Faster spiking neural network model of honey bee mushroom body using adaptive exponential integrate & fire model (AdEx) and its implementation on GeNN

- Shashank Yadav [1,2]

Abstract

Simulations of large spiking neuron networks requires a simple, accurate and computationally fast single-neuron model. Here a simple two equation model: the adaptive exponential integrate-and-fire (AdEx) neuron model is used to describe the neuron dynamics of Kenyon cells in honey bee mushroom body. First, the AdEx model is implemented in GeNN to reproduce the different kinds of firing patterns such as continuous adaption, initial bursting, regular bursting, delayed acceleration and tonic spiking. Secondly, The AdEx model is compared against the Hodgkin-Huxley model for the Kenyon Cells and a parameter exploration is done to reproduce the spiking patterns of Kenyon cells using the AdEx Model. The source code is available on the website https://github.com/xinformatics/genn_adex

Introduction

Large-scale simulations of spiking neural network dynamics require neuron models which are biologically significant and computationally fast. Also a mathematical model should sufficiently versatile to cover the whole range of neuron types and different spiking characteristics, avoiding the need of different models for each type of neuron. Detailed conductance-based neuron model with several ion channels of the Hodgkin-Huxley type are able to capture the behaviour of neurons in great detail, it requires a fine-tuning of hundred or more parameters. Hence, they are computationally restricted. Simplified neuron models such as models of the integrate-and-fire type are certainly less biologically significant, but because they are less complex as they have less number of parameters, parameter optimization from experimental data is feasible. [1]

To make up this trade-off between computational complexity and biological plausibility, a model which has been proposed by Brette & Gerstner 2005 known as adaptive exponential integrate-and-fire model, abbreviated as AdEx wherever mentioned further. This model is shown to be computationally simple and it also explains different spiking neural dynamics. This model is an exponential integrate-and-fire model which provides a more realistic smooth spike initiation zone. It counts for inclusion of subthreshold resonances or adaptation by addition of a second variable. [1-2]

In the current work, the versatility and the biological relevance of the AdEx model is discussed. First, the AdEx models is implemented on GeNN simulator [3] to show that the AdEx reproduces multiple firing patterns and study the spiking type dependence on the model parameters. Secondly, the AdEx model is used to reproduce the spiking patterns Hodgkin-Huxley neuron based Traub-Miles model for the 'Kenyon Cells' in the honey bee mushroom body underlying olfactory learning and memory. [4]

[1] Centre for Computational Neuroscience and Robotics, School of Engineering and Informatics, University of Sussex, Brighton, BN1 9QJ, UK.
[2] Department of Biochemical Engineering and Biotechnology, Indian Institute of Technology Delhi, Hauz Khas, New Delhi, India 110016

Adaptive exponential integrate-and-fire

The adaptive Exponential Integrate-and-Fire model (AdEx) describes the evolution of the membrane potential *V(t)* when a current *I(t)* is injected. It consists of a system of two differential equations:

$$C\frac{dV}{dt} = -g_L(V - E_L) + g_L\Delta_T \exp\left(\frac{V - V_T}{\Delta_T}\right) + I - w$$

$$\tau_w \frac{dw}{dt} = a(V - E_L) - w$$

Followed by reset conditions:

If $V > 20\,mV$ then $V \rightarrow Vr$

$$w \rightarrow w_r = w + b$$

Modification in these parameters brings qualitative changes in behaviour of the system such that the model is able to produce different firing patterns. [2]

g_L is the leak conductance, E_L is the resting potential, Δ_T is the slope factor and V_T is the threshold potential Since it's an exponential integrate and fire model, the potential rapidly grows infinity but after it crosses a threshold of $30mV$, the potential is reset and the integration of equation is started from a reset value Vr. The slope factor determines the sharpness of threshold and in limit $\Delta_T \rightarrow 0$, the model becomes standard integrate-and-model with threshold V_T. w is the adaptation current, τ_w is the time constant, a is the level of subthreshold adaptation & b accounts for spike-triggered adaptation. Whenever the neuron fires, the variable w is increased by an amount b. [2]

The AdEx model is different from the Izhekevich model [5] in terms of usage of the function $f(V)$ characterizing the passive properties and the spiking mechanism. Izhekevich model uses a quadratic dependence on V while AdEx uses an exponential dependence. The aforementioned parameter Vr induces bursting when $Vr > V_T$, high values of a yield subthreshold oscillations while medium values cause a response overshoot and high values of b give strong spike-frequency adaptation. [2]

