

Role of Temporal Integration and Fluctuation Detection in the Highly Irregular Firing of a Leaky Integrator Neuron Model with Partial Reset.

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Submitted: 6 July 1995 (posting date)

Abstract

Partial reset is a simple and powerful tool for controlling the irregularity of spike trains fired by a leaky integrator neuron model with random inputs. In particular, a single neuron model with a realistic membrane time constant of 10 ms can reproduce the highly irregular firing of cortical neurons reported by Softky and Koch (1993). In this paper, the mechanisms by which partial reset affects the firing pattern are investigated. It is shown theoretically that partial reset is equivalent to the use of a time dependent threshold, similarly to a technique proposed by Wilbur and Rinzel, (1983) to produce high irregularity. This equivalent model allows to establish that temporal integration and fluctuation detection can coexist and co-operate to cause highly irregular firing. This study also revealed that reverse correlation curves can not reliably be used to assess the causes of firing. For instance they did not reveal temporal integration when it took place. Further, the peak near time zero did not always indicate coincidence detection. An alternative qualitative method is proposed here for that purpose. Finally, it is noted that, as the reset becomes weaker, the firing pattern shows a progressive transition from regular firing, to random, to temporally clustered and eventually to bursting firing. Concurrently, the slope of the transfer function increases. Thus simulations suggest a correlation between high gain and highly irregular firing.

1. Introduction

It has been reported by (Softky and Koch, 1992, 1993) and (Bugmann, 1990) that the highly irregular firing of cortical neurons cannot be reproduced by a *single neuron* performing the temporal integration of Excitatory Post-Synaptic Potentials (EPSP) generated by independent stochastic input spike trains. They found that only simulations with biologically unrealistic short membrane integration time constants of $RC < 1$ ms allowed to reproduce the observed irregularity.

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While irregular firing at low frequency is commonly obtainable with long membrane time constants (see e.g. Bugmann, 1991a), the specific problem posed by the data of Softky and Koch (1992, 1993) was the high irregularity *at high frequency*.

This result has triggered investigations into alternative ways of producing irregular spike trains, e.g. exploiting dynamic properties of *networks* of spiking neurons (Usher et al., 1994; Zipser et al., 1993) or exploiting *balanced* excitatory and inhibitory inputs (Shadlen and Newsome, 1994, Bell et al, 1995). Recently (Bugmann and Taylor, 1994; Bell et al, 1995) have reminded that incomplete repolarisation (or *partial reset*) of the membrane causes highly irregular firing (for older references to that approach, see (Lansky and Musila, 1991)). The combination of balancing excitation and inhibition and partial reset was advocated in (Tsodyks and Sejnowski, 1995). So far however, it has not been shown that any of these mechanisms allows to reproduce the dependence between irregularity and firing rate shown in (Softky and Koch, 1993).

This paper concentrates on the partial reset technique and demonstrates that it enables a single neuron with a realistic membrane time constant of 10 ms to reproduce the highly irregular firing of cortical neurons. It is shown theoretically that partial reset is equivalent to the use of a time dependent threshold, similarly to a technique proposed by Wilbur and Rinzel, (1983) to produce high irregularity. This equivalent model allows to establish that temporal integration and fluctuation detection can coexist and cause irregular firing. It is shown that, on one hand the potential of the membrane results from the progressive accumulation of input currents, while on the other hand, current peaks are the events causing firing, because the firing threshold remains slightly above the rising potential. Reverse correlation curves are analysed for various strength of reset, in an attempt to establish the causes of firing. However, it is found that they do not reveal temporal integration and peaks near time zero are not reliable indicators of coincidence detection. An alternative qualitative method is proposed for that later purpose.

2. Partial reset and the control of the firing irregularity

Partial reset is a mechanism by which an output spike does not completely reset the membrane potential of a neuron model (Shigematsu et al, 1992). In our simulations of a Leaky-Integrate-and-Fire (LIF) neuron (see a description of that model in (Softky and Koch, 1993) and in Appendix 1) an output spike fired at time t resets the potential of the capacitor to $V(t) = \beta V_{th}$, where V_{th} is the firing threshold and β is the reset parameter, with a value between 0 and 1. By comparing the results from Rospars and Lansky (1993) and those of Christodoulou et al. (1994) who found $CV > 1$ when no resetting was used with the results of Softky and Koch (1993) who found $CV < 1$ for $\beta = 0$, it was inferred that partial reset may allow a fine control of the irregularity of the spike trains. This

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is confirmed in figure 1 which illustrates that CV can be varied over a wide range by varying the reset parameter β .

Partial reset in a leaky integrate-and fire neuron corresponds most likely to partial repolarisation of the somatic membrane in more detailed models (Bell et al., 1995) but it could also reflect a true but incomplete electrical decoupling between axonal trigger zone and neuronal soma (Bras et al., 1988) or between soma and dendrites (Rospars and Lansky, 1993) or be merely a computationally simple way to reproduce the effects of more complex dynamical properties of the membrane (see e.g. (Carpenter, 1979; Lansky and Musila, 1991)).

