Complex Dynamics of Neuronal Thresholds

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Abstract

We study an integrate and fire model of an adapting neuron. Using two dynamic thresholds we account for complex long term behavior of single neurons under periodic pulsed inputs. We find that the pattern of temporal response is that of a staircase of inter-spike interval values. The characteristic time scales of transitions between these ISI values are of the order of tens of seconds. The temporal behavior of our system can be described as a path through the 2-dimensional phase space of dynamic thresholds.

1 Introduction

Single neurons display interesting complex behavior for different inputs. When driven by a constant supra-threshold current, a neuron will usually fire regularly with some frequency. After a while, this frequency will decrease to a steady state value manifesting adaptation of the neuron to the constantly applied stimulus. A totally different temporal behavior is seen when the neuron is driven by a periodic stimulus. In a recent experiment, Tal *et al.* [7] studied the effect of 2 minutes application of 2ms current pulses, using different frequencies. The current amplitude was just above threshold, sufficient for making the neuron fire at 1 Hz when stimulated with 1 Hz pulsed inputs. This behavior we call a "1:1 response". When the input frequency was higher, about 1/2 of the neurons responded with complex firing patterns, and did not display this simple 1:1 response. Examples of ISI series recorded in response to stimulation of 3 and 30 Hz are shown in Fig. 1. It is evident that a high frequency input causes the neuron to respond with a staircase of ISI values. The time

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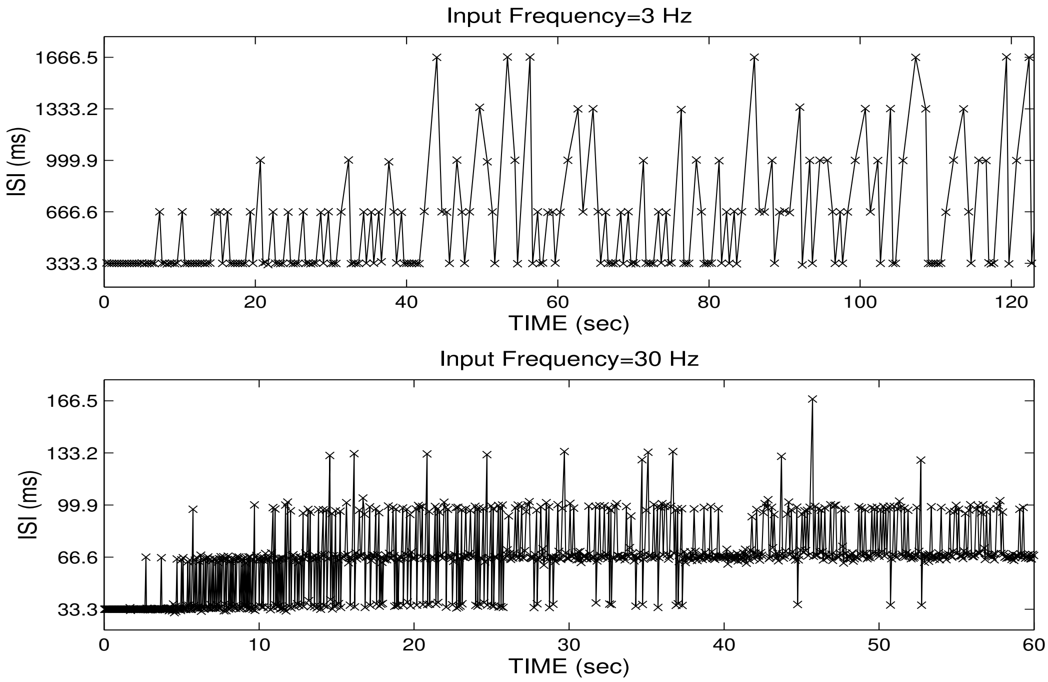

Figure 1: ISI recorded in response to stimulations of 3 Hz (upper frame) and 30 Hz (lower frame). All ISI values are integer multiples of the input period.

intervals between successive spikes grow, but the firing rate does not necessarily reach a steady state value.

