

**INTERSPIKE INTERVAL DENSITY OF THE LEAKY INTEGRATOR
MODEL NEURON WITH A PARETO DISTRIBUTION OF PSP
AMPLITUDES AND WITH SIMULATION OF REFRACTORY TIME**

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Abstract

The main aim of the paper is to arrive at the first passage time for a spike discharge in a single neuron with inputs which produce either inhibition or excitation whose magnitude depend upon the existing membrane potential gathered till that time. This may represent to a certain extent short term accommodation. The refractory time is simulated by having a time dependent threshold. Very interesting closed expressions for the transform of the first passage density and hence their moments for these situations in which we have a moving boundary, are obtained by employing imbedding technique or compensation function method. We are led to Wald identities for such cases of moving boundary problems.

1. Introduction

In previous contributions (Vasudevan *et al.*, 1981; Vasudevan and Vittal, 1981) we have considered membrane potentials gathered by a single neuron with inputs (excitation or inhibition) which were independent. Such models have been treated in the literature (Holden, 1976; Ricciardi, 1976; Sampath and Srinivasan, 1976; Fienberg, 1974; Sugiyama *et al.*, 1970). When the gathered potential exceeds a certain threshold the neuron gives rise to a spike discharge and the interval distribution of these spike trains are of experimental interest. Time-dependent thresholds are considered, to incorporate the idea of refractory time for the neurons. First passage densities for such cases have been investigated in Vasudevan and Vittal (1981), Clay and Goel (1973), Kryukov (1976) and Ricciardi (1976). In our paper (Vasudevan and Vittal, 1981) we have derived Wald identities for the case of moving thresholds using methods quite different from those of Kryukov (1976). Therein by a limiting procedure we also arrived at Wald identities for moving barriers for the diffusion process.

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The input impulses may hit the neuron as Poisson events. However, the response of the neuron, i.e. the jumps induced in the membrane potentials may depend in some way on the existing potential level at that time. The successive responses may not be quite independent. This idea has been supported by the experimental work of Fuortes and Mantegazzini (1962). Tuckwell (1979) also adopts the view that the jumps should in some way depend upon the potential gathered by the neuron just before the excitation or inhibition comes in.

First passage problems have been dealt with in the article of Ramakrishnan (1959). In Vasudevan *et al.* (1981) and Vasudevan and Vittal (1981) we have arrived at the equation for the first passage densities, by an imbedding method and also by the compensation techniques of Keilson (1963) in the case of stationary and moving barriers. In Section 2 we define the jump magnitudes to be governed by Pareto distribution (Mood *et al.*, 1974) and write the forward equation for $f(x, t; x_0)$, the probability density function (p.d.f.) of values of the random variable X , for potential gathered at time t , starting from an initial value x_0 . By a transformation of the variable x and by making use of the method of compensation function we obtain the first passage density. In Section 3 we consider the same problem by the imbedding method and arrive at the moments of the first passage time. In Section 4 we investigate moving boundaries of different types and obtain closed solutions.

2. Forward equation with compensation function

In this section we take the density of the jump magnitude as $a(x, x')$ for the membrane potential to go from a value x' to x in a Poisson jump with frequency ν , as given by

$$(1) \quad a(x, x') = \eta \frac{x'^{\eta}}{x^{\eta+1}}, \quad \eta > 0, \quad x' > 0.$$

Here we consider x and x' to be greater than zero. Alternatively we can say that the ratio of the jump magnitude is governed by the Pareto distribution as

$$(2) \quad P(R)dR = \frac{\eta}{(1 + |R|)^{\eta+1}}dR$$

This is the well known modelling of income distribution in economics (Mood *et al.*, 1974). If X' is large $X - X'$ can also take large values.

Here we consider the case where X , the potential level, is always above zero. We also assume that the excitatory jumps starting from the resting value $x_0 > 0$ at time $t = 0$, occur with a Poisson frequency ν . The stochastic process is defined by

$$(3) \quad X(t) = x_0 + \sum_{n=0}^{N(t)} Z_n e^{-\alpha(t-t_n)}$$

where $\alpha > 0$ is the exponential decay parameter, $N(t)$ the number of jumps in the time interval $(0, t)$ and Z_n are the jumps at time t_n . This means that the neuron is a leaky integrator. The forward equation of such a process is

$$(4) \quad \frac{\partial}{\partial t} f(x, t) - \alpha \frac{\partial}{\partial x} [xf(x, t)] + \nu f(x, t) = \nu \int_0^{\infty} f(x', t) a(x, x') dx'$$

with $f(x, 0) = \delta(x - x_0)$.