3. Equivalence between partial reset and time-varying threshold

A LIF neuron with constant threshold and partial reset is equivalent to a LIF neuron with total reset and a time varying threshold. This is briefly demonstrated analytically in Appendix 1 and is illustrated in figure 2. After a spike is produced, partial reset initially sets the potential $V(t)$ of the capacitor to βV_{th} . If there is no subsequent input, the potential decays according to the curve $V_0(t)$. If there are input spikes, the potential increase due to the inputs builds up on top of the decaying $V_0(t)$ potential. The resulting total potential $V(t)$ is overall relatively constant and firing appears to be controlled by maxima of potential fluctuations, usually attributed to coincidences of input spikes. Another picture emerges when the potential $V_0(t)$ is subtracted from $V(t)$ and from the threshold, an operation which, according to the theory, results in an equivalent model. In the equivalent model, the potential $V'(t)$ of the soma shows now the usual integration and reset cycle seen in LIF models with total reset. In contrast to the constant threshold used in the classical LIF model, the threshold is now increasing with time, according to $V_{th}(t) = V_{th} - V_0(t) = V_{th}(1 - \beta \exp(-t/RC))$. In figure 2, this threshold stays closely above the membrane potential while both increase almost in parallel.

4. Determinants of the firing time

How is the firing time determined in a LIF model with partial reset ? Of special interest is a case of high irregularity and high frequency, for instance the point $T = 10$ ms and $CV = 0.87$ in the curve for $\beta = 0.91$ in figure 1 which is characteristic of the biological data and could not be reproduced in simulations by Softky and Koch (1993). For comparison, points with $T = 10$ ms on the curves for the two other values of β are also discussed. It can be seen in figure 2 that the potential $V'(t)$ of the membrane (of the equivalent model) increases progressively, which is, in the commonly accepted sense, the result of the temporal integration of past input spikes. However, due to the small distance between firing threshold and the potential, potential fluctuations are more likely to cause early firing and can thus become the actual causes of firing. The importance of potential fluctuations for the firing behaviour of the neuron is reflected in the fact that the average interspike interval with a

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fluctuating input, T_f , is shorter than the interspike interval T_c observed with a continuous input current of the same average value¹. For instance, in the case $\beta = 0$, the fluctuations seem to play no role, as $T_f = T_c = 10$ ms. In the case $\beta = 0.98$, when $T_f = 10$ ms, the potential cannot reach the firing threshold with the continuous input current ($T_c = \text{infinity}$), therefore, fluctuations are essential for firing. In the case $\beta = 0.91$, the fluctuations play a significant role, as most spikes are produced early ($T_c = 17$ ms and $T_f = 10$ ms). Therefore, although the potential of the neuron is the result of a standard temporal integration process, the fluctuations of that potential are determining the time of firing, due to the partial reset mechanism or, equivalently, the use of a time dependent threshold.

5. What do reverse correlation graphs tell us ?

What is the time scale over which input current fluctuations (fluctuations of the density of input spikes along the time axis) are integrated to result in potential fluctuations which cause firing ? To answer such a question, one usually turns to reverse correlation graphs, which can "indicate the length of stimulus history that is relevant." (Mainen and Sejnowski, 1995). This interpretation of reverse correlation curves requires some caution (see also Shadlen and Newsome, 1995). For instance, in figure 3, the curve for $\beta = 0$ is almost perfectly flat for times earlier than -0.5 ms, although it is established that, in this case, every input spike arriving during an average of 10 ms before firing is relevant, as firing results from temporal integration of small EPSPs (Softky and Koch, 1992, 1993). An indication on the length of relevant stimulus history is only provided if the temporal organization of the inputs is important for firing. In the case $\beta = 0$, the timing is not important and the graph does not show any feature, even if spikes *are* important for the firing process.

In the curve for $\beta = 0$, the peak at time zero of amplitude 611 Hz is due to the fact that an LIF neuron can only fire when the instantaneous input current is above current threshold (Bugmann, 1991b). In models with EPSP's extended in time, e.g. modeled with alpha functions [Bugmann, 1995], such a current level results from inputs having occurred some time in the past. However, in the model used here, where spikes cause an instantaneous increase in potential (of 0.16 mV), at least one spike must be present during a time step for firing to be possible during that time step. Therefore, the average input firing rate measured by the reverse correlation contains only time steps with one or more spikes for the bin at time zero. This results in large values of the input firing rate. For instance, if one uses only time steps with one or more spikes, the calculated frequency is 380 Hz, while the average input frequency is 295 Hz. If only time steps with two or more spikes are used, the calculations give 673 Hz. Thus, the amplitude of 611 Hz of the central peak indicates that firing mostly occurs during time steps with two or more input spikes. This

¹Each input spike deposits a fixed electric charge $\Delta Q = V_I * C$ (see Appendix 1) in the capacitor, so that a spike trains of frequency f "carries" an average current $I_{AV} = f * \Delta Q$.

