Numerical Frequency Transference Analysis of a Leaky Integrate-and-Fire Neuron

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This work reports a transfer function-based approach to characterizing the operation of single neuronal cells in terms of the instantaneous frequency of the input and output signals. We adopt the leaky integrate-and-fire model. The transfer function is obtained by performing successive numeric-computational simulations and statistical regressions. Several interesting results are reported, including the identification of linearity in the transfer functions, as well as the identification of regions in the parameter space characterized by sharper transfer functions.

I. INTRODUCTION

Neuronal systems have been continuous and intensely investigate along the last decades because of their criticality in underlying human intelligence. The several approaches attempted so far vary in many aspects, focusing on smaller or larger scales of time, space and detail [1–5]. Because a single neuronal cell constitutes the basic processing element of the nervous system, it has received particular attention from both theoretical and experimental points of view. One approach that has been often adopted consists in modeling the electrochemical activity of a single neuronal cell in terms of a set of mathematical dynamical equations [6, 7]. Because these approaches demand substantial computational cost, simplified investigations have been proposed involving only the transmembrane potential value, not taking into account the ionic currents, as in the case of integrate-and-fire models [8]. Neuronal simulations performed in this way typically involve the dynamic unfolding of the neuronal state along time, under control of some mathematical rules such as a differential equation [9, 10]. The analysis of the simulated results obtained by using this type of approaches is often performed taking into account the frequency of neuronal spikes, as this is known to correspond to an important aspect underlying information transfer and processing in neuronal systems [11–15].

Several devices in electronics, such as transistors, are characterized in terms of an input/output formulation in terms of transfer function [16, 17]. More specifically, if the input signal is represented as the time function $x(t)$, and the output as $y(t)$, the transfer function $y(t) = F(x(t))$ defines the mapping from the input into the output signals. This approach is particularly useful because it summarize the operation of the device in terms of a simple functional relationship. Consequently, it becomes particularly simple to simulate the device operation in terms of this methodology. In addition, the shape of the transfer function itself can provide several insights about the processing being performed by the device, including its linearity.

Despite the interesting advantages provided by the transfer function approach, it has rarely applied to characterizing and modeling the nervous system. In the present work, we develop a transfer function approach to characterize the operation of single neuronal cells, with respect to the instantaneous frequency of the action potentials. More specifically, the input signal $x(t)$ is taken as the instantaneous frequency of the input spikes, while the output signal $y(t)$ corresponds to the instantaneous frequency of the output action potential spikes. We adopt the leaky integrate-and-fire model, and several numeric-computational simulations are performed for several model parameters and inputs. This allows us to estimate the transfer function of the instantaneous frequencies. Because of the memory property inherent to these systems, the obtained relationship is not exact in the sense that more than one distinct output can be obtained for the same input signal. In spite of this limitation, it has been possible to infer a linear pattern of relationship for several parametric configurations, which allowed us to estimate the neuronal operation with a good level of accuracy.

This article starts by presenting the adopted model (leaky integrate-and-fire) as well as how the synapses have been approached and modeled. Next, we discuss the choice of the several involved parameters, including time resolution, input currents, and extension of the adopted time window. The obtained results are then reported and discussed, with emphasis on the linearity of the transfer function, and perspectives for future developments are proposed.

II. THE LEAKY INTEGRATE-AND-FIRE MODEL

In the integrate-and-fire model the neuron state is determined only by its membrane potential. The membrane potential is altered by the synaptic inputs and by inject current into it. Each of these synaptic inputs are weighted by their respective synaptic efficacy [18]. When the membrane potential reaches a determined spiking threshold, the neuron generates an action potential as output [19]. The membrane potential is then reset to its rest value and does not change for the time corresponding to its absolute refractory period. The membrane potential decays exponentially with a characteristic time constant, the membrane time constant, and the neuron is...

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said to be leaky. An integrate-and-fire neuron is understood as a ‘point neuron’ since its spatial structures are not considered [8].