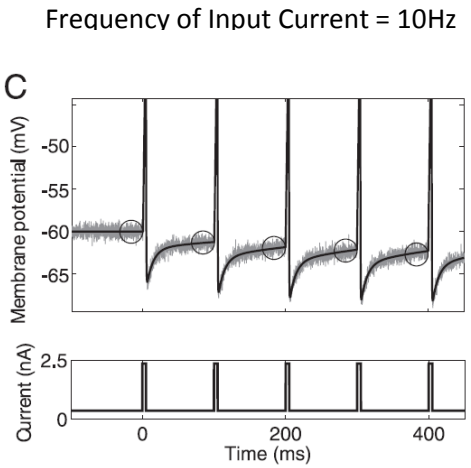

Figure 1: AdEx - Brette & Gerstner 2005 [1]

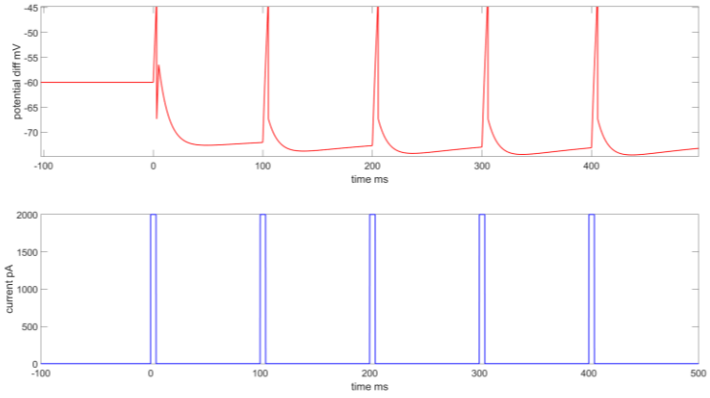

Figure 2: AdEx on GeNN with same parameters as Brette & Gerstner 2005 [1]

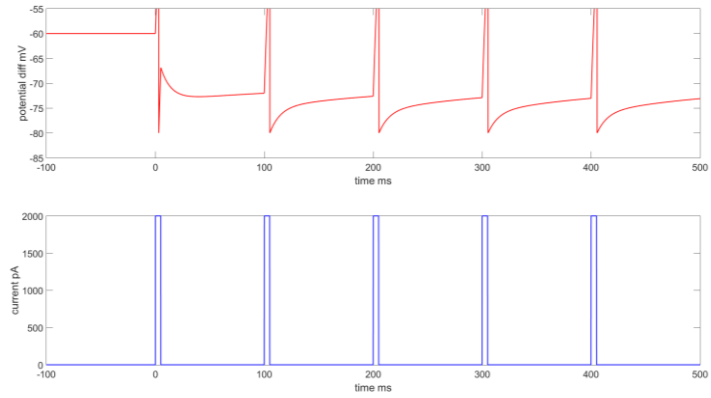

Figure 3: AdEx on GeNN with same parameters as Brette & Gerstner 2005 [1] but with a lower reset

Parameter	Value
C (membrane capacitance)	281 pF
g_L (leak conductance)	30 nS
E_L (leak reversal potential)	−70.6 mV
V_T (spike threshold)	−50.4 mV
Δ_T (slope factor)	2 mV
τ_w (adaptation time constant)	144 ms
a (subthreshold adaptation)	4 nS
b (spike-triggered adaptation)	0.0805 nA

Figure 4: Model Parameters-Brette & Gerstner 2005 [1]

Multiple firing patterns

The AdEx model is able to produce different kinds of spiking behaviour and in order to study the range of firing patterns the single neuron model is simulated with the injection of step current. Analogous to what is seen in real neurons, the behaviour shown by the model to the step current is very diverse, and depends on the choice of parameters.

Regular Bursting: It occurs when there are alternate sharp and broad resets. The reset potential is higher than the effective threshold potential. [2]

Delayed Acceleration: A positive feedback due to negative a is responsible for delayed initiation. Since $a < 0$, the adaptation current is gradually decreasing at a depolarized V, which allows the neuron to spike once the adaptation has suitably decreased. [2]

Table 1: Parameters for firing pattern examples taken from Naud. et. al 2008

Figure	Type	*C* (pF)	*g_L* (nS)	*EL* (mV)	*VT* (mV)	*ΔT* (mV)	a (nS)	*τw* (ms)	*b* (pA)	*Vr* (mV)	I (pA)
5a	Tonic Spiking	200	10	-70	-50	2	2	30	0	-58	500
5b	Adaptation	200	12	-70	-50	2	2	300	60	-58	500
5c	Initial Burst	130	18	-58	-50	2	4	150	120	-50	400
5d	Regular Bursting	200	10	-58	-50	2	2	120	100	-46	210
5e	Delayed Acceleration	200	12	-70	-50	2	-10	300	0	-58	300
5f	Delayed Regular Bursting	200	10	-58	-50	2	-6	300	0	-58	110
5g	Transient Spiking	100	20	-70	-50	2	-10	90	30	-47	350
5h	Irregular Spiking	100	12	-60	-50	2	-11	130	30	-48	160