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sampling effect results in even higher peaks at time zero when smaller simulation time steps are used. This effect added to the fact that the central peak is observed for all three values of β , do strongly suggest that the central peak does not have any computational meaning. For instance, for $\beta = 0$, temporal integration determines the time of firing while in the case $\beta = 0.98$, potential fluctuations determine the time of firing.

In the curve for $\beta = 0$, in the 3-4 time steps before zero, there is a small accumulation of spikes which indicates that, in average, a spike is produced just after a small peak in input current (due to a higher than average arrival rate of input spikes) lasting approximately 0.5 ms. In the case $\beta = 0$, such an accumulation can not be taken as evidence that the neuron is technically a coincidence detector in the sense that only coincidences within a small time window of 0.5 ms cause firing. It merely reflects the fact that, in case of a fluctuating input current, the potential of a LIF neuron usually crosses the threshold during a positive fluctuation. This fluctuation does not need to be large in the case $\beta = 0$ where the saturation potential for an equivalent continuous input current is 24 mV and the potential is rising steeply when crossing the firing threshold. Actually, the comparison of T_c with T_f done earlier shows that fluctuations are not needed at all, because the neuron would fire at the same rate when fed with an average input current.

In the case $\beta = 0.91$, the saturation potential is slightly above the threshold but, at time $T = 10$ ms, the average potential is still below threshold at 14.4 mV (starting with a reset potential $\beta V_{th} = 13.65$ mV). Thus potential fluctuations of sufficient amplitude are required to cause the observed early firing. This is reflected in the reverse correlation curve, where the accumulation before time zero is of larger amplitude and longer duration than in the case $\beta = 0$, indicating that firing is usually preceded by current peaks lasting up to 2 ms (see footnote²). In this case where the input spikes arrive at an average rate of 0.95 per bin (0.1ms), current peaks are not characterized by a clean current plateau of given duration. These are probably best described as clusters of spikes, two of which can be seen in figure 2 before each of the two output spikes. In the case of partial reset, individual spikes have potentially a higher chance to cause firing because the membrane potential is close to the firing threshold. However, the width of the reverse correlation curve indicates that clusters of various duration are contributing to the firing. Firing is therefore better

²To determine this value, the curve was fitted by a simple model based on following assumptions: Input current peaks are defined as having an amplitude larger than the average current and a certain duration. The larger the amplitude, the smaller the necessary duration until firing occurs. Before the peak, the current has the average value. It is assumed that the reverse correlation curve represents an average over all peaks that can cause firing. For instance, current peaks of large amplitude contribute only to the parts of the curve near to time zero. The peaks with smaller amplitude must be of longer duration and contribute also to the tail of the curve. Such a model provides a good fit to the data only if one assumes that peaks can not be of duration larger than a given value (This value is approximately 2ms for $\beta = 0.91$, 0.5ms for $\beta = 0$ and 3ms for $\beta = 0.98$). Somehow, peaks of long duration and small amplitude seem not to contribute to firing. Details of the model will be given in a future publication.

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described as resulting from the integration of input current fluctuations than from the detection of individual input spikes. Thus partial reset is not equivalent to the use of the giant EPSP's of over 10 mV proposed in [Softky and Koch, 1993]. The earlier analysis of the firing times indicates that this neuron has probably a coincidence detection function, where a coincidence is any cluster containing a sufficient number of spikes in a given time window. However, the reverse correlation curve cannot confirm this hypothesis. As seen in the case $\beta = 0$, the fact that firing usually occurs after a peak of above average input current can not be taken as evidence that the neuron is "detecting" this type of peak. In the case $\beta = 0$, many other high current peaks are occurring at random times before firing, do not cause firing and do not appear in the reverse correlation curve.

6. Proving coincidence detection

To prove formally that the neuron operates as a coincidence detector, it has to be shown that *most* current peaks of the same size as those seen before a spike *actually* causes a spike. A theoretical proof is a complex task beyond the scope of this paper. However it can be checked by simulation if current peaks systematically cause firing. For that purpose, simulations are performed with two output neurons receiving the same input spikes, the first being the LIF neuron with partial reset and the second acting as a peak detector. The second LIF neuron has a very short decay time constant of 2 ms (this duration is taken from the reverse correlation curve for $\beta = 0.91$) and its potential is *not reset* after a spike. Due to the fast decay, potential peaks reflect the above-average rate of arrival of input spikes during a preceding time window of up to 2 ms. By placing the firing threshold of this neuron adequately (3.8 mV), its spikes become indicators of peaks in input current. Figure 4 shows that the two neurons fire spikes often at the same time, or within 1-2 ms of each other. Although this is not a formal proof, it strongly suggests that the LIF neurons with partial reset $\beta = 0.91$ operates mainly as a detector of peaks of input current of duration less than 2 ms. As such events are random, this property is the cause of values of CV close to one.

