

Computing with the leaky integrate and fire neuron: logarithmic computation and multiplication

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Abstract

The leaky integrate and fire (LIF) model of neuronal spiking (Stein, 1967) provides an analytically tractable formalism of neuronal firing rate in terms of a neuron's membrane time constant, threshold and refractory period. LIF neurons have mainly been used to model physiologically realistic spike trains but little application of the LIF model appears to have been made in explicitly computational contexts. In this paper we show that the transfer function of a LIF neuron provides, over a wide parameter range, a compressive nonlinearity sufficiently close to that of the logarithm so that LIF neurons can be used to multiply neural signals by addition of two LIF neuron outputs, yielding the logarithm of the product. A simulation of the LIF multiplier shows that under a wide choice of parameters, a LIF neuron can log-multiply its inputs to within a 5% relative error.

1 Introduction

In his book on Mach bands, Ratliff remarks that “often the relation between external stimulus and neural response is approximately logarithmic” (Ratliff, 1965, p. 129). As shown in Figure 1, such a relation is also observed in simulations based on the Hodgkin-Huxley equations (Hodgkin & Huxley, 1952) where a step current of varying amplitudes is applied to a single neuron. A similar compressive response is seen, for example, in M-cells (of the magnocellular stream) of visual cortex. In psychophysics, logarithmic neural transduction has been hypothesized to account for Weber’s law (Cornsweet, 1970; Land, 1977). In the neural modeling literature a logarithmic transfer function is also commonly hypothesized, for example, Koch and Poggio (1992) describe a mechanism for multiplying with neurons whose transfer function is logarithmic. Yeshurun and Schwartz (1989) show that an estimate of the power spectrum of the log power spectrum, which is called the cepstrum in signal processing, provides a simple model for estimating stereo disparity when applied to a columnar image data structure such as the ocular dominance column system of primate visual cortex. These references to logarithmic functionality in neurons lack a generic biophysical justification for this computation on the single cell level. In the present work, the leaky integrate and fire (LIF) model is shown to provide such a justification. Specifically, we show that the ratio of refractory period (t_0) duration to membrane time-constant (τ) controls the degree of compressiveness of a neuron’s transfer function. A cell with small t_0/τ has a quasi-linear transfer function. A broad range of t_0/τ gives a quasi-logarithmic transfer function, and the largest t_0/τ values yield a transfer function more compressive than a logarithm. The paper concludes with a discussion of precision and dynamic range of LIF and other single-cell computational models.

The LIF model used in the simulations below is a lumped model whose few parameters nevertheless correspond to measurable physical quantities. In order to demonstrate how the LIF model’s parameters affect its transfer function, the simplest (four parameter)

model is used, ignoring spike train variability and population coding (See Softky (1993) and Softky (1995) on spike train variability; Knight (1972) and Usher (1993) discuss the improved temporal dynamics of population coding). The work of (Bugmann, 1991) also demonstrates two computational regimes – multiplicative and linear – for a LIF neuron, but it uses a different LIF model than the four parameter model below: for multiplication, a coincidence detector (Srinivasan & Bernard, 1976) is used and the LIF neurons include a model both of spike-train variability and of the relative refractory period. Despite the difficulties with the coincidence detection multiplier discussed in Section 3.2 of this paper, Bugmann’s simulations indirectly demonstrate the same effect of t_0/τ on the cell’s transfer function that is shown below. This suggests that simple integrate and fire properties of a cell such as its refractory period duration and the membrane time-constant continue to affect the cell’s transfer function as described below, even in the presence of spike-train variability and of a relative refractory period model.

