

# [Re] A Generalized Linear Integrate-and-Fire Neural Model Produces Diverse Spiking Behaviors

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The author has declared that no competing interests exist.

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## A reference implementation of

→ A Generalized Linear Integrate-and-Fire Neural Model Produces Diverse Spiking Behaviors, Stefan Mihalas and Ernst Niebur, Neural Computation 21, 704–718, 2009.

## Introduction

Integrate-and-fire neurons are being used extensively in the field of neuroscience for modeling spiking behaviors [1]. In this work we provide a reference implementation of [3], where the authors have introduced a generalization of the leaky integrate-and-fire neuron model. The Mihalas-Niebur Neuron (MNN) model is a linear integrate-and-fire neuron model capable of expressing a rich spiking behavior based on a set of parameters.

An MNN model expresses tonic and phasic spiking, class 1 and 2, spike frequency adaptation, accommodation, threshold variability, rebound spike, integrator, input bistability, hyperpolarizing spiking and bursting, tonic, phasic and rebound bursting, mixed mode, afterpotentials, basal bistability, preferred frequency and spike latency. Due to its simplicity, the MNN model has been used in neuromorphic implementations such as [2].

The model consists of linear differential equations, which describe the membrane and threshold potentials and internal currents. All the results provided in [3] have been obtained by using only two internal currents and thus we use the exact same number of internal currents in this work. The subthreshold dynamics are defined by a set of linear ordinary differential equations, while an instantaneous threshold potential controls when the neuron firing an action potential (spike) in a dynamic way. The ability of the MNN model to generate such a diverse spiking behavior is due to the complex update rules. In this work the MNN model has been implemented in Python (version 3.6.1) using Numpy (version 1.13.1) and Matplotlib (version 2.0.2) packages.

## Methods

In order to implement the model described in [3], we discretized the dynamical system using the forward Euler's integration scheme. The time step is fixed to 0.1 ms for all the simulations, and the total simulation time  $t_f$  varies according to figure 1 of the original paper. Our implementation differs from the one in the original paper, since in [3], authors numerically solve equation 3.5 (algebraic equation) under the constraint

imposed by inequality 3.4 and thus they compute the spike times. On the other hand, in this work we directly compute numerically the solution of the dynamical system defined by equations 2.1 and 2.2 in [3] (see tables 2 and 3).

We provide all equations and parameters of the model in tables as it has been suggested by [4]. Table 1 provides the summary of the model. Tables 2 and 3 give the subthreshold dynamics (differential equations) describing the membrane and the threshold potentials as well as the two internal currents and the update rules. The parameters for all the simulations are given in table 4, while the external current intensities and pulse duration are provided in table 5. The parameters in this work are exactly the same used in the original paper (table 1, pg. 711). We had to infer the time intervals and the total simulation times for the pulses since they are not given explicitly in the original paper. Thus, we extracted the time intervals from figure 1 of [3] by visual inspection. The initial conditions are given in table 6.

All simulations ran on a Dell OptiPlex 7040, equipped with a sixth generation i7 processor, 16 GB of physical memory and running Arch Linux (x86\_64). The total execution time of all simulations was 2.41 seconds and the peak consumed memory was 162 MB<sup>1</sup>.

Model Summary	
Populations	No population – single neuron model
Topology	–
Connectivity	–
Neuron Model	Linear Integrate-and-Fire Neuron
Channel Models	Linear, first order ODEs
Synapse Model	–
Plasticity	–
Input	Constant current or rectangular pulses
Measurements	Membrane potential, phase plane

**Table 1: Summary of the model**

Neuron Model	
Name	Mihalas-Niebur Neuron (MNN)
Type	Linear Leaky Integrate-and-Fire Neuron
Membrane Potential	$\frac{dV(t)}{dt} = \frac{1}{C} (I_e + I_1 + I_2 - G(V(t) - E_L))$
Instantaneous Threshold Potential	$\frac{d\Theta(t)}{dt} = a(V(t) - E_L) - b(\Theta(t) - \Theta_\infty)$
Internal Currents	$\frac{dI_1(t)}{dt} = -k_1 I_1(t)$
	$\frac{dI_2(t)}{dt} = -k_2 I_2(t)$

**Table 2: Description of the subthreshold dynamics of Mihalas-Niebur neuron model.**  $V(t)$  and  $\Theta(t)$  are the membrane and threshold potentials, respectively.  $E_L$  and  $\Theta_\infty$  are the reversal potentials for the membrane and the threshold variables, respectively.  $a, b, k_1, k_2$  and  $G$  are constant parameters.  $I_e$  is the external current applied on the neuron model.



