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Sparse and burst spiking in artificial neural networks inspired by synaptic retrograde signaling

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ABSTRACT

The bursting of action potential and sparse activity are ubiquitously observed in the brain. Although the functions of these activity modes remain to be understood, it is expected that they play a critical role in information processing. In addition, the functional role of retrograde signalling in neural systems is under intensive research. Therefore, we propose a bio-inspired neural network that is capable of demonstrating these activity modes as well as shifting themselves from normal to bursting or sparse modes by changing model parameter values. Accordingly, we model diffused retrograde signalling with different activity patterns in dendrites and presynaptic neurons. Using in a three-layered spiking neural network, simulation studies are conducted using different conditions and parameter values to find factors underlying the change in firing rate of output neurons. Our findings propose the application of retrograde signalling as a known synaptic mechanism for the development of artificial neural systems to encode environmental information by different spiking modes.

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1. Introduction

Neurons communicate with other neurons by transforming synaptic input patterns into output spike trains. This mode of communication strongly depends on the properties of voltage-gated conductance in neuronal membranes. Biological neural systems are equipped with complex molecular and synaptic mechanisms [15,45]. Specifically, synaptic mechanisms play a key role in memory and learning processes that take place across different time scales [40,36]. Although understanding the function of neural systems at different time scales is a challenge for modern neurosciences, theoretical and computational studies may help understand and interpret experimental findings by shedding light on how single neurons and neural populations encode, store and retrieve information [27]. Moreover, to develop artificial architectures that show animal-like behaviours, we must understand the principles of information processing in the neural systems and how they trigger behaviours.

Bursting is a firing mode of neurons which is characterized by high frequency spikes, followed by a period of relative silence [7].

Neurons in a variety of biological neural systems exhibit correlated activity. Understanding how input correlations are processed and transmitted from a layer of neurons to the next neural layer has been studied. Recently, it has been shown

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that neural bursting can be generated intrinsically in neurons themselves or as a result of stimulation by network activity [24] that plays a central role in enhancing output correlations of a neural layer. Another observed firing mode of neurons is sparse spiking –low firing rate- which is observed in some brain regions such as the dentate gyrus in the hippocampus [11] or auditory cortex [26].

Activity in cortical networks is heterogeneous, sparse and often precisely timed. The functional significance of sparseness and precise spike timing has been under intense debates. Some studies have provided an account for the developmental and synaptic mechanisms that shape neuronal discharge sparse patterns in cortical activities [40].

It is believed that feedforward or feedback inhibitory circuits in neural networks plays a role in controlling sparse activity of cortical neural networks [23,32,10]. These inhibition mechanisms play a key role in memory processes in insects [13]. In addition, the homeostatic feedback mechanism in synapses is one of the stabilizing mechanisms in which diffusion of retrograde messengers from postsynaptic to presynaptic neurons as a consequence of action potential reach axonal terminals [35]. These mechanisms equip neurons and neuronal circuits to sense how active they are and to adjust their firing to keep this activity within some target range [34]. In addition, biophysical features of neurons including factors that determine excitability of neurons are other mechanisms that impact sparse and burst spiking neural activities [8].

Although neurons mainly communicate via generating action potentials in short time scales, this is not the only way they transmit information to other neurons in order to induce changes including the stimulation of postsynaptic neurons. In response to stimulation from presynaptic neurons, neurons may generate chemicals of different types that are diffused into presynaptic neurons [15,25]. These chemicals may induce some changes in the cellular and molecular activities that eventually result in a change of electrical activity of neurons at different time scales [4]. The importance of some of these non-synaptic mechanisms in healthy and abnormal neural functions is relatively well-known [14].

Retrograde signalling in neurons plays a role in information processing in healthy brains while abnormal retrograde signalling (low or high levels of retrograde messengers) may lead to brain disorders [28,29,38]. Nitric oxide is one of the well studied fast diffused retrograde messengers, and its abnormal levels are shown to lead to psychiatric disorders [1]. Further, repetitive synaptic activity can induce persistent increase or decrease of synaptic efficacy. Retrograde signalling as diffused chemicals from postsynaptic neuron to presynaptic neurons is essential for the induction of long-term potentiation (LTP) or long-term depression (LTD) [30].

One of the changes that such retrograde signals can induce in presynaptic neurons is an increase or decrease in the probability of neurotransmitter release from presynaptic neurons [9]. The importance of neurotransmitter release probability as a consequence of presynaptic activities of different neuron types and its role in encoding efficiency of neural systems has been studied using computational modelling [9]. Regarding the initial probability of neurotransmitter release in different neurons, synapses are categorized as filters of information [2]. The initial value of release probability is believed to be justified by diffused retrograde signalling from postsynaptic into presynaptic neurons. These mechanisms, in combination with synaptic and intrinsic excitability, have been studied to determine the overall effect on the activity of neural population to encode and store the information from different sources of stimulations [37].