The membrane potential of the leaky integrate-and-fire neuron model is defined by the differential equation:

\[ \tau_m \frac{du(t)}{dt} = u_r + R_m I(t) - u(t) \]  

(1)

Where \( u(t) \) is the membrane potential, \( u_r \) is the resting potential and \( I(t) \) is the total injected current accounting for the the synaptic inputs and the individual injected currents. \( \tau_m \) is the membrane time constant, \( R_m \) is the membrane resistance and \( C_m \) is the membrane capacitance, with the relation between them given by:

\[ \tau_m = R_m C_m \]  

(2)

This equation can be expressed as an equivalent electronic circuit (Figure 1) [20].

![Equivalent Circuit](image)

FIG. 1: The equivalent circuit for the leaky integrate-and-fire model for \( u_r = 0 \).

When the membrane potential reaches the spiking threshold, the neuron generates an action potential. The neuron dynamics that generates the action potential is not treated by the integrate-and-fire model, as it simply defines the instant of time that a action potential is generated.

If we define the set of the instants at which the membrane potential reaches the spiking threshold as \( T_s = \{t_{s_1}, t_{s_2}, ..., t_{s_n}\} \), we can describe the whole dynamics as:

\[ t_{s_i} : u(t_{s_i}) \geq \vartheta \]
\[ \tau_m \frac{du(t)}{dt} = u_r + R_m I(t) - u(t) \quad \text{for} \quad t_{s_i} + \tau_r < t \leq t_{s_{i+1}} \]
\[ \lim_{t \to t_{s_i}^+} u(t) = u_r \]
\[ u(t) = u_r \quad \text{for} \quad t_{s_i} < t \leq t_{s_i} + \tau_r \]  

(3)

Where \( \vartheta \) is the spiking threshold and \( \tau_r \) is the absolute refractory period.

The synaptic inputs current is defined as:

\[ I_s = C_m \sum_{k=1}^{N_E} a_{E,k} S_{E,k}(t) + C_m \sum_{k=1}^{N_I} a_{I,k} S_{I,k}(t) \]  

(4)

Where the indexes \( E \) and \( I \) indicate an excitatory and inhibitory synapses, respectively, and each index \( k \) is an input synapse from a different neuron (or the same neuron but with different synaptic strengths). The \( S(t) \) function is a pulse train usually expressed as:

\[ S_{E,k}(t) = \sum_{t_{E,k}} \delta(t - t_{E,k}) \]
\[ S_{I,k}(t) = \sum_{t_{I,k}} \delta(t - t_{I,k}) \]  

(5)

Where \( t_{E,k} \) and \( t_{I,k} \) are the times of the synaptic input spikes for the excitatory and inhibitory synapses, respectively. This synaptic input model (Equation 4) is said to be a current synapse model because it is independent of the membrane potential [8].

III. ANALYSES OF THE LEAKY INTEGRATE-AND-FIRE MODEL

The solution for the differential Equation 1 for \( I(t) = 0 \) and the boundary condition \( u_r < u(t_0) < \vartheta \) is:

\[ u(t) = u_r + (u(t_0) - u_r)e^{-\frac{t-t_0}{\tau_m}} \]  

(6)

Since Equation 1 is linear on the pre-synaptic spikes, we can use the principle of linear superimposition to solve it by adding the results for each individual delta function, given as \( I(t) = C_m a_E \delta(t - t_s) \). If a single pre-synaptic spike occurs at \( t_s \), and \( u(0) = u_r \), the initial membrane potential equal to resting potential, we have:

\[ u(t) = u_r + a_E e^{-\frac{t-t_s}{\tau_m}} \theta(t - t_s) \]  

(7)

Where \( \theta(t) \) is the Heaviside step function [21]. As the current synapse model is independent of the membrane potential, a single delta spike input adds an \( \epsilon(t, t_s) = a_E e^{-\frac{t-t_s}{\tau_m}} \theta(t - t_s) \) function to the membrane potential \( u(t) \), with \( t_s \) being the arrival time of the spike.