Table 2: Parameters for firing pattern examples used in GeNN

Figure	Type	*C* (pF)	*g_L* (nS)	*EL* (mV)	*VT* (mV)	*ΔT* (mV)	a (nS)	*τw* (ms)	*b* (pA)	*Vr* (mV)	I (pA)
6a	Tonic Spiking	200	10	-70	-50	2	2	30	0	-58	500
6b	Adaptation	200	12	-70	-50	2	2	300	60	-58	500
6c	Initial Burst	130	18	-58	-50	2	4	150	120	-50	400
6d	Regular Bursting	200	10	-58	-50	2	2	120	100	-46	210
6e	Delayed Acceleration	200	12	-70	-50	2	-10	300	0	-58	300
6f	Delayed Regular Bursting	200	10	-58	-50	2	-6	120*	70*	-46*	200*
6g	Transient Spiking	100	20	-70	-50	2	1*	90	120*	-47	380*
6h	Irregular Spiking	100	12	-60	-50	2	-11	130	30	-48	160

*changes in the parameters are according to the reference [6]

Tonic Spiking: It is the simplest of all spiking patterns, a regular discharge of action potential. It resembles the lack of spike triggered adaptation and adaptation sensitivity to sub-threshold voltage. [2]

Adaptation: Largely neurons display some level of spike-frequency adaptation. In this type, the time between subsequent spikes, the inter-spike interval (ISI) grows during a continuous stimulus. [2]

Initial Bursting: It denotes a group of spikes that were emitted at a higher frequency than the steady-state frequency. Considering AdEx model, initial bursting arises when the spiking starts with sharp resets followed by broad resets. [2]

Delayed Regular Bursting: This happens when the value of spike-triggered adaptation is high enough compared to the case of Delayed Acceleration and the adaptation is current decreasing similar to the case of Delayed Acceleration. [2]

Transient Spiking: In transient spiking, during a step of depolarizing current some neurons spike several times before reaching their final state of rest. A spike is produced because the adaptation current is too slow to compensate for the sharp change in the applied injection current. [2]

Irregular Spiking: It happens when the interspike interval changes without periodicity during observation. Irregular spiking is due to chaos. [2]

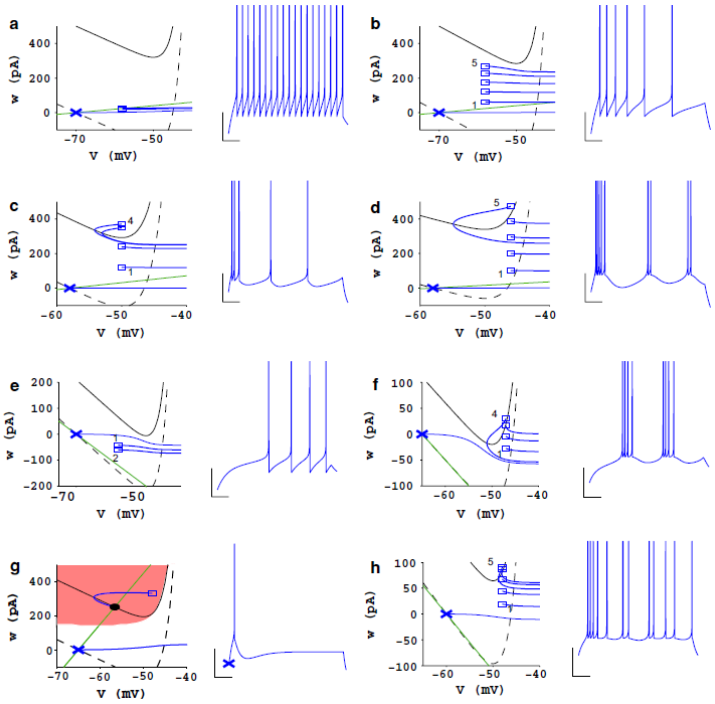

Figure 5: Different spiking behaviour – Naud. et. al 2008 [2]