This small time window of 2 ms and the similarity between the fluctuating portions of two potential curves in full line (figure 4) suggests that the neuron may operate with a small effective time constant. This is however not the case. There is no inhibitory leak in this model which could have such an effect (Softky, 1995). Further, it is shown in Appendix 2 that, when the potential is maintained close to its saturation value by a continuous input current, a small increase in potential decays towards the saturation potential with a time constant of 10 ms. Two factors cause the similarity between the two curves: i) The model uses a step increase of the potential for each input spike. Therefore, there is no difference in the rising phases in both neurons. ii) The reset cuts through the maxima in the potential of the capacitor with $RC = 10$ ms and moves the decreasing parts of potential below the threshold. These are of similar amplitude in both curves, indicating a similar leak current in both neurons. This is due to the difference in average potentials, despite different decay time constants.

7. Temporally clustered firing and neuronal gain

Values of CV larger than one are caused by a temporal clustering process (e.g. bursting) which results from a smooth transition from the peak detection regime described above into a regime where multiple spikes are generated in response to peaks. (Single responses to peaks can only produce values of CV up to 1). As an indicator of clustering, there is an interesting peak at approximately - 2 ms in the reverse correlation curve for $\beta = 0.98$ (figure 3). The interpretation of this peak requires several logical steps. To start with, it is not sensible to take this peak as evidence that an input current peak occurs frequently 2 ms before a spike is fired. More plausible is the assumption that the peak has caused a first spike followed by a second one, 2 ms later. One notes that there is no current peak at $t = 2$ ms in the reverse correlation curve. This indicates that the first spike is generally not followed by an increased input current 2 ms later. Thereby, the accumulation of current just before time zero does not occur in the same run as the accumulation before the spike 2 ms before. The picture that emerges is that, either a first spike is followed by a second spike 2 ms later which is not caused by a peak in input current, or an isolated spike is produced by a current peak. The simplest interpretation is that a current peak produces either a single spike or a pair of spikes separated by the minimum interspike interval (for $\beta = 0.98$ the reverse correlation curve shows only a faint indication for triplets, which becomes much stronger for $\beta = 0.995$ (not shown)). Two effects favour clustered firing: i) the small reset enables long lasting current peaks to cause repeated firing and ii) a decreasing average potential favours a bimodal firing pattern. For instance, in the case $\beta = 0.98$, the reset potential is initially 0.3 mV below threshold but then decreases towards the saturation potential which is 0.8 mV below threshold. Thus it is just after a spike that the firing conditions are the most favourable³, however, the more the firing is delayed after that initial period, the higher the current peaks required and the longer the average time to the next peak. While the first effect causes generally clear bursts of spikes, the second causes a more discrete clustered firing.

Interspike interval distribution curves (ISI) show a transition from regular, to random, to clustered and eventually to bursting firing (Bugmann, 1995) when the value of β increases. This transition can be described as a progressive replacement of single spikes with regular interspike intervals by clusters with a larger and larger number of spikes per cluster, a process which enhances the ISIs at small intervals and depletes them at large intervals. Such a process increases the value of CV (Bugmann, 1995). Clusters can also be seen as multiple responses to favourable input events⁴, which increase the gain of the neuron, as illustrated in figure 5. The higher gain observed with

³Firing is only possible after the refractory time (2 ms in this case), so the average potential at that time is relevant for fluctuation detection.

⁴This is consistent with the observation that, in bursting neurons, information is carried by the rate of bursts, rather than the rate of spikes (Bair et al., 1994).

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high values of β can be also be inferred from the small change in average potential which is required to cause a large change in firing rate, see e.g. figure 4. Thus, simulations suggest a correlation between high gain and highly irregular firing.

8. Summary

The effects of strength of reset on the irregularity of firing can be summarized as follows:

i) With total reset, for a spike to be produced after 10 ms, the average potential must rise steeply during the interspike interval. This favours the late production of spikes with relatively regular interspike intervals. When the potential crosses the threshold, fluctuations play a minor role in determining the exact time of firing. This explains a small non-zero CV for the model with total reset⁵.

ii) With partial reset and a reset parameter $\beta = 0.91$, the average potential remains relatively constant and close to the threshold, so that random firing results from the detection of current peaks. The amplitude of reset can be seen as a way of selecting the amplitude of the fluctuations which are able to cause firing. This also determines the average interspike interval.

iii) With partial reset and a reset parameter $\beta = 0.98$, the potential is very close to the threshold after firing and repetitive firing occurs during periods of maintained high input current. As each detected current peak can produce multiple spikes, to achieve an average interval of 10 ms, the number of detected current peaks must be small. For that purpose, a lower average potential is used which causes long silent periods between bursts. This bimodal firing pattern results in values of $CV > 1$.