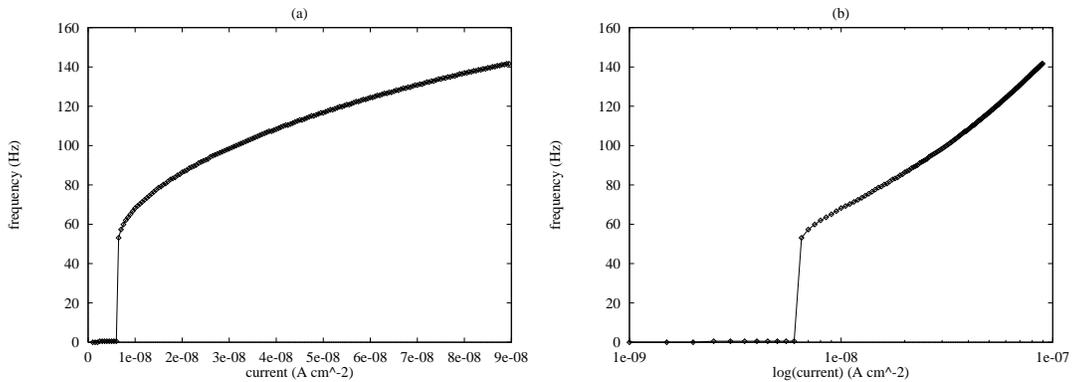


Figure 1. (a) Current-frequency curve resulting from uniform depolarization of a membrane modeled by the Hodgkin-Huxley equations, using the giant squid axon parameters (Hodgkin & Huxley, 1952); (b) semi-log plot of the curve in (a).

It is worth noting that logarithmic computation in the models below do not address sensory transduction neurons *per se* but rather, the models suggest that quasi-logarithmic computations could occur in any neuron for which the LIF model is a reasonable approximation. For this reason, parameter values are based on physiological measurements in

cat and rat pyramidal cells (see Section 3.1).

2 Properties of the LIF transfer function

Agin (1964) appears to have been the first to relate Hodgkin-Huxley simulations of a uniformly polarized membrane to “the logarithmic law of sensory physiology” by fitting the curve in Figure 1(a) to the equation $f = 27 \log(I + 1)$, where f is firing frequency and I is applied current. Although the Hodgkin-Huxley model is sufficient to produce a log-like transfer function, as is evident in Figure 1, its complex dynamics are not necessary for explaining the nature of the compressiveness. The much simpler LIF model is all that is required to account for the transfer function shown in Figure 1. As shown below, a neuron’s membrane resistance and capacitance and the duration of its absolute refractory period are sufficient to account for the log-like transfer-function shown in Figure 1, without a need to model the detailed dynamics of action potential generation.

2.1 The LIF model

In the LIF model, a steady current source, I , uniformly depolarizes the membrane causing an exponential increase in its potential, V . When the membrane potential reaches a threshold, V_{Th} , a spike occurs (at this point we shall assume the spike to take an infinitesimal amount of time). At the spike onset, the membrane capacitance discharges instantaneously and the membrane potential is reset to the resting potential. This firing process repeats for as long as the input current is on (see Figure 2(b)).

A resistor and a capacitor in parallel model the membrane’s charging process (see Figure 2(a)). The RC integrator of the LIF model relates membrane potential to input current via the usual exponential charging relationship (Horowitz & Hill, 1989):

$$V = IR[1 - e^{-t/\tau}] \tag{1}$$

where $\tau = 1/RC$ is the membrane time-constant.