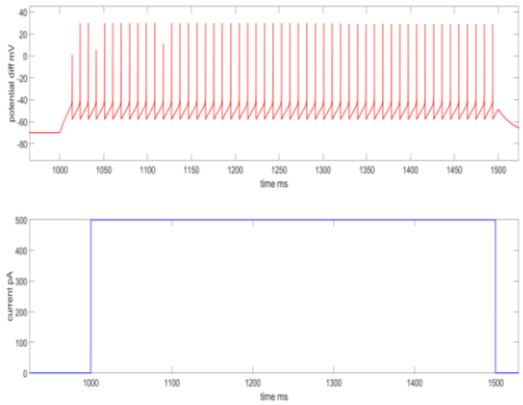

Figure 6a: Tonic Spiking

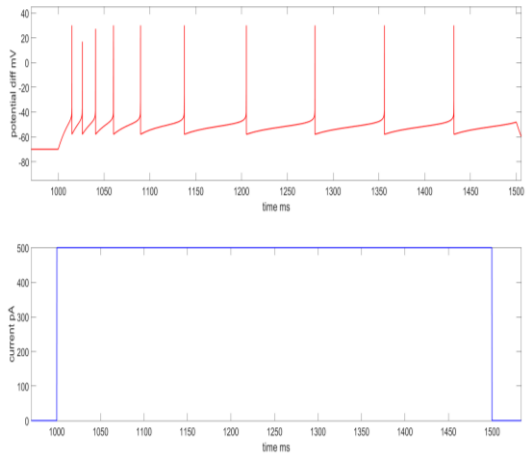

Figure 6b: Adaptation

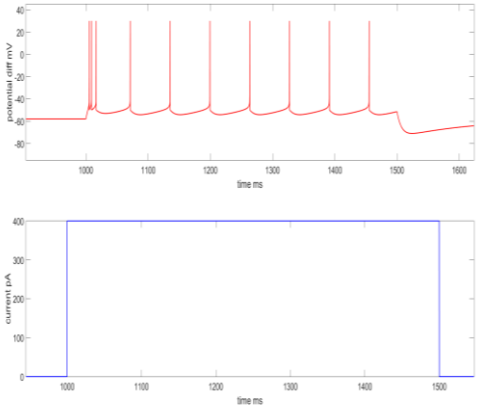

Figure 6c: Initial Bursting

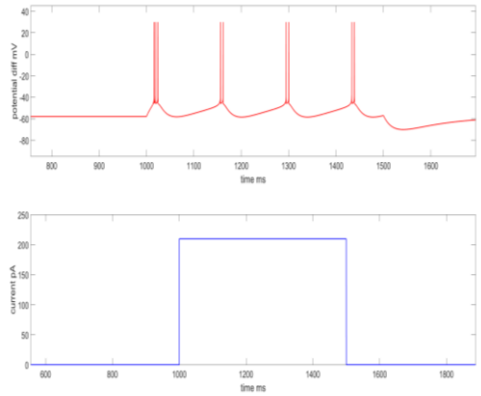

Figure 6d: Regular Bursting

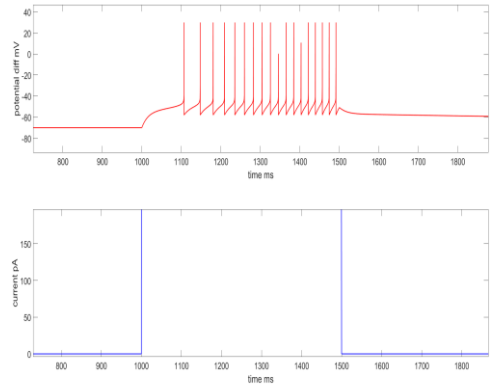

Figure 6e: Delayed Acceleration

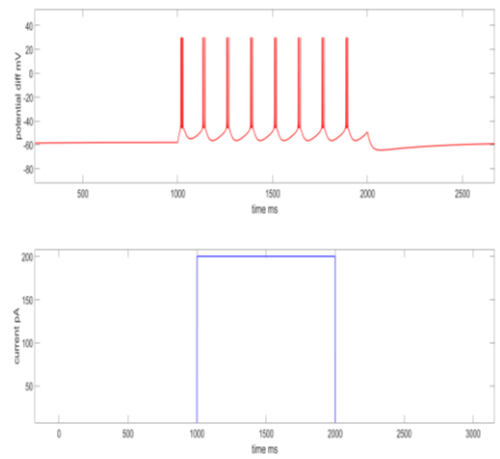

Figure 6f: Delayed Regular Bursting

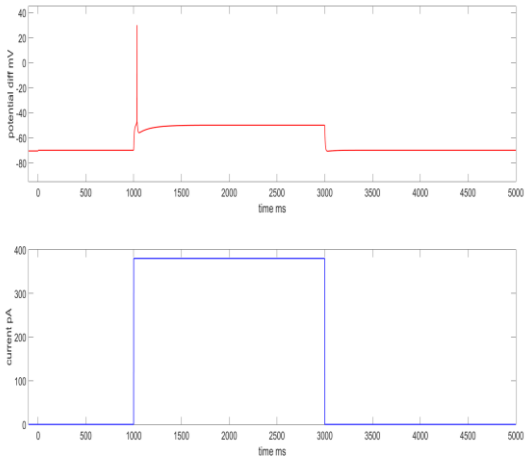

Figure 6g: Transient Spiking

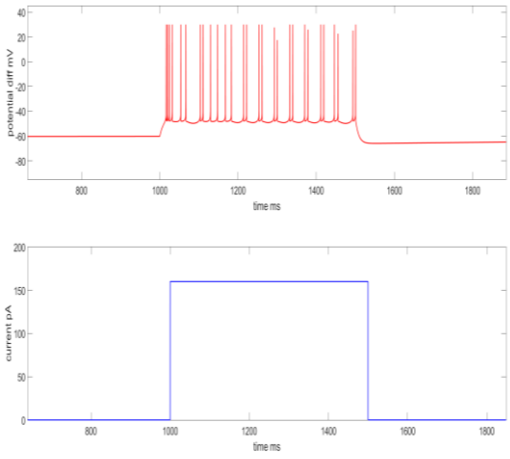

Figure 6h: Irregular Spiking

Reducing Hodgkin-Huxley model to AdEx model

Starting with the single-compartment Hodgkin-Huxley equations:

$$C\frac{dV}{dt} = -g_M(V - E_M) - g_{Na}m^3h(V - E_{Na}) - g_K n^4(V - E_K) + I$$

$$\tau_x \frac{dx}{dt} = -x + x_\infty$$

τ_x and x_∞ are dependent on V, x being any of the gating variables *m, h* or *n*.

Under voltage-clamp conditions (when membrane potential is held at a constant value), the equations governing the dynamics of the gating channels reduces to the following equations:

$$m(t) = m_0 - \left[(m_0 - m_\infty)\left(1 - e^{-\frac{t}{\tau_m}}\right)\right]$$

$$n(t) = n_0 - \left[(n_0 - n)\left(1 - e^{-\frac{t}{\tau_n}}\right)\right]$$

$$h(t) = h_0 - \left[(h_0 - h_\infty)\left(1 - e^{-\frac{t}{\tau_h}}\right)\right]$$

Now assuming $\tau_m \ll \frac{C}{g_L}$, this gets rid of the changes in sodium channel activation variable.

$$m(t) = m_\infty$$

Another assumption is that when the voltage reaches some relatively high value (e.g. V > 0mV), which corresponds to a spike being emitted, the voltage is reset to 'V_r' (reset potential), while the potassium channel gating variable 'n' undergoes a conventional change and a small δ_n is added to it.

$$n \rightarrow n + \delta_n$$

Now assuming that the sodium inactivation variable has no effect in during sub-threshold dynamics and spike initiation.

$$h(t) = h_0$$

Now remains the only variables 'V' and 'n' and the dynamics of n can be linearized around E_L.

Hence, the system reduces to the following equations:

$$C\frac{dV}{dt} = I - g_L(V - E_L) - g_{Na}h_0m_\infty^3(V - E_{Na}) - w$$

$$\tau_w \frac{dw}{dt} = a_w(V - E_0) - w$$

$$\text{if } V > 0mV \text{ then } V = V_r, w = w + b$$

With the corresponding parameters:

$$w(t) = 4g_K(n(t) - n_\infty)n_\infty^3(E_0 + E_K)$$

$$a = 4g_K n_\infty^3(E_0 + E_K)\left.\frac{\partial n_\infty}{\partial V}\right|_{E_\infty}$$

$$\tau_w = \tau_n$$

$$b = 4g_K\delta_n n_\infty^3(E_0 + E_K)$$

where n_∞ and τ_w are function of E_0 [7]

Neuron Dynamics of Kenyon Cells

Kenyon cells are mushroom body neurons and are considered to represent a neuronal substrate underlying olfactory learning and memory. Kenyon cells receive input from projection neurons (PNs). Kenyon cells are organized into a structure called the mushroom body calyx, where some projection neurons from the antennal lobe provide olfactory information. Kenyon cells encode information about odours by their sparse responses (identities of the responding neurons) as well as the timing of their spikes. [4]

Currently GeNN [] uses Traub-Miles implementation of the Hodgkin-Huxley model and the dynamics is shown in figure 8.

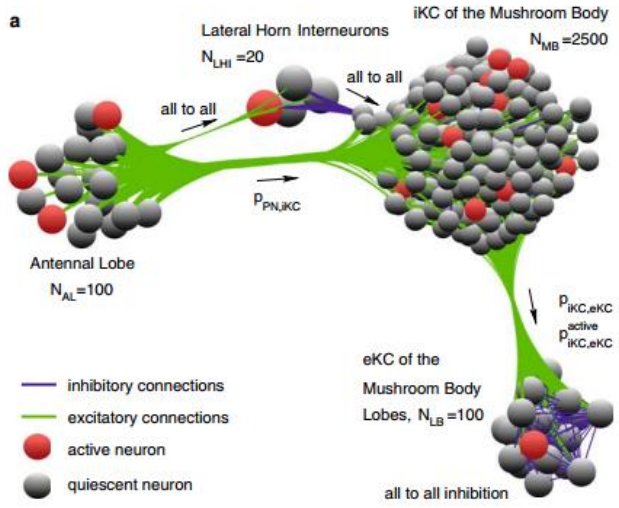

Figure 7: Mushroom body model from [4]