For a given average interspike interval, with strong reset, the duration of the interspike interval is determined by the time taken to integrate the input current. With weak reset, the random occurrence of current peaks determines the firing time. Currently, reverse correlation graphs do not allow to quantify the contribution of each of these mechanisms in intermediate cases. While reverse correlation graphs show that current peaks of given sizes usually precede spikes, they do not indicate if the neuron was integrating current before the peak or if it was waiting for a peak of sufficient amplitude. Further analytical work is needed to determine if it is possible to extract this information. Probably, a reverse correlation graph of the membrane potential would be more informative. Alternatively, useful indications can be obtained by comparing the firing times caused by a fluctuating current and by an equivalent continuous current, as done in earlier in this paper.

In conclusion, highly irregular firing similar to the one observed in biological neurons can be produced with a simple leaky integrator model provided with a partial reset mechanism. This mechanism is a simple way to improve the realism of spike trains produced by simulated neurons.

⁵When the average potential input current approaches the threshold very slowly, fluctuations become the main cause of firing. Therefore, neuron models with total reset also show high values of CV at low frequency.

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It is also a powerful parameter to control the gain of a neuron. One may note that none of the mechanisms suggested by Softky and Koch (1993) is at work here: Strong inhibitory leak, individual input spikes with high amplitude or strong dendritic amplification, or non-random synchronized inputs. By using partial reset, the temporal integration of random input spikes is exploited for maintaining the average potential of the neuron at a small distance from the threshold during the whole integration time, allowing input current fluctuations (made of small EPSPs) to cause firing at random times.

Acknowledgements:

We are thankful to Christian Lehmann, Sue McCabe, Mike Denham and Jack Boitano for helpful discussions and comments on earlier versions of this paper. We are also very grateful to anonymous referees for their stimulating criticisms and pointers to the literature. One of us, C.C., gratefully acknowledges the support of The Leverhulme Trust for the grant ref. nb. F.40Z, awarded to King's College London.

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Appendix 1. Equivalence between a model with partial reset and a model with time dependent threshold:

The demonstration has two steps. First, it is shown that the potential of the membrane, in case of partial reset is the sum of a decaying reset potential $V_o(t)$ and a potential $V_s(t)$ due to the integration of input spikes in a neuron with total reset. Let us assume that the input current $I(t)$ is made of very short impulses of duration Δt carrying each a charge $V_I * C$. It is then straightforward to show that the membrane potential $V(t)$, which is a solution of the leaky integrator equation (1):

$$C \frac{dV(t)}{dt} = -\frac{1}{RC} V(t) + I(t) \quad (1)$$

has the following form:

$$V(t) = \beta V_{th} \exp\left(-\frac{t}{RC}\right) + V_1 \sum_j \exp\left(-\frac{t-t_j}{RC}\right) = V_o(t) + V_s(t) \quad (2)$$

where t_j is the time of arrival of an individual spike. When the reset is total, i.e. $\beta = 0$, then $V(t) = V_s(t)$, which shows that $V_s(t)$ has the desired property, i.e. is the potential of a neuron with total reset.

The second step is to show that the firing time is the same for the model with partial reset and constant threshold V_{th} and the model with total reset but varying threshold $V_{th}(t)$. The neuron with partial reset fires an interval T after the last spike if the firing condition (3) is satisfied.

$$V(T) = V_{th} = V_o(T) + V_s(T) \quad (3)$$

This is equivalent to the firing condition (4) describing the firing time in a model with total reset and a time dependent threshold $V_{th}(t)$:

$$V_{th}(T) = V_{th} - V_o(T) = V_s(T) \quad (4)$$

Thereby it is shown that with same input conditions, both models fire at the same time and are therefore equivalent. In the model of (Wilbur and Rinzel, 1983), the threshold increases with a function of shape $\tanh(t)$, while partial reset results in an exponential increase, from (4) and (2).

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Appendix 2: Decay time constant for fluctuations

Let us assume that the input current is made of a continuous background I_0 to which a fluctuating component with average zero is added. The continuous component brings the potential of the neuron up to a saturation value V_0 . A positive current fluctuation has brought the potential to $V_0 + \Delta v$. At time $t=0$, the current becomes equal to I_0 and the potential decays. At time zero, the following equation describes the decay of the potential from a value $V_0 + \Delta v$:

$$\frac{dV}{dt} = -\frac{V_0 + \Delta V}{RC} + \frac{I_0}{C} \quad (5)$$

As $V_0 = I_0 * R$, equation (5) simplifies to:

$$\frac{dV}{dt} = -\frac{\Delta V}{RC} \quad (6)$$

Equation (6) describes the discharge of a capacitor with time constant RC and no external input current. If the continuous input current I_0 is also switched off at time zero, the capacitor would discharge at a larger rate $(V_0 + \Delta V)/RC$.

