the probability density of particle trajectories (Wiener measure) is proportional to  $\exp[-\int_0^t ds[\dot{x}(s) + \gamma x(s)]^2/2]$ , where  $\dot{x}(s) \equiv dx(s)/ds$ . Using a Fourier

representation of the delta-function, we have

$$\begin{aligned} \phi(\tau) = & \int_{-\infty}^{\infty} \frac{d\lambda}{2\pi} e^{i\lambda\tau} \int_{-\infty}^{\infty} dy \exp[-\gamma y^2/2 + \gamma t/2] \times \\ & \times \int_{x(0)=0}^{x(t)=y} d[x] \exp\left[-\int_0^t [\dot{x}^2(s)/2 + \gamma^2 x^2(s)/2 + i\lambda\Theta(x(s))] ds\right]. \end{aligned} \quad (4)$$

Here  $\int_{x(0)=0}^{x(t)=y} d[x] \dots$  denotes a functional integral over trajectories that start at position 0, at time 0, and end at position  $y$ , at time  $t$  (see, *e.g.*, [9]), and the factor  $\exp[-\gamma y^2/2 + \gamma t/2]$  originates from an integration by parts and the Ito definition of time-splitting underlying the functional integral [3]. With the conventional definition of an imaginary time functional integral [9], it may be verified that  $\phi(\tau)$ , as given in eq. (4), is correctly normalised over all  $\tau$  to unity:  $\int_{-\infty}^{\infty} \phi(\tau) d\tau = 1$ .

Completely equivalent to the functional integral appearing in eq. (4), is an imaginary time, quantum-mechanical propagator which, in Dirac representation, is  $\langle y | \exp[-\hat{H}_\lambda t] | 0 \rangle$ , where carets denote operators,  $\hat{p}$  ( $\hat{x}$ ) is the momentum (coordinate) operator,  $\hat{x}|y\rangle = y|y\rangle$  and

$$\hat{H}_\lambda = \hat{p}^2/2 + \gamma^2 \hat{x}^2/2 + i\lambda\Theta(\hat{x}). \quad (5)$$

Thus

$$\phi(\tau) = \int_{-\infty}^{\infty} \frac{d\lambda}{2\pi} e^{i\lambda\tau} \int_{-\infty}^{\infty} dy \exp[-\gamma y^2/2 + \gamma t/2] \langle y | \exp[-\hat{H}_\lambda t] | 0 \rangle. \quad (6)$$

For the special case,  $\gamma = 0$ , the propagator in eq. (6) reduces to that of a particle in a piecewise-constant potential and the Laplace transform of the propagator can be found in closed form:

$$\int_0^\infty e^{-zt} \langle y | \exp[-\hat{H}_\lambda(\gamma=0)t] | 0 \rangle dt = \frac{2 \exp[-\sqrt{2[z + i\lambda\Theta(y)]}|y|]}{\sqrt{2(z + i\lambda)} + \sqrt{2z}}.$$

Carrying out the  $y$  and  $\lambda$  integrals in eq. (6), for this special case, and inverting the Laplace transform yields, for  $t \geq \tau \geq 0$ , the original results of Levy:  $\phi(\tau) = \pi^{-1}[\tau(t - \tau)]^{-1/2}$  and  $\int_0^\tau \phi(\sigma) d\sigma = 2\pi^{-1} \arcsine(\sqrt{\tau/t})$ .

For the general case at hand,  $\gamma \neq 0$ , and despite the fact that the Hamiltonian in eq. (5) is that of a simple harmonic oscillator plus an additional piecewise-constant potential, there does not appear to be a simple analytical expression for  $\phi(\tau)$ . We proceed, therefore, by establishing properties of the distribution by computing exact moments of  $T$ . As an example,

$$\begin{aligned} E[T] &= \int_{-\infty}^{\infty} \tau \phi(\tau) d\tau = i \frac{\partial}{\partial \lambda} \int_{-\infty}^{\infty} dy e^{-\gamma y^2/2 + \gamma t/2} \langle y | \exp[-\hat{H}_\lambda t] | 0 \rangle \Big|_{\lambda=0} \\ &= \int_{-\infty}^{\infty} dy \int_0^t ds e^{-\gamma y^2/2 + \gamma t/2} \langle y | e^{-\hat{H}_0(t-s)} \Theta(\hat{x}) e^{-\hat{H}_0 s} | 0 \rangle, \end{aligned} \quad (7)$$