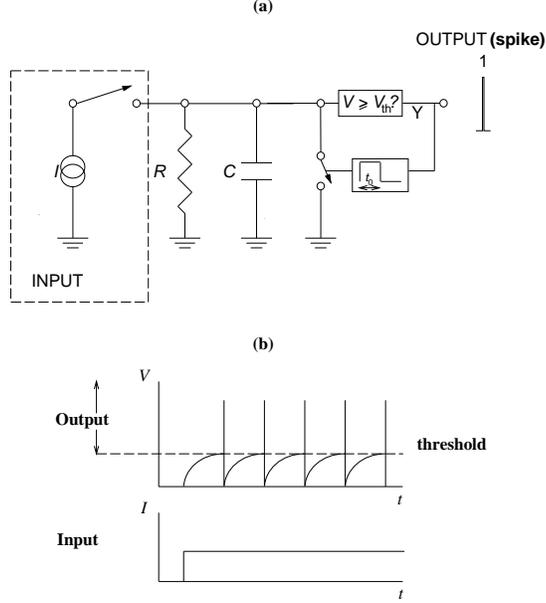


Figure 2. (a) RC circuit used to model charging of a neuron's membrane from its resting potential to V_{Th} . C corresponds to the membrane capacitance, R corresponds to the membrane resistance and I corresponds to an excitatory input such as a current injection or a steady current produced by a train of excitatory post-synaptic potentials. t_0 is the duration of the absolute refractory period; (b) membrane voltage vs. time in an RC-circuit IAF model, in response to a step current. Only the suprathreshold spikes are produced in the output.

We now outline Stein's analysis of the leaky integrate and fire model. The time t_{isi} (the time it takes the membrane to reach V_{Th}), also called the inter-spike interval, can be calculated by setting $V = V_{Th}$, $t = t_{isi}$ in Equation 1, and solving for t_{isi} :

$$t_{isi} = -\tau \ln \left(1 - \frac{V_{Th}}{IR} \right). \quad (2)$$

The rheobasic current, I_{th} , is defined as the smallest value of current that can drive the membrane potential to V_{Th} :

$$I_{th} = \frac{V_{Th}}{R}. \quad (3)$$

Substituting Equation 3 for I in Equation 2, t_{isi} can be rewritten as

$$t_{isi} = -\tau \ln \left(1 - \frac{I_{th}}{I} \right). \quad (4)$$

The cell's firing frequency f is the reciprocal of the period of each action potential. Since an action potential is considered to have infinitesimally small duration, the period of each

action potential is just the inter-spike interval (Equation 4). The firing frequency as a function of current is therefore

$$f = \frac{1}{-\tau \ln(1 - I_{th}/I)}. \quad (5)$$

The LIF model described so far does not produce a compressive or quasi-logarithmic current frequency relation. As current is increased in Equation 5, the current frequency relation becomes linear. Stein has shown that Equation 5 becomes linear for large I by expansion of its power series:

$$\begin{aligned} f &= \frac{1}{-\tau[(I_{th}/I) + \frac{1}{2}(I_{th}/I)^2 + \frac{1}{3}(I_{th}/I)^3 + \dots]} \\ &= \frac{1}{\tau} \left[(I/I_{th}) - \frac{1}{2} - \frac{1}{12}(I/I_{th})^{-1} - \dots \right]. \end{aligned} \quad (6)$$

From Equation 6, we see that as I grows larger than I_{Rh} , the frequency becomes proportional to the line with slope RC intersecting the abscissa at $1/2$. The inverse frequency, or rate, is thus quasi-linear in the approximation considered here, which ignores the effect of refractory period(s) (see Figure 3).

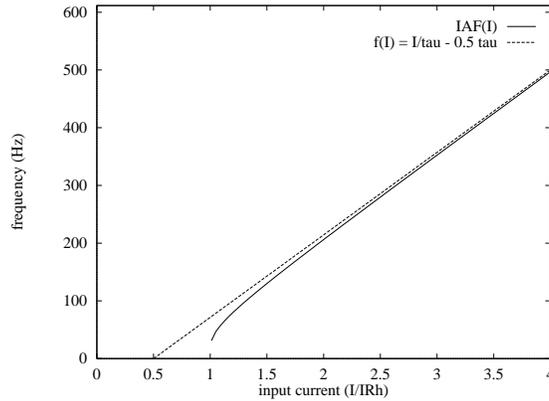


Figure 3. Plot of the integrate and fire transfer function (solid line) with no absolute refractory period (i.e. $t_0 = 0$). This transfer function approaches the line $I/\tau - 0.5\tau$ (I in units of the rheobasic current). Thus if the time constant of a neuron is much larger than the refractory period duration, the transfer function of the cell is quasi-linear. All other parameter values are shown in Table 1.