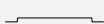
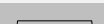


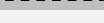
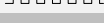
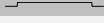
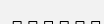
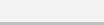

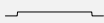

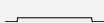
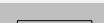
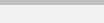

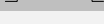

<sup>1</sup>Python memory profiler used ([https://pypi.python.org/pypi/memory\\_profiler](https://pypi.python.org/pypi/memory_profiler)).

Update rules	
Variable	Rule
$V(t)$	$V_r$
$\Theta(t)$	$\max\{\Theta_r, \Theta(t)\}$
$I_1(t)$	$R_1 \times I_1(t) + A_1$
$I_2(t)$	$R_2 \times I_2(t) + A_2$

**Table 3: Update rules.**  $V_r$  and  $\Theta_r$  are the reset values for the membrane and threshold potentials, respectively.  $R_1, R_2, A_1$  and  $A_2$  are constants.

Model Parameters				
Figure	$a$ ( $s^{-1}$ )	$A_1/C$ (V/s)	$A_2/C$ (V/s)	$t_f$ (s)
1A	0	0	0	0.2
1B	0	0	0	0.5
1C	5	0	0	0.2
1D	5	0	0	0.5
1E	5	0	0	1.0
1F	5	0	0	0.4
1G	5	0	0	1.0
1H	5	0	0	0.3
1I	5	0	0	0.4
1J	5	0	0	1.0
1K	30	0	0	0.4
1L	30	10	-0.6	0.4
1M	5	10	-0.6	0.5
1N	5	10	-0.6	0.5
1O	5	10	-0.6	1.0
1P	5	5	-0.3	0.5
1Q	5	5	-0.3	0.2
1R	0	8	-0.1	0.2
1S	5	-3	0.5	0.8
1T	-80	0	0	0.05
Common Parameters				
$b = 10 s^{-1}$ , $G/C = 50 s^{-1}$ , $k_1 = 200 s^{-1}$ , $k_2 = 20 s^{-1}$ , $\Theta_\infty = -0.05 V$ , $R_1 = 0$ , $R_2 = 1$ , $E_l = -0.07 V$ , $V_r = -0.07 V$ , $\Theta_r = -0.06 V$ .				

**Table 4: Simulation Parameters**

Model Parameters		
Figure	Type	$I_e/C(\text{V/s})$
1A		1.5
1B		$1 + 10^{-6}$
1C		2
1D		1.5
1E		1.5(0.1s), 0(0.5s), 0.5(0.1s), 1(0.1s), 1.5(0.1s), 0(0.1s)
1F		1.5(0.02s), 0(0.18s), -1.5(0.025s), 0(0.025s), 1.5(0.025s), 0(0.125s)
1G		0(0.05s), -3.5(0.756s), 0(0.194s)
1H		$2(1 + 10^{-6})$
1I		1.5(0.02s), 0(0.01s), 1.5(0.02s), 0(0.25s), 1.5(0.02s), 0(0.02s) 1.5(0.02s), 0(0.04s)
1J		1.5(0.1s), 1.7(0.4s), 1.5(0.1s), 1.7(0.4s)
1K		-1
1L		-1
1M		2
1N		1.5
1O		0(0.1s), -3.5(0.5s), 0(0.4s)
1P		2
1Q		2(0.015s), 0(0.185s)
1R		5(0.01s), 0(0.09s), 5(0.01s), 0(0.09s)
1S		5(0.005s), 0(0.005s), 4(0.005s), 0(0.385s), 5(0.005s), 0(0.045s) 4(0.005s), 0(0.345s)
1T		8(0.002s), 0(0.048s)

**Table 5: External current.** This table provides the external current for each panel in Figure 1. There are two types of external currents, constants and pulses. In the case of pulses the duration of each pulse is given in seconds along with its intensity.

Initial Conditions	
Variable	Initial Value
$V(t)$	-0.07 V / -0.03 V (Figure 1H)
$\Theta(t)$	-0.05 V / -0.03 V (Figure 1H)
$I_1(t)$	0.01 V
$I_2(t)$	0.001 V

**Table 6: Initial conditions.** In all simulations have been used the same initial conditions, except from the one illustrated in Figure 1H.

## Results

All three figures from the original article have been successfully replicated. All the different spiking behaviors of the model are illustrated in Figure 1, where the black solid line indicates the membrane potential ( $V(t)$ ), the red dashed line illustrates the instantaneous threshold potentials ( $\Theta(t)$ ), and the gray line shows the input to the neuron ( $I_e/C$ ). The  $x$ -axis scale in all the panels are exactly the same as in the original paper (indicating the total simulation time ( $t_f$ ), while the  $y$ -axis scale differs from the one in the original paper. In this work the  $y$ -axis scale is the same same for all the subplots ( $[-95, -25]$  mV), except from panels G and O ( $[-145, -25]$  mV).