Let us consider only positive jumps; i.e. $(X - X')$ is always positive. $X = 0$ is a natural barrier in this problem and the threshold value for a given neuron serves as another absorbing barrier which we take as the constant K . The problem of first passage time to cross the barrier $X = K$ can easily be solved in closed form if one considers the transformation of the variable X to Y where $X = e^Y$. When this transformation is effected $a(x, x')dt$ becomes $b(y, y')dy$ where

$$(5) \quad b(y, y') = \eta e^{-\eta(y-y')}$$

Also

$$(6) \quad f(x, t) = \pi(y, t) \left| \frac{dy}{dx} \right|$$

Now $\pi(y, t)$ satisfies the forward equation

$$(7) \quad \frac{\partial}{\partial t} \pi(y, t) - \alpha \frac{\partial}{\partial y} (y, t) + \nu \pi(y, t) = \nu \eta \int_{-\infty}^{\infty} \pi(y', t) e^{-\eta(y-y')} dy'$$

with $\pi(y, 0) = \delta(y - y_0)$ where $y_0 = \log x_0$. Thus the effect of the transformation is that the problem with exponential decay with a parameter α is converted into a linear drift problem with drift coefficient α . The constant barrier $X = K$ becomes $Y = \bar{K} = \log K$ in the Y space. The problem of linear drift is presented in Section 2 of Vasudevan *et al.* (1981).

To take into account the boundary we introduce the compensation function into the differential equation (7). The equation can now be treated as an equation with no barrier. We write

$$(8) \quad \frac{\partial}{\partial t} \pi(y, t) - \alpha \frac{\partial}{\partial y} (y, t) + \nu \pi(y, t) = \nu \eta \int_{-\infty}^{\infty} \pi(y', t) e^{-\eta(y-y')} dy' + c(y, t)$$

The compensation function is given by

$$(8A) \quad c(y, t) = -\nu H(y - \bar{K}) \int_{-\infty}^{\infty} \pi(y', t) b(y - y') dy'$$

where $H(y)$ is the Heaviside function and $b(y)$ is the p.d.f. for the positive jumps. With the introduction of the compensation function for the source term in equation (8) it can be seen that $\pi(y, t) = 0$ for $Y \geq \bar{K}$ with $y_0 < \bar{K}$. We take the double transform with respect to y and one-sided transform with respect to t , as in Keilson (1963). Denoting $\bar{\pi}(s, l)$, $\bar{c}(s, l)$ and $\bar{b}(s)$ as the transforms of $\pi(y, t)$, $c(y, t)$ and $b(y)$ respectively we get from (8)

$$(8B) \quad [l + \alpha s + \nu(1 - \bar{b}(s))] \bar{\pi}(s, l) = e^{s y_0} + \bar{c}(s, l)$$

$$(9) \quad l + \alpha s + v[1 - \bar{b}(s)] = 0$$

If σ_1 is the root of equation (9) for $Re(s) > 0$ we have

$$(10) \quad \bar{c}(\sigma_1, l) = -e^{\sigma_1 y_0}.$$

It is evident from the definitions of $c(y, t)$ and $M(t)$,

$$(11) \quad M(t) = M(y_0, \bar{K}, t) = - \int_{\bar{K}}^{\infty} c(y, t) dy.$$

For the density $b(y)$ of (5) $M(t)$ is given by

$$(12) \quad M(t) = -e^{-\eta \bar{K}} S(\bar{K}, t)$$

where

$$(13) \quad S(\bar{K}, t) = -v \int_{-\infty}^{\bar{K}} \pi(y', t) e^{\eta y'} dy'$$