The quasi-linear output of the simple LIF model above, therefore, does not provide a compressive transduction function. However, the analysis of the effects of refractory

behavior (both relative and absolute refractory period), which was included in the LIF analysis of Stein(1967), changes the output function of the LIF model from linear to quasi-logarithmic, in suitable parameter ranges, as follows: Let the absolute refractory period take time t_0 †; the inter-spike interval in Equation 2 is then $t_{\text{isi}} + t_0$, and the frequency is

$$f = \frac{1}{t_0 + t_{\text{isi}}} = \frac{1}{t_0 - \tau \ln(1 - I_{\text{th}}/I)} \quad (7)$$

Note that as I grows arbitrarily, f in Equation 5 grows without bound while in Equation 7, f remains bounded at $1/t_0$. This boundedness compresses high I values and yields a log-like response. The larger t_0 is in Equation 7, the more f is compressed. The current frequency relation expressed by Equation 7 maintains the same shape when the ratio t_0/τ remains constant. Figure 4(a) shows plots of Equation 7 for different ratios t_0/τ . Of the curves in Figure 4(b), we see that the one whose corresponding t_0/τ is between 0.1 and 0.2 best approximates a log, since it produces the most linear curve on a semi-log plot.

One critical issue is the “goodness-of-fit” of the LIF transfer function to the logarithm. We have taken the approach of defining “goodness-of-fit” in terms of the operation of multiplication. In other words, if the compressive non-linear transduction function supports an accurate multiplication model, then we deem it to be a good “quasi-logarithmic” function. In the following section, an LIF neuron with biologically reasonable parameter values is quantitatively shown to within a 5% relative error.

In summary we conclude that the log-like response of neurons depends on two properties of the LIF model:

1. The neuron’s *time constant* (affecting integrative behavior).
2. The existence of a *refractory period* (affecting rate saturation).

†Note that the relative refractory period – the time period after a spike during which it is difficult but not impossible to generate another action potential – is not taken into account in this model, but Stein (1967) has shown that the effect of including a relative refractory period modeled by rising and falling exponentials is qualitatively the same as that of increasing the value of parameter t_0 in the current model, that is, as either the absolute refractory period or the relative refractory period are increased, the current frequency relation becomes more compressive. The parameter t_0 can therefore be thought of as lumping the effects of both the absolute and relative refractory periods.

We can now see why the Hodgkin-Huxley equations produce a log-like behavior, as per Agin’s original observation. The underlying passive circuit in the Hodgkin-Huxley model is an RC circuit with an active component – voltage dependent conductances – that corresponds to the LIF model’s firing mechanism. Although it is difficult to make general statements about the detailed behavior of the Hodgkin-Huxley dynamics (due to its mathematical complexity), it appears that the logarithmic behavior observed by Agin (1964), and replicated in Figure 1 is accounted for by the passive integrative component alone, i.e., it is captured by the LIF model. In any event, the LIF model is sufficient to account for Agin’s observation of the logarithmic behavior of the Hodgkin-Huxley model.

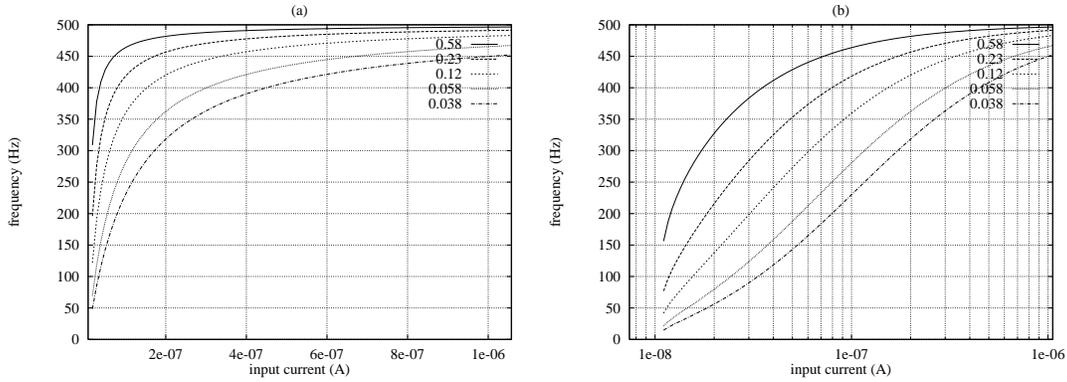


Figure 4. (a) Plots of Equation 7 for different values of t_0/τ (key shows t_0/τ); (b) semi-log plot of the curves in panel (a). Parameter values are shown in Table 1.