For simplicity’s sake we will assume, without loss of generality, that \( u_r = 0 \). Recall that the dynamics of the system is influenced only by the difference between the spiking threshold and the resting potential. In addition, here we consider a null absolute refractory period \( \tau_r = 0 \) and only excitatory synapses.

In order to construct the frequency transfer relation we assume that the neuron has only one input. This situation can be achieved in cases where one input of the neuron is much more active and intense than the others, or when in a small time window the neuron receives
many inputs that so the sum of the intensities is nearly constant.

For the stationary frequency case, when the frequency of the synaptic inputs is constant in time, it is easily verified that the output frequency will be constant and the relation between the input and output frequencies is linear. Consider a sequence of input spikes with interspike interval \( (t_{\text{isi}} = \gamma) \), depending of \( a_E \) a number \( N \) of input spikes will be necessary to generate one output spike, and based on Equation 7 the number \( N \) is defined as the smallest value that obeys the relationship:

\[
N - 1 \sum_{i=0}^{N-1} a_E e^{-\frac{\gamma i}{\Delta t}} \geq \vartheta
\]  

As \( N \) is constant, the output interspike interval will also be constant and given by:

\[
d = N\gamma
\]

In this case, the input frequency is \( f_i = \frac{1}{\gamma} \) and the output frequency \( f_o = \frac{1}{N\gamma} \) so that \( f_o = \frac{f_i}{N} \) with \( N \) given by Equation 8, establishing a linear stationary frequency relation.

In the general case, the input instantaneous frequency varies over time. There are more than one way to define instantaneous frequency of a spike train [22]. Here, we adopt the following window method:

\[
f(t) = \frac{1}{\Delta t} n(t; t + \Delta t)
\]

Where \( n(t; t + \Delta t) \) is the number of spikes between \( t \) and \( t + \Delta t \). In this context, when the input instantaneous frequency varies over time it is not possible to have a function that describes the relation between the input and the output instantaneous frequencies of a integrate-and-fire neuron.

Observe that it is not possible to construct a function between the instantaneous frequencies with the examples of Figure 2 and Figure 3. Considering a frequency window \( \Delta t = 20ms \) the Figure 2 shows that two input spike trains with the same instantaneous frequencies (both have 13 spikes in the 20ms interval) can generate different output instantaneous frequencies in the same interval. Contrariwise, Figure 3 shows that two input spike trains with different instantaneous frequencies can generate equal output instantaneous frequencies.

Therefore, it is not possible to build a function between the input and output frequencies based only on their instantaneous values, but as will be shown below it is possible to obtain a relationship between them.

IV. DEVELOPMENT

As seen previously, at an instant \( t \) the output instantaneous frequency of a leaky integrate-and-fire neuron depends of the input current not only at that moment but also at the moments prior of \( t \). When working only with the frequencies of the spikes and with instantaneous relations, we do not have the complete information about the input current and therefore we have to use a statistical relation between the frequencies.

The dynamic of the leaky integrate-and-fire model was simulated using the Equation 7 with total execution time of 10000ms and a simulation time interval of \( dt = 0.1ms \). So, at each \( dt \), the membrane potential value is calculated and compared to the spiking threshold in order to know if a spike was generated or not. The dynamic constants were configured as: membrane rest potential \( u_r = 0mV \), spiking threshold \( \vartheta = 25mV \), absolute refractory period \( \tau_r = 0ms \) and membrane resistance \( R_m = 10M\Omega \).

The input current was chosen to be an homogeneous Poisson process [23], the input current is generally modeled in this way [19, 24], which at every simulation time interval has a chance of 5% to generate an input spike. This chance of spike was chosen because it generates, in the period of time used for the simulations and for the adopted frequencies windows, consistently both null and small input frequencies as well as relatively high input frequencies. This is illustrated in the histogram of interspike intervals (ISI) shown in Figure 4.