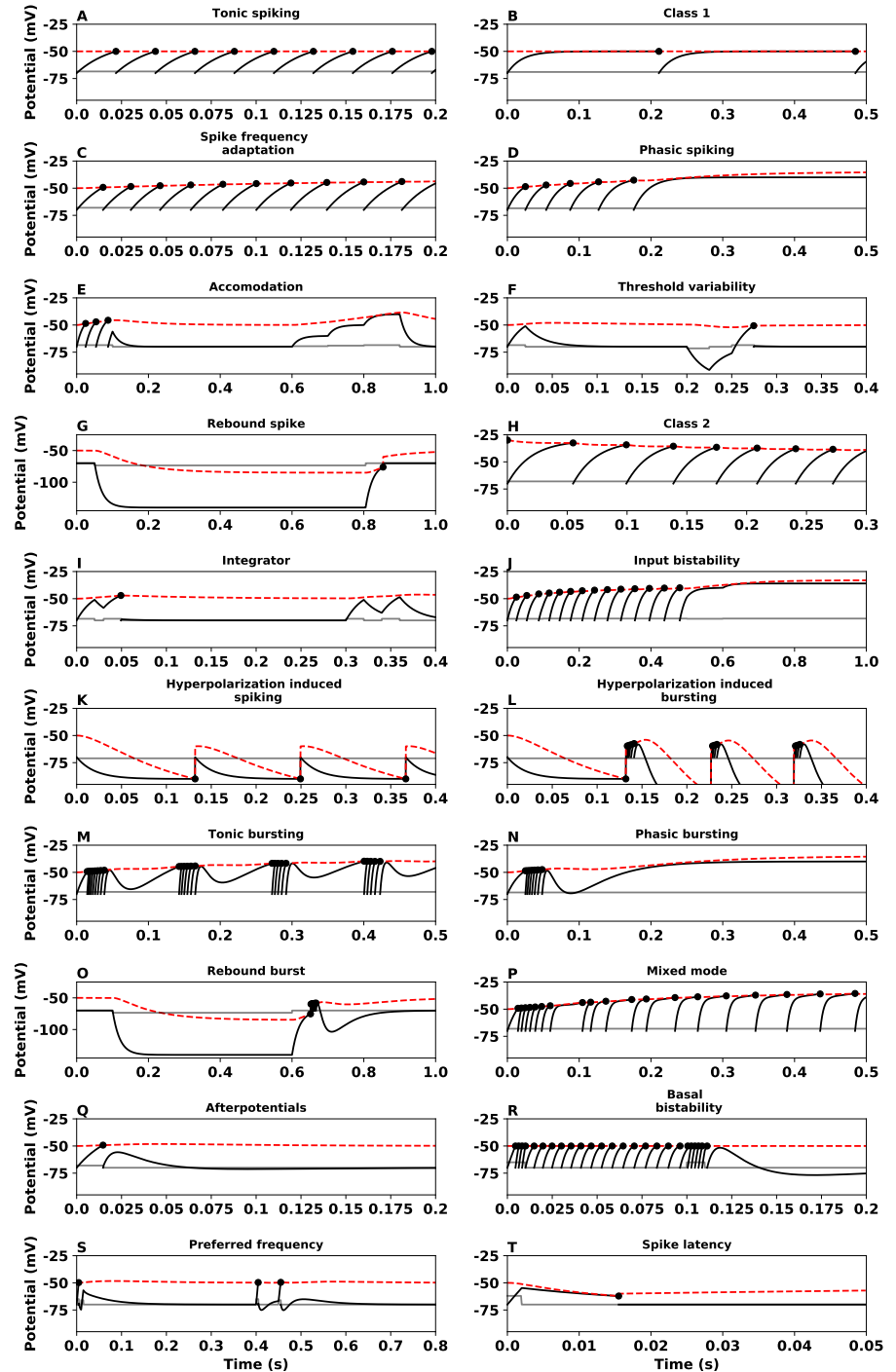
Figures 2 and 3 depict the phase space of the phasic spiking ( $V(t)$  and  $\Theta(t)$ ) and phasic bursting ( $V(t)$ ,  $I_1(t)$ , and  $I_2(t)$ ). In both figures the blue curves and the black dots indicate the trajectory of the system and spike events, respectively. In Figure 2 the gray arrows show the evolution of the system (vector field of the system). Figure 3 has a different orientation from the original one but both illustrate the same trajectories and spike events of the system. All the figures express the same qualitative behavior as the original figures in [3].