In this paper we present a minimal model that describes such complex and variable behavior. It is based on dynamic thresholds associated with an $I\&F$ neuron.

2 Dynamical Thresholds in an Integrate-and-Fire Neuron

An Integrate-and-fire ($I\&F$) neuron [3] can be defined by the formula

$$C\frac{dV}{dt} = -g_L(V - V_{rest}) + I \tag{1}$$

where V is the membrane potential, C is the capacitance, g_L is the leak conductance and I is the external input current. When V reaches threshold a spike is emitted and V is reset to V_{reset} such that

$$V_{rest} < V_{reset} < V_{threshold} \equiv V_{reset} + \theta. \tag{2}$$

Refractoriness may be added as a short dead-time after firing.

When the external current has a constant component that is much larger than statistical fluctuations, one can approximate the inter-spike-interval by

$$ISI = -\frac{C}{g_L}\log(1 - \frac{g_L\theta}{I_{eff}}). \tag{3}$$

where $I_{eff} = I - g_L(V_{reset} - V_{rest})$. It follows then that the firing rate will be $I_{eff}/C\theta$ for large input currents.

MacGregor[5, 6] discusses the use of dynamical changes of the threshold parameter as suggested by various authors since the early 30s. One natural extension [2] is using the threshold to describe adaptation, or fatigue, accounting for the fact that the firing rate decreases in time for a given constant input. This can be done by hypothesizing a behavior of

$$\tau_\theta \frac{d\theta}{dt} = -(\theta - \theta_0) \tag{4}$$

with an updating prescription such that after every a spike is emitted

$$\theta \to \theta + \alpha_\theta. \tag{5}$$

A typical value for τ_θ is in the range of 100-400 msec, which is the range in which different types of neurons display adaptation.

Alternatively one can introduce a 'current threshold', a term which appears naturally if we try to account for after-hyperpolarization effects by modifying the $I\&F$ equation:

$$C\frac{dV}{dt} = -g_L(V - V_{rest}) + I - g_x x(V - V_x) \tag{6}$$

x denotes a variable like the concentration of Ca^{++} in the cell. In that case $g_x = g_{AHP}$ and $V_x = V_K$, the K^+ reversal potential. This current threshold is linearly dependent on x and has also fatigue type effects on the firing rate of the neuron. x is increased after every spike

$$x \to x + \alpha_x \tag{7}$$

and is endowed with decay dynamics of the type

$$\tau_x \frac{dx}{dt} = -x, \tag{8}$$

where now τ_x determines the temporal scale of adaptation.

This problem was recently investigated in detail by Liu and Wang [4] whose notation we have adopted in the description so far. They point out that the AHP current leads to adaptation, and can therefore act as the equivalent of the voltage-threshold θ. They compare the two in light of experimental findings by Ahmed *et al.* [1] and conclude that the current-threshold serves as a better description.

3 Model of Two Dynamical Thresholds

The model we propose for qualitative description of the data[7] discussed in the Introduction relies on using both types of thresholds together. In doing so we assume that there is a new behavior associated with time scales of tens of seconds, that has to operate in addition to the conventional adaptation represented by either the voltage-threshold or the current-threshold terms. Our description is therefore represented by the set of equations 4-8, where 6 describes the membrane potential and all the other the behavior of both dynamical thresholds. The interplay of both thresholds gives us the richness of many different ISI patterns for a given high-frequency input.

We have run simulations with the 2ms pulse protocol, using different input frequencies. The structures we obtain can be characterized as a staircase of ISI values. This is because the dynamics of the thresholds change slowly and the system stays for long times at metastable values of the $m : n$ ratio between input and output frequencies, as can be seen in Fig. 2a. Such a staircase is the backbone of the ISI structure observed experimentally, as seen in Fig. 1. Once noise is added to the system, as in Fig. 2b, the results can be made to fit the data observed experimentally.