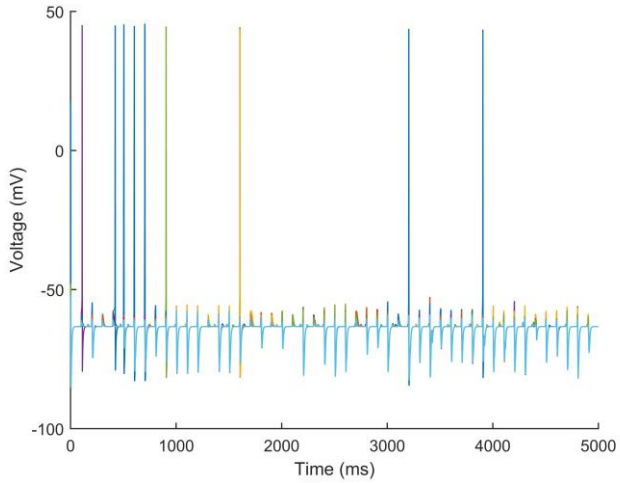

Figure 8: Neuron dynamics of first 20 KC's

For a single KC using Hodgkin-Huxley model the dynamics is shown in figure 9:

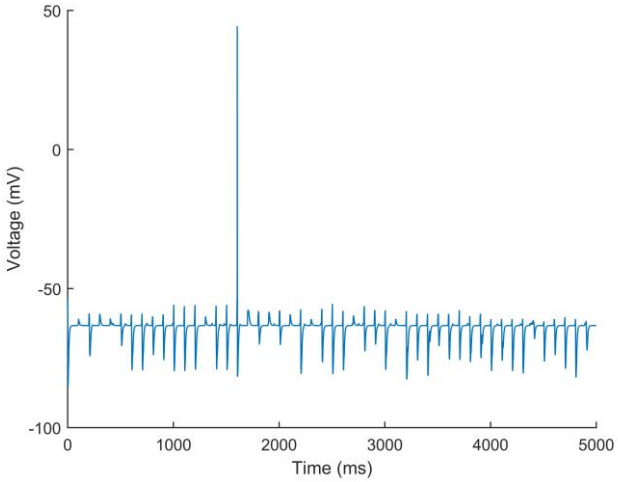

Figure 9: Dynamics of a single Kenyon Cell using HH model

After replacing the current model by AdEx model the dynamics of the same neuron is shown in Figure 10

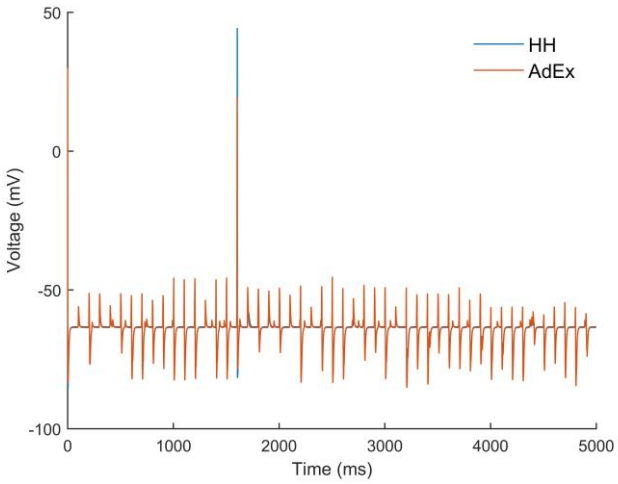

Figure 10: Dynamics of a single Kenyon Cell using AdEx model

The parameters for AdEx model are given in the following table:

Table 3: Parametes for AdEx model for KC's

C (pF)	*g_L* (nS)	*EL* (mV)	*VT* (mV)	*ΔT* (mV)	a (nS)	*τw* (ms)	*b* (pA)	*Vr* (mV)	I (pA)
20.0	2.62	-63.5	-50	2.0	1	1.0	100	-45	$500*I_{syn}$

For a neuron which doesn't spike during simulation, the dynamics in shown in Figure 11 and Figure 12.

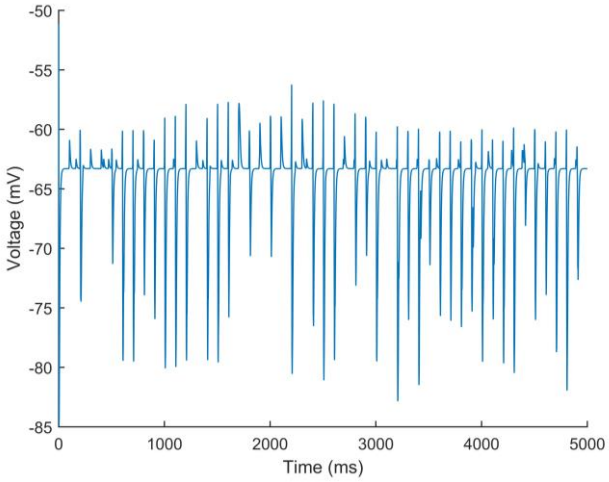

Figure 11: Neuron dynamics of a KC using Hodgkin-Huxley model which didn't spike.