Under the previous assumptions and settings, the \( EPSP \) (excitatory postsynaptic potential) \( a_E \) and the membrane time constant \( \tau_m \) become the principal parameters that can be altered for the study of the dynamic of the model. Due to the relation \( \tau_m = R_mC_m \), variations of \( \tau_m \) are equivalent to variations of the membrane resistance \( R_m \) and the membrane capacitance \( C_m \). And variations of the \( EPSP \) are related to variations of the spiking threshold \( \vartheta \).

The plot of the output instantaneous frequency in terms of the input instantaneous frequency for several values of \( EPSP \) is illustrated in Figure 5. The possible values of the instantaneous frequency is given by intervals of \( \frac{1}{\Delta t} \) as a consequence of the instantaneous frequency window method, as implied by Equation 10. Its possible to identify a linear relationship between the frequencies, which becomes more defined with the increase of the \( EPSP \).

This behavior makes sense if we analyze what is expected from the plot of an \( EPSP \geq 25 \). In this case the system is completely determined as each input spike generates an output spike, so the instantaneous frequency plot is a perfect line with the slope \( a = 1 \). It remains to be seen how the relation between instantaneous frequencies approaches a straight line for the different values of \( \tau_m \), \( EPSP \) and the window size of the frequency calculation \( \Delta t \), whether it is a smooth or abrupt transformation.

In order to reach conclusions about the dynamics of the model in a way that is not too variant with the frequency window \( \Delta t \) used, several values for the frequency window were adopted for the simulations performed. The windows size \( \Delta t \) was taken as 1,5,10,15 and 20ms.

The way in which the instantaneous frequency has been
defined implies it to assume only discrete values. After a simulation, the quantity of points found with a particular combination of an input frequency and an output frequency at any time of the simulation is based on the probability density of the input interspike intervals, since it determines the amount of times an input pattern is repeated, and on the simulation time. Observe that the possibility of one of these points exist with a determined combination of input and output instantaneous frequency is determined only by the model dynamic and parameters.

It will be assumed that the execution time of the simulations with the probability density of the input pulses and the model parameters are sufficient to generate at least one result respective to each of all the possible combination of input and output instantaneous frequency for
small frequencies values. Therefore, for a study of frequency transfer that does not depend on the probability density of the input interspike intervals, only one value of each combination of input and output instantaneous frequency were considered for the next analyzes.

A. Correlation

The relationship between the input and output instantaneous frequencies at the same instant of time has a linear shape that depends on the parameters of the neuron (Figure 5). A neuron for which the transference of the instantaneous frequencies is a straight line acts as a linear frequency attenuator.

In order to know when an integrate-and-fire neuron can be approximated by a frequency attenuator and how well this approximation can be, it is necessary to measure the linearity of the instantaneous frequencies relationship of the neuron. For this, we used the Pearson correlation as a measurement of how linear is a relationship, high values of Pearson correlation mean that the system can be well represented by a linear function [25].

The plot of the Pearson correlation coefficient in terms of $EPSP$ and $\tau_m$, can be seen in Figure 6 for different values of $\Delta t$. The plot shows a crescent behavior of the correlation with $EPSP$ and $\tau_m$. This is expected because the higher the $EPSP$, the closer the neuron is to the saturation, which has a linear characteristic. The higher the membrane time constant, the closer the neuron is to a perfect integrator.

The Figure 6 shows that there are no major differences in the behaviors obtained for different frequency window sizes, besides some variation which decreases with the increase of the frequency window size, as expected. These characteristics are found in all results of this work, which shows that these frequency window sizes are in a stable region, which does not change the results of the dynamics of the system. In the rest of this work, we will use mostly the frequency window size of $\Delta t = 10ms$ and, in some cases where less variation is desired, we will adopt $\Delta t =$ 20$ms$.

An important characteristic about the Person correlation is that it is a measurement of the quality of a least squares linear regression. In this context the Pearson correlation is called coefficient of correlation $R$ and its square is named coefficient of determination $R^2$ and both values are often used as measures of quality, each with its advantages, of a least squares linear regression [20].