Also $c_1(s, t)$, the Laplace transform of $c(y, t)$ with respect to y is

$$(14) \quad c_1(s, t) = \frac{-\eta}{\eta - s} e^{s \bar{K}} M(t)$$

Hence the transform $\bar{M}_y(l)$ of the first passage density in Y space is

$$(15) \quad \bar{M}_y(l) = \left(1 - \frac{\sigma_1}{\eta}\right) e^{\sigma_1(y_0 - \bar{K})}$$

where σ_1 is the root of the equation (9). We are automatically led to the solution (Vasudevan and Vittal, 1981)

$$(16) \quad M_y(t) = \left(1 - \frac{1}{\eta} \frac{d}{dy_0}\right) \frac{|y_0 - \bar{K}|}{t} g_{oy}(\bar{K} - y_0 + \alpha t, t)$$

where g_{oy} is the well known Green's function of the unbounded process with jump p.d.f. $b(y)$ with no barriers. Going back to the original space variable x ,

$$(17) \quad M(t) = \left(1 - \frac{x_0}{\eta} \frac{d}{dx_0}\right) \frac{1}{t} \log\left(\frac{K}{x_0}\right) g_{oy}\left(\frac{K}{x_0} + \alpha t, t\right)$$

Here, by g_y we mean the Green's function in the y -space with corresponding variable transformations into the x -space.

3. Imbedding analysis

This first passage problem can also be solved by writing down the imbedding equation for $M(u, k, t)$, the probability that the barrier $X = K$ is crossed for the first time at time t starting from $X = u$ at $t = 0$ (Vasudevan *et al.*, 1981). The imbedding equation for M can be arrived at as

$$(18) \quad \frac{\partial M}{\partial t} + \alpha u \frac{\partial M}{\partial u} + vM = v \int_u^K M(z, K, t) a(z, u) dz + \delta(t)v \int_K^\infty a(z, u) dz$$

with the initial condition $M(y, k, 0) = 0$. On taking Laplace transform with respect to t (18) becomes

$$(19) \quad \alpha u \frac{\partial \bar{M}}{\partial u} + (l + v)\bar{M} = v\eta \int_u^K \bar{M}(z, K, l) \frac{u^\eta}{z^{\eta+1}} dz + v\eta \int_u^K \frac{u^\eta}{z^{\eta+1}} dz$$

with $a(z, z')$ as defined in (1).

Transforming the variable $u = e^y$ the equation (19) becomes

$$(20) \quad e^{-\eta y} \left[\alpha \frac{\partial \bar{M}}{\partial y} + (l + v)\bar{M} \right] = v \int_y^{\bar{K}} \bar{M}(y', \bar{K}, l) e^{-\eta y'} dy' + v e^{-\eta \bar{K}}$$

Differentiating with respect to y , we get the second order differential equation

$$(21) \quad \alpha \frac{\partial^2 \bar{M}}{\partial y^2} + (l + v - \eta\alpha)\bar{M} - \eta l \bar{M} = 0$$

The range of y will be $(-\infty, \bar{K})$ resulting from the range of the variable in the X -space from 0 to ∞ . Since M has to be finite the solution for the equation (21) is

$$(22) \quad \bar{M}(y, \bar{K}, l) = A \exp(m_1 y)$$

where m_1 is the positive root of the equation

$$(23) \quad \alpha m^2 + (l + v - \eta\alpha)m - \eta l = 0$$

and A , which is independent of y , is to be determined. This can be found by substituting the solution (22) in the first order equation (20). Thus we find

$$(24) \quad A = \left(1 - \frac{m_1}{\eta}\right) e^{-m_1 \bar{K}}$$

and the solution in the Y -space is

$$(25) \quad \bar{M}(y, \bar{K}, l) = \left(1 - \frac{m_1}{\eta}\right) e^{m_1(y - \bar{K})}.$$

It can be easily seen that the root σ_1 of the equation (9) is the same as the root m_1 of the equation (23). Hence

$$(26) \quad \bar{M}(y, \bar{K}, l) = \left(1 - \frac{\sigma_1}{\eta}\right) e^{\sigma_1(y - \bar{K})}.$$

When inverted this is expressed in terms of the Green's function in the Y -space. If one wants to express $M(l)$ in X -space we have

$$(27) \quad \bar{M}(x_0, K, l) = \left(1 - \frac{\sigma_1}{\eta}\right) \left(\frac{u}{K}\right)^{\sigma_1}$$

We can verify that this solution satisfies the first order equation (18) in the X -space.