<i>parameter</i>	<i>value</i>	<i>units</i>
t_0	0.002	S
τ	varies	S
V_{th}	0.015	V
C	$6 \cdot 10^{-11}$	F
R	τ/C , varies	Ω
I_{rh}	V_{th}/R , varies	A

Table 1: Parameter values used in LIF multiplication and in Figures 3 and 4: t_0 = absolute refractory period; τ = time-constant (t_0/τ is varied in the simulations by keeping t_0 constant and varying τ); V_{th} = membrane threshold voltage; C = soma capacitance; R = soma membrane resistance, I_{rh} = Rheobasic current.

3 LIF Multiplication

Many arguments have been proposed for the usefulness of multiplication in the nervous system. Functionally, the product of two signals produces an analog measure of their correlation, or in boolean terms, their conjunction, implemented by the 'AND' operator. Barlow (1969) argues that selectivity and generalization in the visual system require multiplication and summation operations. The Reichardt motion detector (Reichardt, Egelhaaf, & Ai-ke, 1989) relies on a multiplicative operation. For a review of neural uses and neural models of multiplication see Koch and Poggio (1992). A simple scheme for neural multiplication mentioned by Koch and Poggio (1992) involves neurons with a logarithmic transfer function that excite or inhibit each other additively or subtractively. Under these assumptions, if x_1 is the input to neuron A and x_2 is the input to neuron B and the outputs of both neurons A and B add, then the sum is

$$\log(x_1) + \log(x_2) = \log(x_1 x_2) \quad (8)$$

which is a multiplicative relation. Thus multiplication and division can be implemented by adding and subtracting outputs of neurons with a logarithmic transfer function.

In order to evaluate to what extent, and over what parameter ranges, the transfer function of a neuron is logarithmic, the multiplication model of Equation 8 was simulated using a single LIF neuron receiving two simultaneous constant current injections. A log-product provides the functionality of multiplication or correlation, simply because it is a monotonic function of the product. The analysis below uses the multiplication model to demonstrate that a quasi-logarithmic computation in neurons can occur accurately across a biologically reasonable t_0/τ range.

3.1 Parameter choices

Since the ISI does not vary in this model and inputs are held constant through time, the equilibrium solution (Equation 7) is used. To solve Equation 7, four parameters need to be

specified: t_0 , τ , V_{th} and C . Parameter choices are based on physiological values observed in cortical pyramidal cells of the rat and the cat, summarized and derived in (Bugmann, 1991). The input injection current, I_{inj} , varies over a realistic range of current injection: $[1I_{\text{th}}, 13I_{\text{th}}]$ Amperes. Threshold potential, $V_{\text{th}} = 15\text{mV}$ (see (Wolfson, Gutnick, & Baldino, 1989)). V_{th} lies between the axon hillock threshold and the soma fast sodium conductance threshold (Schwindt & Crill, 1982). The capacitance, $C = 6 \cdot 10^{-11}$, agrees with published values of the neural membrane capacitance ($1\text{-}2\mu\text{F cm}^{-2}$ (Jack, 1979; Kawato, Hamaguchi, Murakami, & Tsukahara, 1984)) and surface area of the soma of pyramidal neurons ($200\text{-}700\mu\text{ m}^2$ (Hillman, 1979)). The refractory period, $t_0 = 2\text{ms}$, is comparable to that used in other biologically motivated simulations of LIF neurons (see (Harmon, 1961; Amit, Evans, & Abeles, 1990)). Table 1 summarizes the parameter values and derived constants in the model.