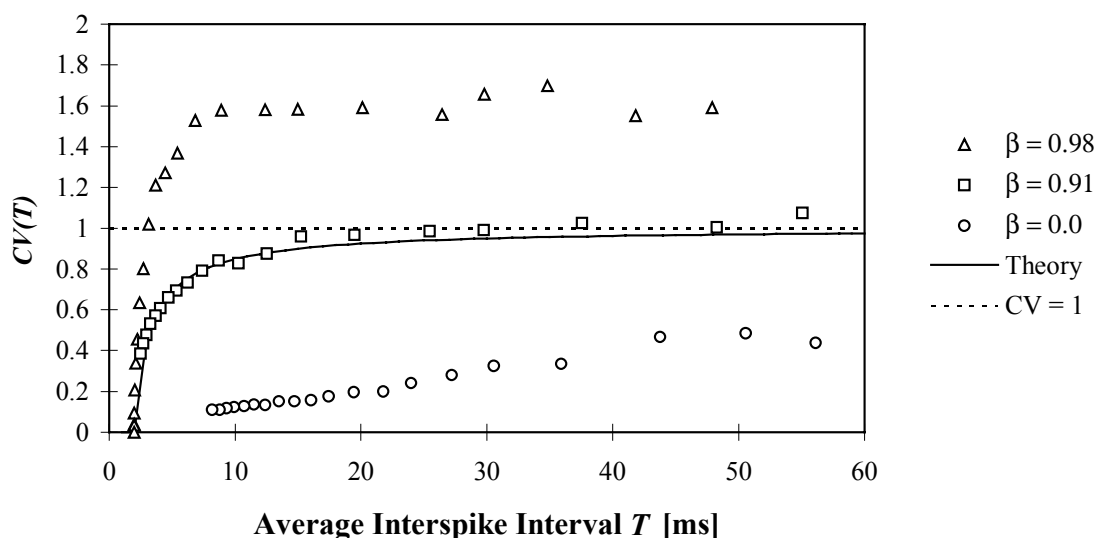
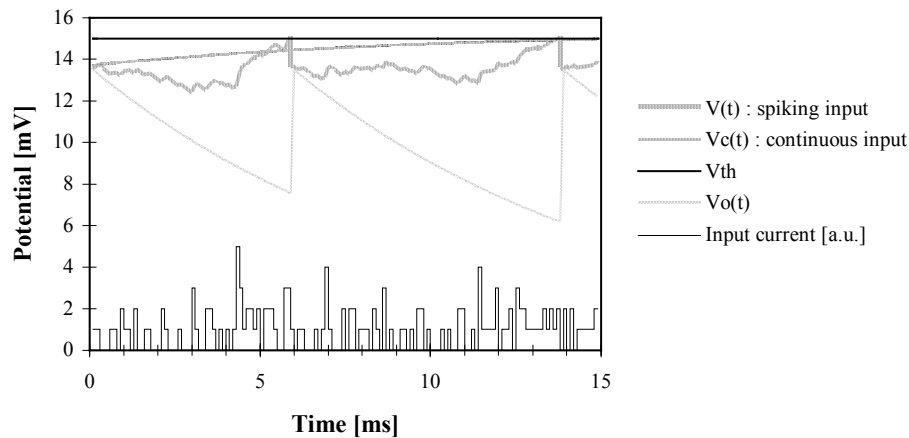
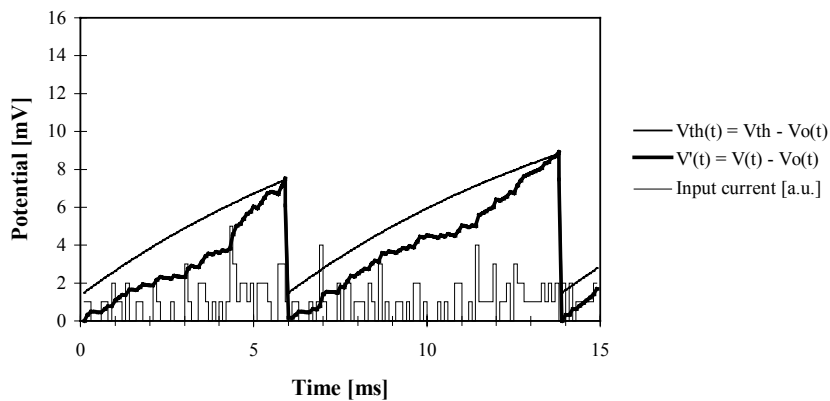


Figure 1. Dependence of the coefficients of variation of the interspike intervals CV on the average interspike interval T , for three values of the reset parameter β .