It is useful to establish categories of linearity of the frequency transference, and this can be done by taking into account the fact that the Pearson coefficient increases with $EPSP$ and $\tau_m$. Using a determined value of the Pearson coefficient, it is possible to adjust the points with lowest correlation values that are greater than or equal to the determined value in order to construct a curve of $EPSP$ in terms of $\tau_m$. Due to the increasing behavior of the Pearson coefficient, it is possible to infer that for values of $EPSP$ and $\tau_m$ above this curve the Pearson coefficient will result above the initially determined value.

For this curve adjustment, we adopted the least squares method with a model function of $ax^{-b} + c$ where $a$, $b$ and $c$ are the adjustment coefficients [27]. The results are showed in the Table I and the curves are showed in the Figure 7.

![Histogram of the interspike intervals (ISI) of consecutive spikes in the current input. It is possible to identify the exponential behavior characteristic of a homogeneous Poisson process.](image)

**FIG. 4:** Histogram of the interspike intervals (ISI) of consecutive spikes in the current input. It is possible to identify the exponential behavior characteristic of a homogeneous Poisson process.

| Pearson Coefficient | Bounding Curve | Standard Error |
|---------------------|----------------|---------------|
| $\geq 0.95$         | $\frac{30.61}{20.28} - 8.35$ | 0.73         |
| $\geq 0.9$          | $\frac{18.71}{20.47} + 0.50$ | 0.47         |
| $\geq 0.8$          | $\frac{14.24}{20.47} + 1.00$ | 0.38         |
| $\geq 0.7$          | $\frac{12.12}{20.35} + 1.09$ | 0.33         |
| $\geq 0.6$          | $\frac{12.27}{20.47} + 0.81$ | 0.33         |

**TABLE I:** Curves that delimit an area of the $EPSP$ and $\tau_m$ plane. For values of $EPSP$ and $\tau_m$ higher than the curve the Pearson Correlation is higher than a determined value. The standard error is the average of the vertical distance between the data and the adjusted curve.

B. Linear Regression

As seen in the previous section, the relationship between the frequencies is a scatter of points with a linear behavior for some model parameters. The method used to study this linear behavior involves fitting the set of points of the instantaneous frequencies relationship (Figure 5) by a straight line, by using the least squares method.

The parameters of the adjusted straight line in terms of the model parameters $EPSP$ and $\tau_m$ is illustrated in...
FIG. 5: Left: plots of both instantaneous frequency input and output along time. Right: plots of the respective instantaneous frequency output in terms of the input at the same instant of time. The simulations adopted $\tau_m = 20\text{ms}$, the window size of the frequency $\Delta t = 10\text{ms}$, the total time of $10000\text{ms}$ and the EPSP varies in each subplot: a) $3\text{mV}$; b) $5\text{mV}$; c) $10\text{mV}$; d) $15\text{mV}$.
FIG. 6: Each line is a plot of the Pearson correlation by $EPSP$ and $\tau_m$ in two different angles, the window size of the frequency $\Delta t$ varies in each subplot: a) 5ms; b) 10ms; c) 15ms; d) 20ms.

Figure 8. It is possible to see, for the slope $a$, that some well delimited regions are obtained, which have almost
FIG. 7: Plot of the adjusted curves of the Table I. Each curve delimits the plane $EPSP$, $\tau_m$ according with the value of the Pearson coefficient of the same color found in the legend.

constant value.

One characteristic that can be extracted from the Figures 8 and 6 is that the measurements vary with $\tau_m$ only for small values of $\tau_m$ and $EPSP$ remaining practically constant after that. This characteristic is found in all measures that vary with $EPSP$ and $\tau_m$ performed in this work. As showed, the model does not have a frequency transference with a linear behavior for small values of $\tau_m$ and $EPSP$, and therefore this region is not part of the focus of this work. Additionally the $\tau_m$ estimated to simulate biological cells is reasonable with these values [28, 29]. All this motivates us to analyze the model only for $\tau_m = 20$ ms, i.e. in the region where the frequency transfer exhibits some remarkable linearity and the behavior in terms of $\tau_m$ is almost constant.