3.2 Precision and dynamic range

The firing rate of neurons typically extends from a few Hertz to a few hundred Hertz. The utility of any numerical function dependent on firing rate is thus limited to this range. We have examined the precision of a multiplier that is constructed from two summed quasi-logarithmic LIF neurons. We used the LIF transfer function (Equation 7), for a range of different t_0/τ , (as plotted in Figure 4) and defined the error by “multiplying” several thousand combinations of input currents. This was done by summing the corresponding “quasi-log” firing rates using the LIF curve, and comparing this method of multiplication with the correct numerical answer. We defined error, δ , by the average relative error, i.e. as

$$\delta = 1/N \sum_{i=1}^N \frac{|(L(\overline{a_i b_i}) - a_i b_i)|}{a_i b_i}, \quad (9)$$

where a_i and b_i are two “input” currents to be multiplied. The estimate of their product, $\overline{a_i b_i}$, is obtained by summation of the “quasi-logarithmic” LIF transfer function as follows: Let $f_{\text{LIF}}(I)$ be the frequency-current relation expressed by Equation 7. We first generated a

number of random current value pairs $\{a_i, b_i\}$. Multiplication of each pair was performed by the equation

$$f_{\text{LIF}}^{-1} (f_{\text{LIF}}(a) + f_{\text{LIF}}(b)) , \quad (10)$$

where f_{LIF} is Equation 7 and f_{LIF}^{-1} is its inverse. Using the inverse function permits the unit of the multiplier (current squared) to be the same unit as the actual product of currents, $a_i b_i$, and thus the degree of correlation between the two products can be determined.

The products obtained by Equation 10 are then fitted using linear interpolation to the numerically correct products, $a_i b_i$, obtaining an equation for a straight-line, $L(I)$ [‡]. A new set of LIF-products is then generated, and the LIF-products are interpolated via $L(\overline{a_i b_i})$ and then subtracted from $a_i b_i$, as in Equation 9.

Equation 9 provides a measure of the average deviation from a perfect multiplication, as a fraction of the product itself. Figure 5(a) shows the average relative error of the LIF products as a function of t_0/τ . This error, expressed as a percentage, is around 5% for $0.13 < t_0/\tau < 0.23$, indicating that in this input range the “quasi-logarithmic” LIF transfer function is useful as an approximate four-bit multiplier. Figure 5(b) shows the data points used for the error estimate for the case of $t_0/\tau = 0.2$ in Fig 5(a).

The timing constraints of the LIF model above can be considered by measuring the time to equilibrium of the LIF differential equation as it is iterated in time. As shown in Figure 6 the voltage of a LIF neuron reaches equilibrium (that is, the membrane capacitance saturates) after about 25 msec, across a range of biologically reasonable current input levels. This means that the multiplication model above can only work when the input to a cell varies temporally with an average period on the order of 25 msec. This time-resolution corresponds to a maximum input frequency of 40Hz that can be resolved by the LIF model presented above.

[‡]Note that this linear regression is used simply to rescale the output in order to compare it to mathematically correct multiplication. In neuronal terms, this implies a gain and offset at the summing neuron that would need to be specified if actual numerical multiplication were desired in a particular model. However, without this, the simple model of summing of the output of two “logarithmic” neurons provides a result which is proportional (with an offset) to the desired numerical (log)product over the entire dynamic range of the neuron.