The symbols show the effects of partial reset on the irregularity of spike trains produced by an LIF neuron simulated with 1 ms integration time steps. The coefficients of variation obtained with $\beta = 0.91$ (square symbols) are very similar to those observed in cortical neurons (figure 9 in (Softky and Koch, 1993)). Each point is based on 20,000 simulation time steps. As inputs we used 50 random spike trains without refractory time. All inputs were excitatory and had the same average firing frequency, increased step by step from 150 Hz to 400 Hz to vary the average output interspike interval T . The membrane potential was increased stepwise by 0.16 mV by each input spike assumed to be of zero width. Between spikes, the potential decreased with a decay time constant of 10 ms (13 ms in (Softky and Koch, 1993)). During the refractory time, integration of inputs continued but the value of the potential was not compared with the firing threshold $V_{th} = 15$ mV, as in (Christodoulou et al., 1994). **The full line** shows the theoretical curve for a random spike train with discrete time steps Δt and a refractory time of Tr time steps: $CV(T) = \sqrt{\sigma^2(T)/T^2} = \sqrt{1-\alpha}/(1+\alpha Tr)$. This expression was developed assuming that in each time step, except the Tr time steps following a spike, there is a probability α of observing a spike (Bugmann, 1995). For the plotted curve and the simulations we used $\Delta t = 1$ ms and $Tr = 1$ ms (causing a minimum interspike interval $Tr + \Delta t = 2$ ms). The actual average interspike interval T is related to α by: $T = (1+\alpha Tr)/\alpha$.



A)



B)

Figure 2. Membrane potentials of the LIF model with partial reset (figure 2a, grey lines) and its equivalent model with total reset (figure 2b, black lines). The curve $V(t)$ is observed in the case $\beta=0.91$ with an average interspike interval of $Tf=10$ ms. The simulation it is done assuming that a spike has just been fired so that the initial potential is βV_{th} . The output spike train is very irregular and has a $CV=0.87$. The curve $V_c(t)$ is obtained with a continuous input current equal to the average input current in the case of the curve $V(t)$. The time taken to reach the threshold is now $T_c=17$ ms. This shows that a fluctuating input current leads to higher firing rates. For comparison, in the case $\beta=0.98$ one finds $T_c=Infinity$ but $Tf=10$ ms, and in the case $\beta=0$, $T_c=Tf=10$ ms. The curves $V_o(t)$ and $V_{th}(t)$ are explained in the text. The curve $V'(t)$ is calculated from $V(t)$ and $V_o(t)$. The input current corresponds to the total number of input spikes in each timestep. The simulation time step is 0.1 ms.

"Role of Temporal Integration and Fluctuation Detection in the highly irregular firing of a Leaky Integrator Neuron Model with Partial Reset", Bugmann G., Christodoulou C. and Taylor J.G. (1997) Neural Computation, 9, pp. 985-1000.

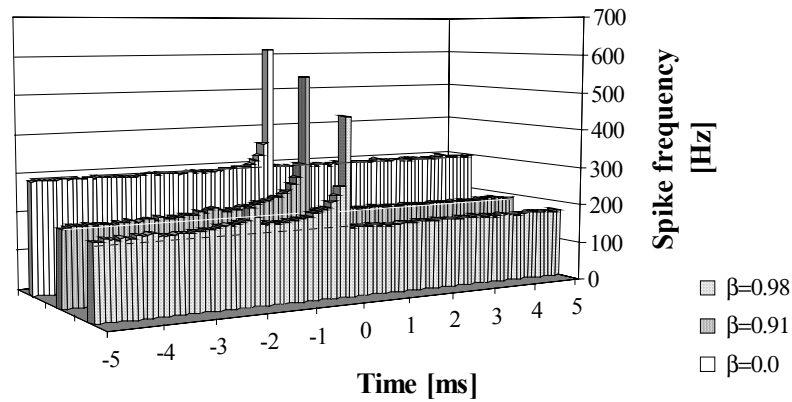


Figure 3. Reverse correlation graphs for the three indicated values of the reset parameter β . The average interspike interval is $T=10$ ms in all three cases. The graphs represent input firing frequencies based on number of input spikes observed in 0.1 ms time steps, at the indicated delay before and after a spike is produced. The frequencies stay at the same levels on both sides up to + 15 ms and - 15 ms. The fine lines indicate the level of the average input frequencies. Lower average input firing rates are needed as β increases (295 Hz for $\beta = 0$, 189 Hz for $\beta = 0.91$ and 178 Hz for $\beta = 0.98$) because partial reset removes less charges after each spike than total reset. Amplitude of the peak at time zero: 611 Hz for $\beta = 0$, 546 Hz for $\beta = 0.91$ and 455 Hz for $\beta = 0.98$. Data are averaged over 10000 output spikes (100 sec simulated operation). Decay time constant $RC=10$ ms.