The slope $a$ and the intercept $b$ of the adjusted line in terms of the $EPSP$ for $\tau_m = 20$ ms is illustrated in Figure 9. The slope $a$ has a small dispersion and for $EPSP$ values above about 9 mV it has a strong plateau-based behavior. This occurs because the higher the $EPSP$, the set of train of spikes that generate an output spike does not change considerably in the time scales used here, with the exception of changing plateaux regions.

The intercept $b$ has a higher dispersion and varies greatly with the $EPSP$. Additionally the intercept $b$ assumes small values, in the case presented that $\Delta t = 10$ ms the instantaneous frequencies have differences of 0.1 ms that is higher than the highest value that the intercept $b$ assumes. Therefore it’s possible to discard the intercept $b$, and work with a adjusted straight line of the type $y = ax$.

V. CONCLUSIONS

In the last years, the use of neuron models and numeric simulations to explain certain characteristics of the nervous system has greatly increased. This increase can be related to the success of this approach under certain circumstances and the ever increased processing power. However, most of these works focus on modeling neuronal activity in terms of differential equations, often solved by numerical means. The current work intends to study the relationship between input and output instantaneous frequencies of single neuronal cells by using a transfer function formalism. Widely used in areas such as electronic engineering, the transfer function allows the understanding of a system in terms of a graphic-functional relationship between its input and output. We adopted the leaky integrate-and-fire as the basic neuronal model, due to its simplicity and the fact that it has been used systematically in previous related works (e.g. [??]).

By using one input excitatory synapse, we derived relationships between the input and output instantaneous frequencies, at the same instant of time, for different model parameters. Because the integrate-and-fire system has memory, this relationship is not deterministic and, therefore, it is possible to have one input instantaneous frequency associated to more than one output instantaneous frequency. However, the possible values of this transference relationship still exhibit much linearity that varies with the model parameters. To quantify this linearity we calculated the Pearson coefficient of the relationship for different values of the model parameters: excitatory postsynaptic potential ($EPSP$), membrane time constant ($\tau_m$) and window size of the frequency ($\Delta t$) (Figure 6). Based in this information, we then applied the least squares method to relate regions of the param-
FIG. 8: a) Plot of the slope $a$ in terms of $EPSP$ and $\tau_m$ in three different angles. b) Plot of the intercept $b$ of the adjustment in terms of $EPSP$ and $\tau_m$ in three different angles.

ceter space with the adjust quality of the instantaneous frequencies transference by a straight line (Figure 7 and Table I). In this way, it became possible to determine the quality of the instantaneous frequencies transference approximation by a straight line, yielding a model in which the neuron acts as a frequency attenuator.

We also determined the parameters of the aforementioned straight line for the different model parameters (Figure 8), showing that the intercept of the line is not much relevant and that the slope has a nearly constant value in many regions of the parameters space. In addition, we showed that in the cases in which the neuron can be well approximated as a frequency attenuator, i.e. the instantaneous frequency transference relationship can be well approximated by a straight line, the membrane time constant ($\tau_m$) does not affect the frequency transference.

As future developments, it would be interesting to analyze how the behavior of the frequencies transference in the cases in which the neuron has more than one presynaptic input with different $EPSP$ and instantaneous frequencies. It would also be promising to study the transfer relationship for other neuron models, or even real neurons.

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FIG. 9: a) Slope $a$ of the transference frequency adjust in terms of $EPSP$. b) Intercept $b$ of the transference frequency adjust in terms of $EPSP$. In both plots $\Delta t = 10\, ms$ and $\tau = 20\, ms$. $EPSP$ values varies from $0.5\, mV$ to $30\, mV$ in intervals of $0.05\, mV$ (green squares). The blue points define the line and are given by the mean of the squares in a $0.5\, mV$ interval of $EPSP$. The dot line is the standard error.

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