and to obtain the last expression, we utilised a time-ordered series expansion of the propagator in powers of  $\lambda$ . Note that  $\int_{-\infty}^{\infty} dy e^{-\gamma y^2/2} |y\rangle$  is, up to a normalisation, the ground state of  $\hat{H}_0$ , and has an eigenvalue of  $\gamma/2$ . Thus we can simplify eq. (7) to  $E[T] = \int_{-\infty}^{\infty} dy \int_0^t ds e^{-\gamma y^2/2 + \gamma s/2} \langle y | \Theta(\hat{x}) e^{-\hat{H}_0 s} | 0 \rangle = \int_0^\infty dy \int_0^t ds e^{-\gamma y^2/2 + \gamma s/2} \langle y | e^{-\hat{H}_0 s} | 0 \rangle$  and a straightforward calculation, using the exact propagator of a simple harmonic oscillator [9], yields  $E[T] = t/2$ .

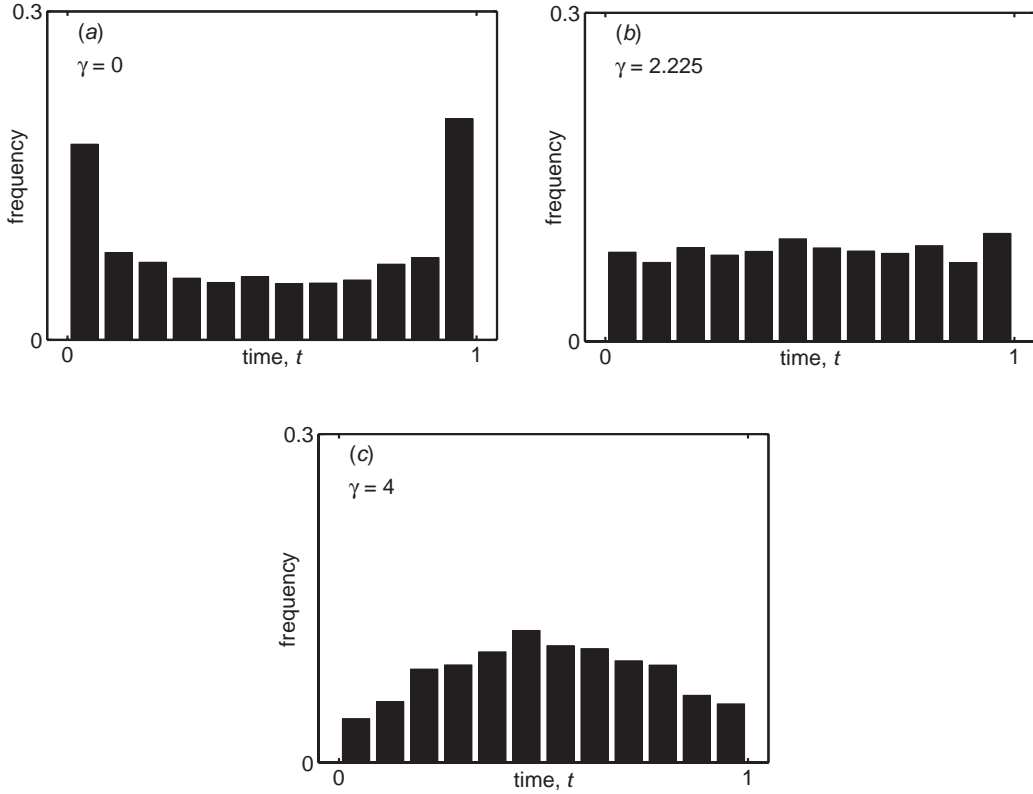


Fig. 1 – Histograms of normalised frequencies are plotted that illustrate the distributions of residence times,  $\phi(\tau)$  of eq. (3), for a time window of  $t = 1$ . The histograms were determined from  $2 \times 10^5$  independent replicate trajectories of a discretised version of eq. (1), with time splitting 0.01. Each trajectory was subject to  $X(0) = 0$  and the parameter  $\alpha$  had the value  $\alpha = 1$ . When  $\gamma = 0$  (a), the original result of Levy (corresponding to the so-called arcsine law) is obtained. The value of  $\gamma$  of (b), corresponding to the variance of residence times having the value of a uniform distribution,  $\text{Var}(T) = t^2/12$ , was numerically determined, from eq. (8), to be  $\gamma = 2.225$ . When  $\gamma$  is appreciably larger than this value, as in (c), the distribution has the opposite convexity to that of the distribution of (a).