We can also find the moment of $M(t)$ from (27) as we know that the n th moment is

$$(28) \quad E(T^n) = (-1)^n \frac{d^n}{dl^n} \bar{M}(l) \Big|_{l=0}$$

The mean passage time is given by

$$(29) \quad E(T) = \frac{1 - \eta \log\left(\frac{u}{K}\right)}{v - \eta\alpha}$$

Since $E(T)$ is always to be positive we should have the condition $v/\eta > \alpha$. In the Y -space we know that η^{-1} is the average value of the jump magnitude. The average of the Poisson jumps per unit time is v . Hence v/η represents the average upward increase in Y -space per unit time and α is the deterministic downward drift per unit time. Hence $v > \eta\alpha$ is a necessary condition for the ‘particle’ to cross the barrier in any time.

The second moment of T about the origin is

$$(30) \quad E(T^2) = \left(\frac{1 - \eta \log\left(\frac{u}{K}\right)}{v - \eta\alpha}\right)^2 + \frac{v\left(1 - 2\eta \log\left(\frac{u}{K}\right) + \eta\alpha\right)}{(v - \eta\alpha)^3}$$

4. Refractoriness

Barrier decaying exponentially

We consider here a moving barrier of the type

$$(31) \quad K(t) = K_0 e^{-\beta t},$$

K_0 being a constant with a large value to simulate the refractoriness of the neurons just after a spike. This type of boundary has been treated in Clay and Goel (1973) and Ricciardi (1976). The barrier in Y -space is $F(t) = \log K - \beta t$. This linear problem in Y -space is equivalent to the problem of finding the first passage time density with constant barrier $\bar{K} = \log K$ and a downward linear drift. The solution of this problem can be easily obtained as outlined in Sections 2 and 3. The first passage density in the Y -space, can be obtained as in equations (16) and (17) as

$$(32) \quad M_y(t) = \left(1 - \frac{1}{\eta} \frac{d}{dy_0}\right) \frac{|y_0 - \bar{K}|}{t} g_y[\bar{K} - y_0 + (\alpha - \beta)t, t]$$

This can be easily transformed to the X -space, where g is the same function as g_y with suitable transformation for y .

Hagiwara threshold

Another type of model simulating a refractory threshold was introduced by Hagiwara (1954). Here the boundary is

$$(33) \quad K(t) = Ke^{\beta t}$$

This boundary in Y space is

$$(34) \quad K(t) = \bar{K} + \beta/t$$

The forward equation for the density function $f(y, t)$ in the Y -space is

$$(35) \quad \frac{\partial}{\partial t} f(y, t) - \alpha \frac{\partial}{\partial y} (y, t) + \nu f(y, t) = \nu \int_{-\infty}^{\infty} f(y', t) b(y - y') dy' + c(y, t).$$

$c(y, t)$, the compensation function responsible for the boundary effect is given by

$$(36) \quad c(y, t) = -\nu \eta H[y - (\bar{K} + \beta/t)] \int_{-\infty}^{\infty} f(y', t) e^{-\eta(y-y')} dy' = H[y - (\bar{K} + \beta/t)] \eta e^{-\eta y} S(t)$$

$M_y(t)$, the first passage density, is given by

$$(37) \quad M_y(t) = - \int_{\bar{K} + \beta/t}^{\infty} c(y, t) dy = \exp[-\eta(\bar{K} + \beta/t)] S(t)$$

As seen in the previous cases we can obtain

$$(38) \quad \bar{c}(s, l) = \frac{-\eta}{\eta - s} e^{s\bar{K}} \mathcal{L} \left\{ \sum_{n=0}^{\infty} \frac{(s\beta)^n M(t)}{n! t^n} \right\}$$

or

$$(39) \quad \frac{-(\eta - s)}{\eta} \bar{c}(s, l) e^{-s\bar{K}} = \bar{M}(l) + \mathcal{L} \left\{ \sum_{n=1}^{\infty} \frac{(s\beta)^n M(t)}{n! t^n} \right\}$$

Using the identities in Hildebrand (1964) we obtain a series for $\bar{M}(\xi)$ as

$$(40) \quad -\left(1 - \frac{s}{\eta}\right) e^{-s\bar{K}} \bar{c}(s, l) = \bar{M}(l) + \sum_{n=1}^{\infty} \frac{(s\beta)^n (-1)^{n-1}}{n! (n-1)!} \int_l^{\infty} (l - \xi)^{n-1} \bar{M}(\xi) d\xi$$