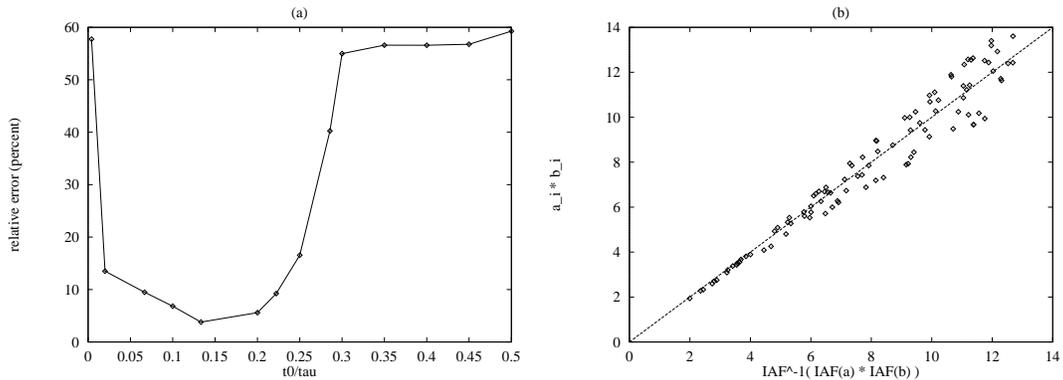


Figure 5. (a) A plot of Equation 9, the average relative error of the IAF products as a function of t_0/τ . N , the number of samples used for each point, is 10,000 (see text for details of this simulation). Solid line is the identity function $y = x$. (b) A sample of 100 data points $a_i b_i$ (abscissa) vs. $a_i b_i$ (ordinate) used to obtain the sixth point from the left in panel (a). t_0/τ for this point is 0.2, and the relative error in multiplication is approximately 5%. Both ordinate and abscissa in (b) have units of I_{Rh}^2 .

A known model of multiplication that takes into account spike timing is the coincidence detector (Srinivasan & Bernard, 1976) (this model is also the multiplicative mechanism used in Bugmann’s (1991) LIF model). One difficulty with coincidence detection is that for low spike rates modelled by a Poisson distribution, its accuracy grows as the logarithm of the time window used to count coincidences. Thus, the activity of a single-cell coincidence detector whose inputs spike at a mean rate of 20 Hz would have to be integrated for approximately 20 seconds in order to achieve a 5% accuracy in its multiplication estimate. It has been argued, however, that the coincidence detector could be functioning on the faster temporal scale of dendritic summation (Softky, 1995) (see also the reply by Shadlen & Newsome (1995) in the same issue, which analyzes the temporal summation properties of LIF coincidence detectors).

4 Conclusion

In this paper, we provide a model for multiplication with neurons that depends only on the generic properties of the leaky integrate and fire model of neural transduction. The range over which LIF neurons have a sufficiently compressive transfer function to

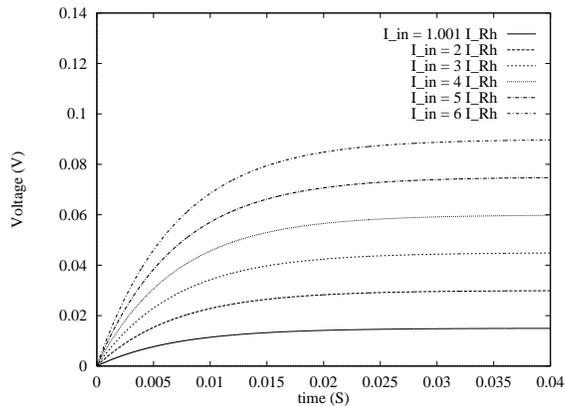


Figure 6. An integrate and fire neuron’s response over time to varying constant input values. Equilibrium is approximately reached in 25 msecs, meaning that for logarithmic computation to occur to within a 5% accuracy, the input’s frequency cannot exceed 40Hz, a reasonable requirement for cortical neurons.

multiply their inputs to within a 5% accuracy is quite broad in the parameter space of the LIF model. Thus, in the case that the LIF model is a reasonable approximation to neural transduction, a simple and generic model for neural multiplication is provided. The single dimensionless parameter t_0/τ determines the shape of a LIF neuron’s current frequency transfer function, changing it from linear (small t_0/τ) to quasi logarithmic (larger $t_0\tau$) under a biologically reasonable parameter ranges. Thus, parameters such as the refractory period duration, membrane resistance and membrane capacitance are linked with computational properties of the transfer function of single neurons.

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