An analogous calculation for  $E[T^2]$  yields

$$E[T^2] = 2 \int_{-\infty}^{\infty} dy e^{-\gamma y^2/2 + \gamma t/2} \times \int_0^t ds_1 \int_0^{s_1} ds_2 \langle y | e^{-\hat{H}_0(t-s_1)} \Theta(\hat{x}) e^{-\hat{H}_0(s_1-s_2)} \Theta(\hat{x}) e^{-\hat{H}_0 s_2} | 0 \rangle.$$

From this we can calculate the variance of  $T$ ,  $\text{Var}(T) = E[T^2] - (E[T])^2$ , with the result

$$\text{Var}(T) = t^2 \times g(\gamma t), \tag{8}$$

where

$$g(\zeta) = \frac{1}{\pi} \int_0^1 ds_1 \int_0^{s_1} ds_2 \arctan \left( e^{-\zeta s_1/2} \sqrt{\frac{\sinh(\zeta s_2)}{\sinh(\zeta[s_1 - s_2])}} \right). \tag{9}$$

We find  $g(0) = 1/8$ ,  $g(\zeta) \underset{\zeta \rightarrow \infty}{\sim} 1/(\pi\zeta)$ , which are suggestive of  $\phi(\tau)$  being bimodal (U-shaped) for small  $\gamma t$  and unimodal (bell-shaped) for large  $\gamma t$ , in agreement with what is observed numerically (see fig. 1a and c).

There is a crossover between the bimodal and unimodal forms of  $\phi(\tau)$  (or, equivalently, in the convexity of  $\phi(\tau)$ ) and the value of  $\gamma t$  at the crossover point corresponds to  $\phi(\tau)$  being close to a uniform distribution (see fig. 1b). Given that a uniform distribution on  $[0, t]$  has a variance of  $t^2/12$ , we can determine the crossover point in behaviour, as that value of  $\gamma t$  where  $\text{Var}(T) = t^2/12$ . From eq. (9), we numerically find that  $g(\zeta) = 1/12$  when  $\zeta \simeq 2.225$ , thus the crossover value of  $\gamma t$  is  $\gamma t \simeq 2.225$ .

*Application of calculation.* – Let us return to the two-compartment neuron model discussed above, and now apply the results derived. We note that in this model, a neuron is composed of two compartments: a somatic compartment and dendritic compartment. Suppose that a neuron receives EPSPs (excitatory postsynaptic potentials) at a number,  $q_E$ , of excitatory synapses and IPSPs (inhibitory postsynaptic potentials) at  $q_I$  inhibitory synapses and that  $V_s(t)$  and  $V_d(t)$  are the membrane potential of the soma and dendritic compartments at time  $t$ , respectively.

When the somatic membrane potential,  $V_s(t)$ , is between the resting potential,  $V_{\text{rest}}$ , and the threshold voltage,  $V_{\text{thre}}$ , we have, in the language of stochastic calculus typically employed in the neuroscience literature,

$$\begin{aligned} dV_s(t) &= -\gamma(V_s(t) - V_{\text{rest}})dt + g_c \frac{V_d(t) - V_s(t)}{p} dt, \\ dV_d(t) &= -\gamma(V_d(t) - V_{\text{rest}})dt + g_c \frac{V_s(t) - V_d(t)}{1-p} dt + \frac{di_{\text{syn}}(t)}{1-p}. \end{aligned} \quad (10)$$