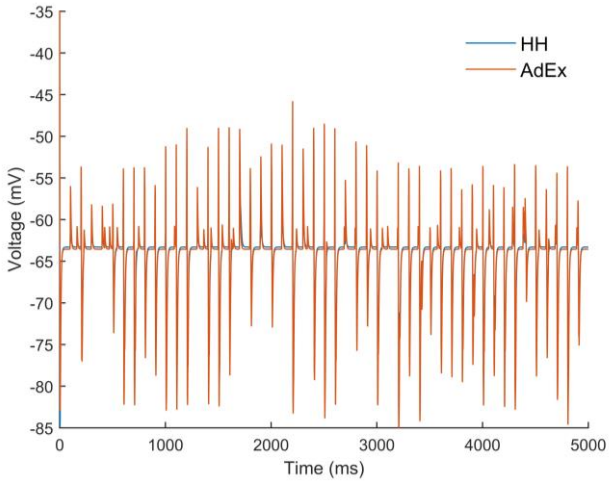

Figure 12: Comparison of depolarization dynamics of a non-spiking KC during the 5 second simulation

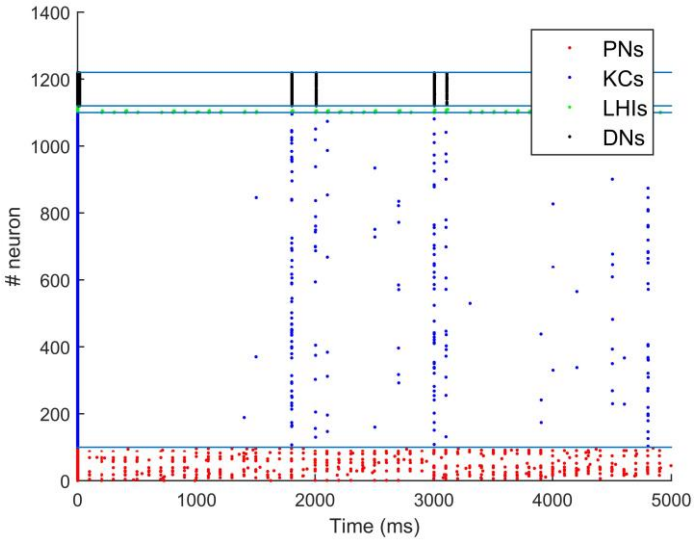

Figure 13 Raster Plot of the network

Raster Plot of the network is shown in Figure 13 corresponding to spiking in neuron population. During parameter exploration, several plots deviating from the actual dynamics were obtained. Some neurons were found to have an extra spike shown in Figure 14a, 14b, 14c and 14d.

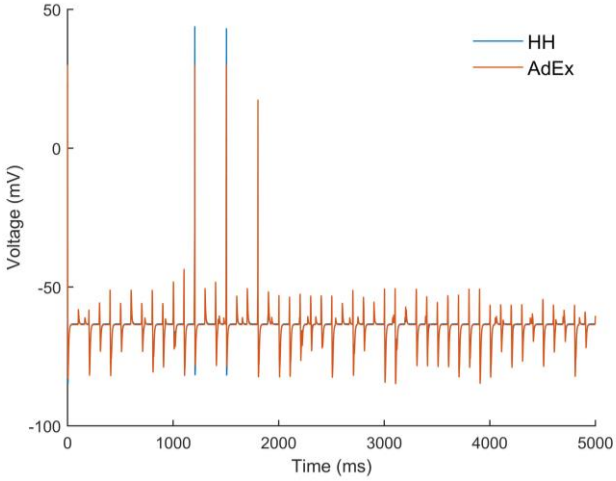

Figure 14a: KC with an extra spike at t=1.804ms

For the parameter set

C (pF)	*g_L* (nS)	*EL* (mV)	*VT* (mV)	*ΔT* (mV)	a (nS)	*τw* (ms)	*b* (pA)	*Vr* (mV)	I (pA)
20.0	2.62	-63.5	-50	2.0	1	100	100	-45	$500*I_{syn}$

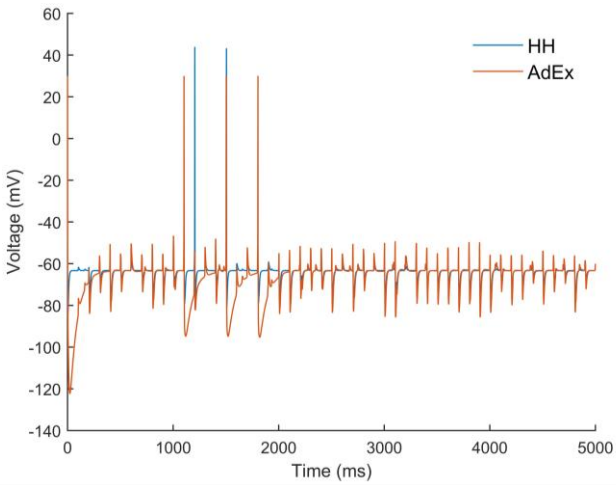

Figure 14b

For the parameter set

C (pF)	*g_L* (nS)	*EL* (mV)	*VT* (mV)	*ΔT* (mV)	a (nS)	*τw* (ms)	*b* (pA)	*Vr* (mV)	I (pA)
20	2.62	-63	-50	2	-2	1	100	-45	$500*I_{syn}$