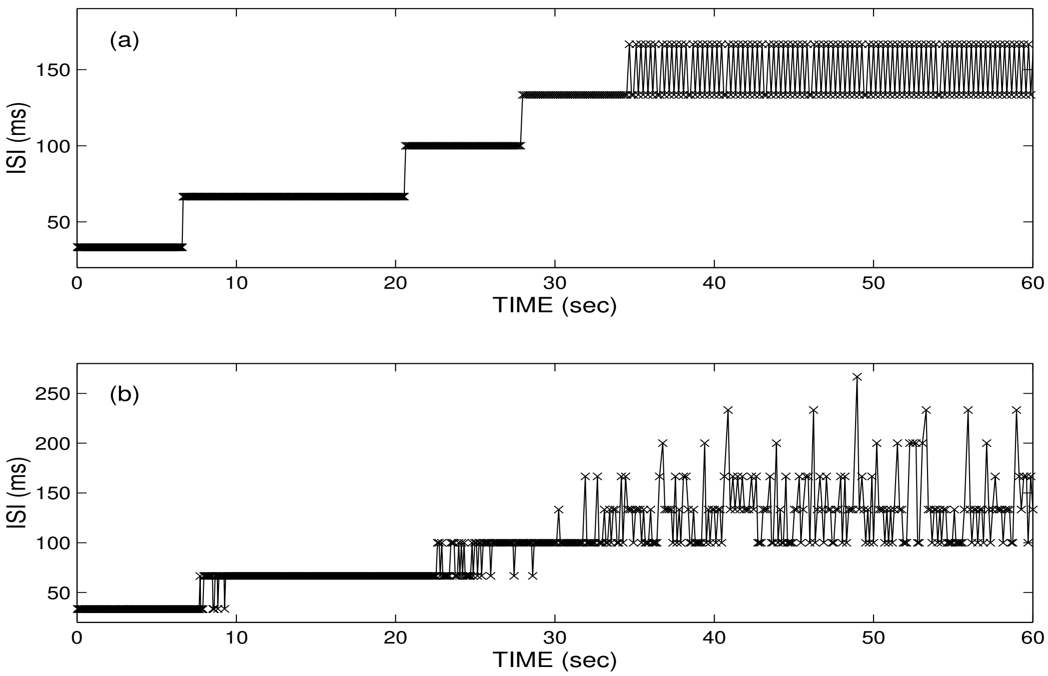

Figure 2: Examples of staircase of ISI values for a 30 Hz stimulus in our model: a. In the absence of noise, the system stays for rather long times in fixed $m : n$ ratios of input to output frequencies. The ratios 1:1, 2:1, 3:1 and 4:1 are metastable. At later times we observe more complex behavior of oscillations between the ratios of 4:1 and 5:1. b. When little noise is added to the input, we get time series that resemble experimental results. The basic staircase structure can still be seen, but the pattern is less regular.

Using our simple model we were able to mimic the behavior of many neurons. In each case, the distribution of ISI as well as the temporal behavior of the neuron were successfully reconstructed. An example is shown in Fig. 3, resembling the temporal pattern of the neuron shown in the top frame of Fig. 1.

4 Phase Space Analysis

The dynamics of our combined model can be separated into fast and slow components. The temporal integration that the neuron performs during the 2 ms current pulse is the fast component. The dynamics of the thresholds, whose values vary considerably only after a large number of spikes have been emitted, is the slow component.