## Conclusion

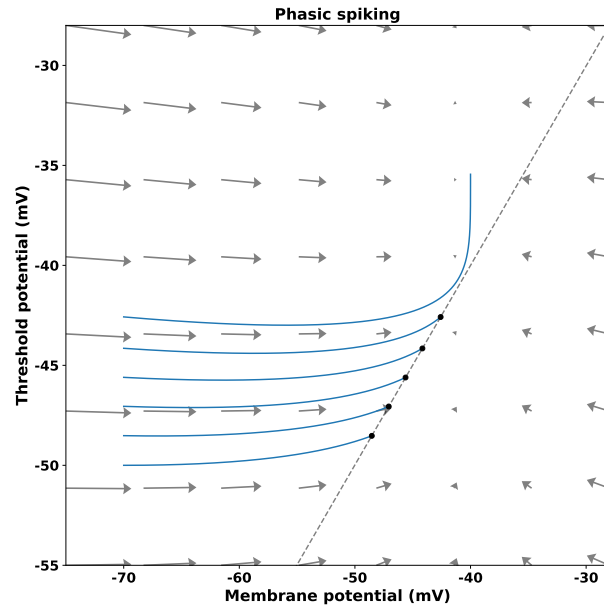
All figures in Mihalaş and Niebur [3] have been successfully replicated with high fidelity. Overall, the whole reproducing process was smooth and without obscure points since most of the parameters are provided in the original article. Only the time intervals for which the external current is applied to the model and the initial conditions are not provided explicitly. Therefore, we had to extract that information from figure 1 of the original article. To conclude, the article [3] has been successfully reproduced without any discrepancy.

## References

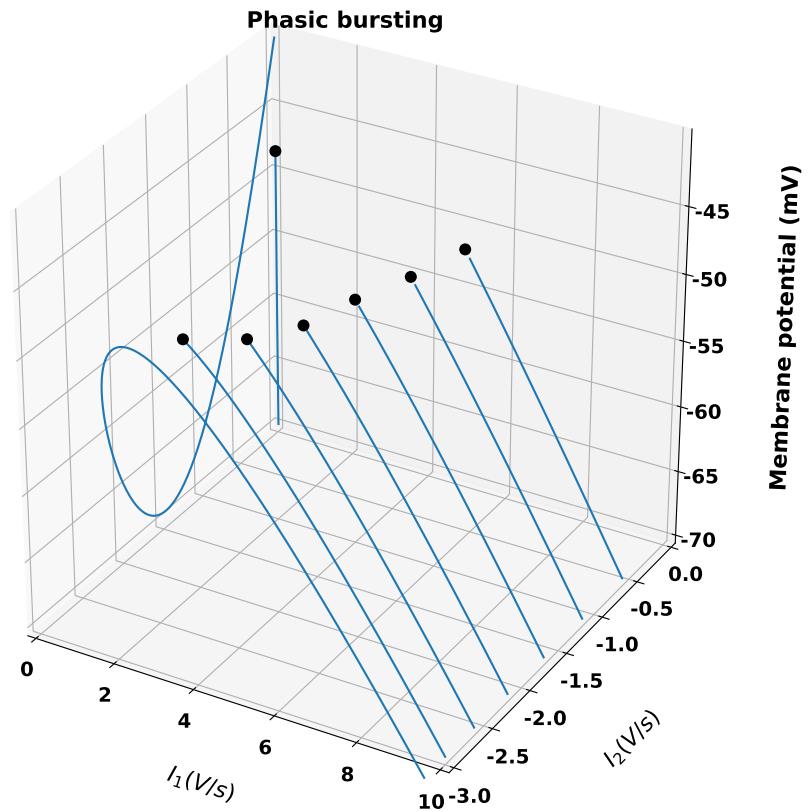
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- [4] Eilen Nordlie, Marc-Oliver Gewaltig, and Hans Ekkehard Plesser. "Towards reproducible descriptions of neuronal network models". In: *PLoS computational biology* 5.8 (2009), e1000456.



**Figure 1: Neural responses of MNN.** Black solid lines indicate the membrane potential ( $V(t)$ ), the red dashed lines show the threshold potentials ( $\Theta(t)$ ), and the gray lines the external currents applied on each case. **A** tonic spiking, **B** class 1, **C** spike frequency adaptation, **D** phasic spiking, **E** accommodation, **F** threshold variability, **G** rebound spike, **H** class 2, **I** integrator, **J** input bistability, **K** hyperpolarization induced spiking, **L** hyperpolarization induced bursting, **M** tonic bursting, **N** phasic bursting, **O** rebound burst, **P** mixed mode, **Q** afterpotentials, **R** basal bistability, **S** preferred frequency, **T** spike latency.



**Figure 2: Phase space of phasic spiking.** Blue solid lines indicate the trajectories of the model in the phase spiking behavior (Figure 1D). The dashed line corresponds to  $V(t) = \Theta(t)$ , and the black dots represent spike events. The parameters for this simulation are the same as in Figure 1D.



**Figure 3: Phase space of phasic bursting.** Blue solid lines represent the trajectories of the system and the black dots indicate spiking events. The parameters for this simulation are the same as in Figure 1N.