Going back to the equation (35) one finds that

$$(41) \quad \bar{c}(s, l) = -e^{s y_0}$$

where $s = \sigma_l$ is the root of the equation

$$(42) \quad l + \alpha s + \nu[1 - \bar{a}(s)] = 0$$

with a positive real part. Hence the Wald identity in this case is

$$(43) \quad \left(1 - \frac{1}{\eta} \frac{d}{dx_0}\right) e^{\sigma_l(y_0 - \bar{K})} = \bar{M}(l) + \sum_{n=1}^{\infty} \frac{(\sigma_l \beta)^n (-1)^{n-1}}{n! (n-1)!} \int_l^{\infty} (l - \xi)^{n-1} \bar{M}(\xi) d\xi$$

$$= \bar{M}(l) + \sigma_l \beta \int_l^\infty \sum_{n=0}^{\infty} \frac{(\sigma_l \beta)^n}{n!} \frac{(-1)^n}{(n+1)!} (l-\xi)^n \bar{M}(\xi) d\xi$$

The coefficient of $\bar{M}(l)$ in the integral of (43) can be expressed in terms of the J_1 function

$$(44) \quad J_1(x) = \frac{x}{2} \sum_{r=0}^{\infty} \frac{(-1)^r}{r!(r+1)!} \left(\frac{x}{2}\right)^{2r}$$

Hence we rewrite the Wald identity in (43) as

$$(45) \quad \left(1 - \frac{1}{\eta} \frac{d}{dy_o}\right) e^{\sigma_l(y_o - \bar{K})} = \bar{M}(l) + 2\sigma_l \beta \int_l^\infty \frac{J_1(2\sqrt{(l-\xi)\sigma_l\beta})}{2\sqrt{(l-\xi)\sigma_l\beta}} \bar{M}(\xi) d\xi.$$

If $l = 0$ we observe that both sides of (45) become unity since $\sigma_l = 0$ at $l = 0$. σ_l can be computed for a given density function $b(y)$ from the equation (42).

To derive some meaningful results from the expression (45) let us assume that β is small which is reasonable if we realise that the threshold from a very high value just after a spike gets down to values near K quite rapidly. Hence we now approximate the J_1 function (44) by its value for small arguments and write an approximate integral equation as

$$(46) \quad \left(1 - \frac{1}{\eta} \frac{d}{dy_o}\right) e^{\sigma_l(y_o - \bar{K})} = \bar{M}(l) + \sigma_l \beta \int_l^\infty \bar{M}(\xi) d\xi - C\sigma_l^2 \beta^2 \int_l^\infty (l-\xi) \bar{M}(\xi) d\xi$$

where C is a constant. When l is large we see from the solution of the equation (42)

$$(47) \quad \frac{1}{2\alpha} \sigma_l = \{-l + v - \eta\alpha\} + [(l + v - \eta\alpha)^2 + 4\eta\alpha l]^{1/2} \simeq \eta$$

This means that we are interested in small time region. For this approximation we find from the equation (47) after inversion

$$(48) \quad \left(1 - \frac{1}{\eta} \frac{d}{dy_o}\right) \frac{y_o - \bar{K}}{t} g(y_o - \bar{K} + \alpha t, t) = M(t) + \eta\beta \frac{M(t)}{t} - \frac{C\eta^2 \beta^2 M(t)}{t^2} + \text{higher order terms.}$$

Here g is the well-known Green's function for the unrestricted process in Y -space. We can easily convert the above result into the original X -space variable. Since l is taken to be large the solution corresponds to small values of t . Even if the above result happens to be an approximation for small time, we have an analytical expression to compare with the experimental data.

In conclusion we want to point out that by the compensation technique as well as by the imbedding method we have found the transform of first passage density

for crossing the threshold level with jumps which are not independent of membrane potential. We have assumed that the excitation or inhibition produced by the external stimuli depend on the existing level of the membrane potential.

Suitable time-dependent barriers are considered to simulate the refractory period in the spike phenomena. Closed expressions for the transforms of the first passage time density have been obtained. This has been possible by adopting a transformation for the random variable corresponding to the membrane potential $X(t)$ at time t . The calculation thereafter becomes much simpler.

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