Here  $\gamma$  is the decay rate and  $p$  is the ratio between the membrane area of the somatic compartment and the whole cell. The quantity  $g_c > 0$  is a constant, and the synaptic input is  $i_{\text{syn}}(t) = a \sum_{i=1}^{q_E} dE_i(t) - b \sum_{j=1}^{q_I} dI_j(t)$ , where  $E_i(t)$ ,  $I_i(t)$  are Poisson processes with rates  $\lambda_E$  and  $\lambda_I$ , respectively, and  $a$ ,  $b$  are the magnitudes of each EPSP and IPSP. After  $V_s(t)$  crosses  $V_{\text{thre}}$  from below, a spike is generated and  $V_s(t)$  is reset to  $V_{\text{rest}}$ . This is the essence of the two-compartment, integrate-and-fire model. The interspike interval of efferent spikes is the smallest value of  $t$ , where  $V_s(t)$  equals or is larger than  $V_{\text{thre}}$ :  $S(p) = \inf\{t : V_s(t) \geq V_{\text{thre}}\}$  for  $1 > p > 0$ . A neuron shows bursting activity if  $S(p)$  can be divided into two disjoint groups  $A$  and  $B$ , with all interspike intervals in  $A$  being much smaller than in  $B$  (see, for example, [2]). It is well known that Poisson input can be approximated by [10]  $I_{\text{syn}}(t) = \mu t + \alpha B_t$ , where  $B_t \equiv \int_0^t \xi(s) ds$  is the so-called standard Brownian motion,  $\mu = aq_E\lambda_E - bq_I\lambda_I$  and  $\alpha = \sqrt{a^2q_E\lambda_E + b^2q_I\lambda_I}$ . Thus, eq. (10) can be approximated by

$$\begin{aligned} dV_s(t) &= -\gamma(V_s(t) - V_{\text{rest}})dt + g_c \frac{V_d(t) - V_s(t)}{p} dt, \\ dV_d(t) &= -\gamma(V_d(t) - V_{\text{rest}})dt + g_c \frac{V_s(t) - V_d(t)}{1-p} dt + \frac{dI_{\text{syn}}(t)}{1-p}. \end{aligned} \quad (11)$$

It is known that when  $p$  is small enough,  $V_s$  bursts whenever  $V_d$  is above zero [5], where  $V_d$  is given by

$$dV_d(t) = -\gamma(V_d(t) - V_{\text{rest}})dt + dI_{\text{syn}}(t). \quad (12)$$

In particular, when  $\mu = 0$ , the model receives exactly balanced synaptic inputs and with the identification  $X(t) = V_d(t) - V_{\text{rest}}$ , eq. (12) coincides with eq. (1). The possible significance

of an exactly balanced synaptic input has been extensively discussed in the literature [11,12]. Hence we conclude that the total bursting length of the model, within a time window  $t$ , is  $T$ , *i.e.* the *residence time* of  $V_d$ . Given that the typical value of  $\gamma$  is  $\gamma = 1/20$  [12], we can conclude that the mean bursting length is  $t/2$ , and the variance in bursting lengths is  $t^2g(\gamma t)$  (eq. (9)). Hence when  $t \gg 2.225 \times 20$ , the distribution of  $T$  is bell-shaped, but when  $t \ll 2.225 \times 20$ , the distribution is  $U$ -shaped. We note that many promising hypotheses have been put forward in the literature on the significance associated with bursting activity for the information processing power of bursting [2]. However, our results tell us that in the case of exactly balanced synaptic inputs, *i.e.* when  $\mu = 0$ , the complete distribution of  $T$  (*i.e.* all moments) contain *no information* of synaptic inputs, *i.e.* it is independent of  $\alpha$ . Hence the moments of  $T$  are not informative and the bursting length in a two-compartment model is not a candidate of an information carrier, at least under the conditions considered.

It is illuminating to note that the distribution of  $T$  relies on  $t$ , the observed time window. Hence from the distribution of  $T$ , we can tell the length of the time window in which the bursting is observed. In particular, at the critical point  $2.225/\gamma$ , the distribution changes from a convex function to a concave function.

The coefficient of variation of  $T$  defined by  $\sqrt{\text{Var}(T)}/E[T] = 2\sqrt{g(\gamma t)}$  is a decreasing function of  $t$  with a maximum value of  $1/\sqrt{2} \simeq 0.7$ . Hence, the distribution of  $T$  is less irregular than the distribution of interspike intervals of a Poisson process, which has a coefficient of variation of  $T$  of unity.

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