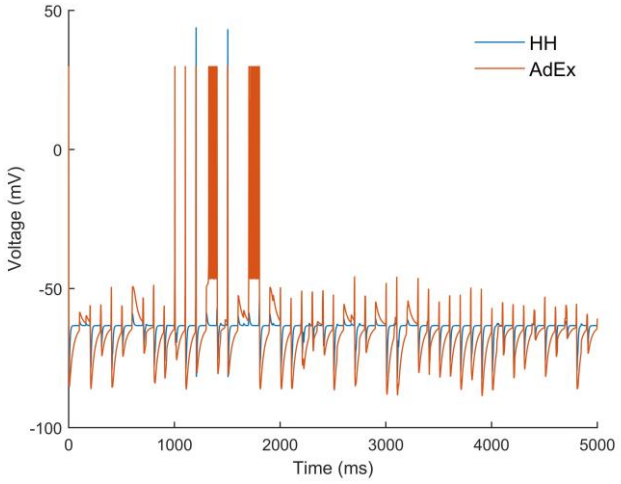

Figure 14c

Running Time Comparison

Running time for both the network simulation differing only in the type of neuron being used for Kenyon Cell is shown in Table 4. First, the network is initialised by 100 Projection Neurons (PNs), 1000 Kenyon cells (KCs), 20 Lateral Horn Interneurons (LHIs) and 100 Detector Neurons (DNs). Subsequently, the number of KCs were increased in the network in order: 10x, 50x and finally 100x.

Discussion

The AdEx model is able to produce multiple firing patterns depending on parameters. The model neuron can exhibit initial bursting, regularly bursting, tonic spiking, adaptation, acceleration, irregular spiking and delayed initiation.

Table 4: Running Time comparison between Hodgkin-Huxley and AdEx* on KCs using GeNN

Model	PN/PN_spike	KC/ KC_spike	LHI/LHI_spike	DN/ DN_spike	Time (s)	Ratio
HH_KC	100/546	1000/1020	20/207	100/1570	18.35	
AdEx_KC	100/546	1000/2772	20/207	100/1730	17.95	1.02
HH_KC	100/562	10000/10795	20/243	100/1862	39.55	
AdEx_KC	100/562	10000/31682	20/243	100/2342	21.31	1.86
HH_KC	100/566	50000/59986	20/248	100/2501	133.26	
AdEx_KC	100/566	50000/158164	20/248	100/2393	29.99	4.44
HH_KC	100/562	10^5/117310	20/237	100/2678	249.54	
AdEx_KC	100/562	10^5/299684	20/237	100/2278	40.54	6.23
AdEx_ALL	100/546	1000/1663	20/175	100/1666400	31.09	

**all simulations done with a time step DT=0.1ms*

For the parameter set

C (pF)	*g_L* (nS)	*EL* (mV)	*VT* (mV)	*ΔT* (mV)	a (nS)	*τw* (ms)	*b* (pA)	*Vr* (mV)	I (pA)
20	2.62	-63	-50	2	-2	100	120	-45	$500*I_{syn}$

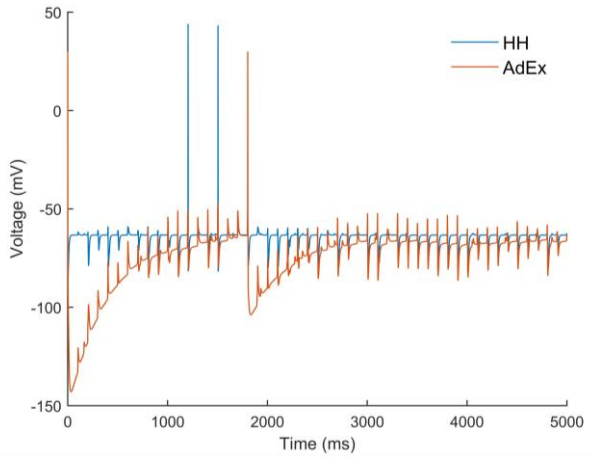

Figure 14d

During network simulations, the AdEx model is able to reproduce the spiking behaviour of the Kenyon Cells and during simulation of large networks it is 6 times faster than the Hodgkin-Huxley model when simulated on GPU.

References

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