This separation allows us to calculate, for each point (θ, x), the expected $m : n$ ratio

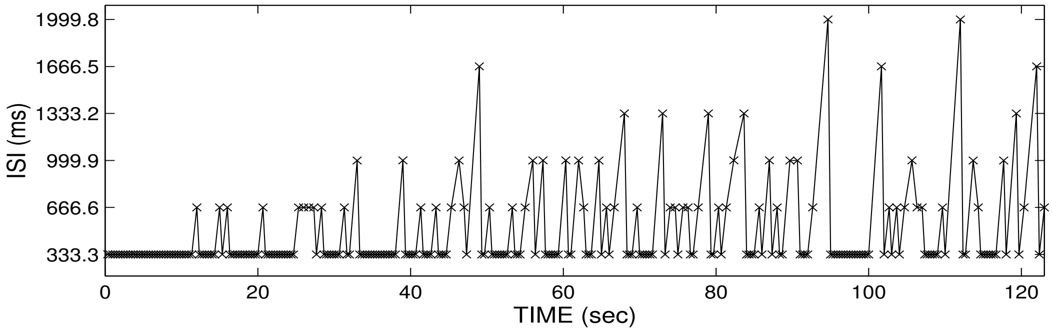

Figure 3: Simulation results that resemble the experimental example of 3 Hz shown in Fig. 1. The similarity between the two time series is evident. Furthermore, statistical properties of these two series are the same.

between input and output frequencies. It follows that we can construct a two-dimensional phase space where the temporal development of the system is represented as a trajectory. An example that corresponds to the ISI staircase of Fig. 2a is shown in Fig. 4.

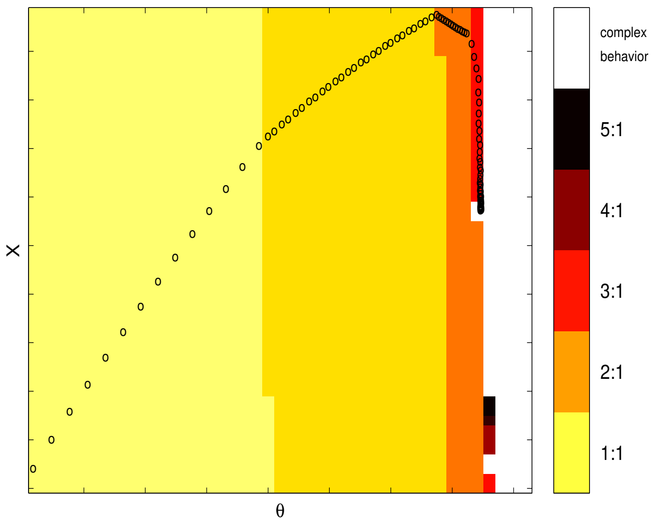

Figure 4: A two dimensional phase space of our system. Different areas in this phase space correspond to different $m : n$ ratios between input and output frequencies. The circles represent the trajectory corresponding to the ISI time series of Fig. 2a.

This representation opens the possibility for an investigation of the behavior of the same neuron under input currents of different frequencies. So far we have allowed ourselves the freedom of choosing appropriate parameters for different runs even for the same neuron. We hope to obtain a consistent description that will allow us to fit the different runs on the same phase space, and find the correct dynamics that will consistently account for all of the behavior displayed by the same neuron.

Acknowledgment

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References

[1] B. Ahmed, J.C. Anderson, R.J. Douglas, K.A.C. Martin and D. Whitteridge, 1998. Estimates of the net excitatory currents evoked by visual stimulation of identified neurons in cat visual cortex. *Cerebral Cortex* submitted.

[2] D. Horn and M. Usher, 1989. Neural Networks with Dynamical Thresholds. Phys. Rev. A40, 1036-1044.

[3] B. W. Knight, 1972. Dynamics of encoding in a population of neurons. J. of Gen. Physiol. 59, 734-766.

[4] Y.-H. Liu and X.-J. Wang, 1998. Adaptation and decorrelation in cortical pyramidal neurons: A generalized integrate-and-fire model with stochastic inputs. to be published in Behavioral/Systems Neuroscience.

[5] R. J. MacGregor, 1977. *Neural Modeling*, Plenum Press.

[6] R. J. MacGregor, 1987. *Neural and Brain Modeling*, Academic Press.

[7] D. Tal, E. Jacobson, V. Lyakhov and S. Marom, 1998. Frequency-tuning of a single neuron transfer function. Preprint.