"Role of Temporal Integration and Fluctuation Detection in the highly irregular firing of a Leaky Integrator Neuron Model with Partial Reset", Bugmann G., Christodoulou C. and Taylor J.G. (1997) Neural Computation, 9, pp. 985-1000.

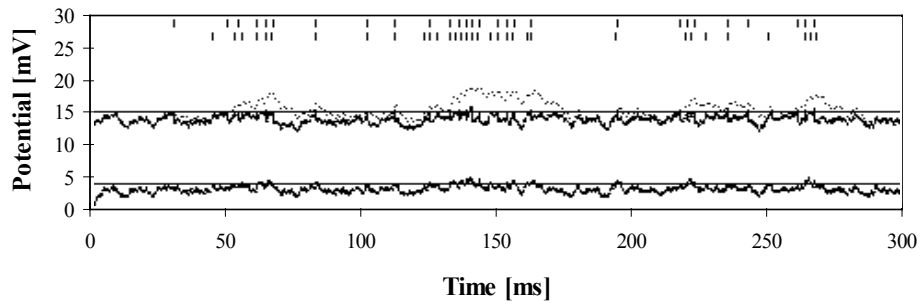


Figure 4. Membrane potentials and firing times of two neurons with the same input spike trains simulated during 300 ms. The upper row of spike times and the upper membrane potential (in full line) belong to a LIF neuron with partial reset ($\beta = 0.91$) and a membrane time constant of $RC = 10$ ms. The firing threshold is $V_{th} = 15$ mV. The dotted line represents the free evolution of the potential with neither spiking nor resetting. The lower row of spike times and the lower membrane potential belongs to a LIF neuron with a membrane decay time constant of $RC = 2$ ms and a firing threshold $V_{th} = 3.8$ mV. This neuron is not reset after a spike and is used to detect peaks of input current, or equivalently peaks of spike input rate. Further simulation conditions as in figure 2.

"Role of Temporal Integration and Fluctuation Detection in the highly irregular firing of a Leaky Integrator Neuron Model with Partial Reset", Bugmann G., Christodoulou C. and Taylor J.G. (1997) Neural Computation, 9, pp. 985-1000.

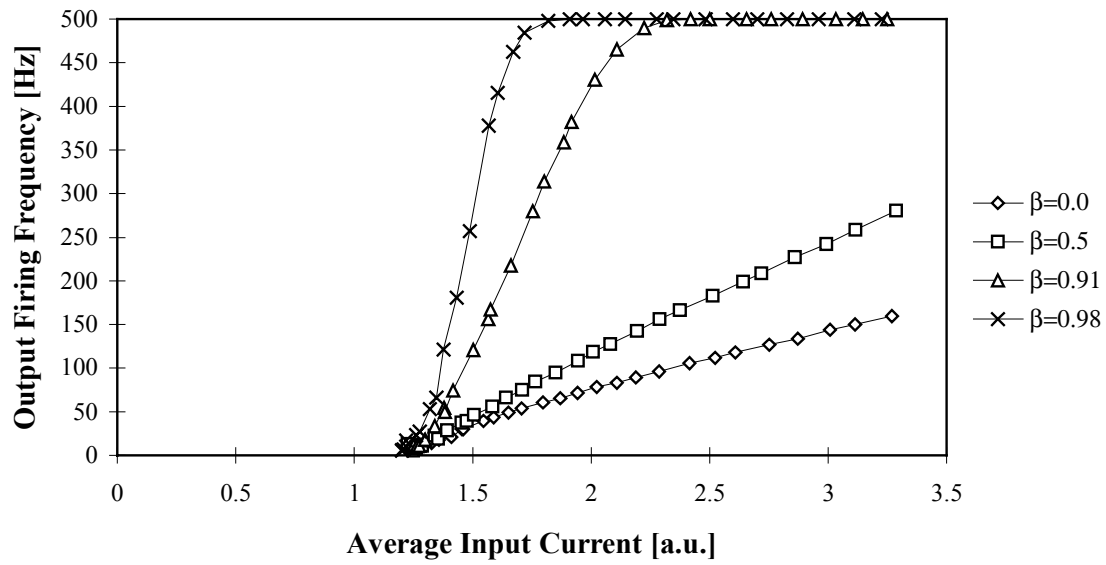


Figure 5. Transfer function of the LIF neuron model with various values of the reset parameter β . With $\beta=0$ our model is equivalent to the one used in Softky and Koch (1993). The theoretical current threshold is 1.5 but due to the long integration time steps used (1 ms) the model underestimates leaks and shows a smaller threshold of 1.41. Firing below that threshold is due to fluctuations. Note that partial reset modifies the gain and not the current threshold. Simulation conditions as in figure 1.