Biological neurons have complex and diverse shapes and sizes, and electrophysiological features. Therefore, to simulate their function in a network, it is necessary to simplify biological features of neurons. Artificial Neural Networks incorporate basic information processing from biological neurons and their biophysical features that process sensory input processing and generate action potential to transfer information to the networks [21]. Models that simplify neuronal electrophysiology are computationally efficient but they are generally very abstract to be used in biologically realistic simulations [20].

Some simulation techniques of neuron models that consider biophysical feature of neurons in details are computationally expensive and unsuitable for the simulation of large aggregate of neurons, such as network simulations [20].

Bio-inspired neural networks developed with different architectures (e.g., multilayer perceptron classifiers [19]) have many industrial applications including optimization [41], dealing with large scale datasets [6], and image processing (e.g., handling the human pose recovery problem [17,18]). For this purpose, retrieving of images with sparse coding by artificial neurons has been effectively used.

One of such bio-inspired neural systems is deep neural networks which have been used to solve image processing problems by high-dimensional sparse representation [43]. In this line of research, to obtain an appropriate description of images, multimodal features have been considered for describing images. For this purpose, recently, a novel deep multimodal distance metric learning combines these multimodal features [44].

In this study, we have developed a three-layer feedforward neural network model using a hypothetical mechanism of changing the probability of neurotransmitter release that is induced by diffused retrograde messengers from postsynaptic neurons. Synapses that show production and diffusion of retrograde messengers from a postsynaptic neuron in response to presynaptic stimulation are considered as a closed loop [22]. In this study, we have modelled controlling of neurotransmitter release by a closed loop in presynaptic and postsynaptic cellular machinery. The neural system is able to decrease or increase the probability of neurotransmitter release in response to different levels of stimulation. The role of different model parameter values is examined using simulation studies to investigate neural system's dynamic activation in different conditions of stimulation. Such feedforward neural system as divergence-convergence architecture is found in many sensory-perception loops in animals' brains. Two well-known examples are *Drosophila* olfactory system and information processing in hippocampus. In the insect brain, activated neurons in Antennal Lobe (about 150 neurons) transmit information to Mushroom Body (memory center of insects that includes about 2500 neurons) [16]. The activated neurons in Mushroom Body project to few Output Neurons that elicit avoidance behavior. In the rat hippocampus, about 200,000 neurons in the

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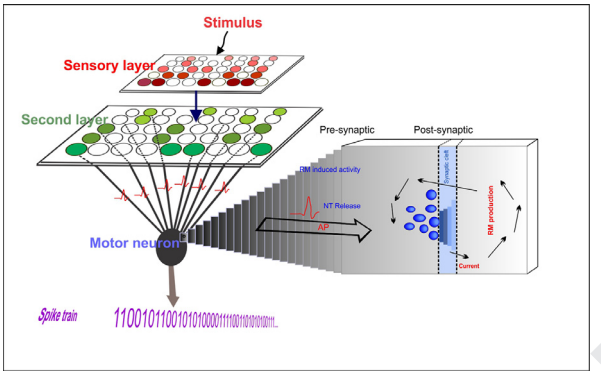

Fig. 1. The neural network architecture. The neural network is composed of three layers: sensory, hidden and motor neurons layer (the spiking of one neuron of the motor neurons layer is studied in the simulations). A presented stimulus activates a set of neurons in the sensory layer and consequently leads to the activation of neurons in the hidden layer. The stimulation may trigger the motor neurons layer to spike with different rates depending on the incoming input. The spike trains of the motor neurons are used to measure mutual information between the motor neurons and the stimulus. Moreover, the spiking pattern can be used to evaluate the system efficiency to encode stimuli. The dynamic model of the synapses between hidden neurons and motor neurons include production and diffusion of retrograde messenger (RM) as chemicals from a post-synaptic site (motor neurons) into a presynaptic site (hidden neurons layer) induced by action potential of the hidden layer (AP). According to the concentration of a diffused retrograde messenger in the hidden layer neurons in a successive time bin the probability of neurotransmitter release in the next time bin is determined.

Table 1
Parameters of the Integrate and Fire neuron model used in the neural system.

Parameter	value
$\mathbf{V_{rest}}$ resting potential	−84mV
$\mathbf{V_{thresh}}$ threshold of spiking	−25.8mV
$\mathbf{V_{recov}}$ recovery threshold	−40.2mV
$\mathbf{V_{spike}}$ spike potential	9.5mV
$\mathbf{g_{leak}}$ membrane conductance	0.26nS
$\mathbf{C}$ membrane capacitance	0.26nS

Entorhinal Cortex are connected to about 1,200,000 neurons in the dentate gyrus. Activated neurons in the dentate gyrus send information to about 300,000 neurons of CA3 [5,31]. The connectivity rate of these layers is not known. However, by following the neural architecture of layers that demonstrate divergence-convergence we are able to consider different connectivity rates in simulation studies.

2. Model

2.1. Neural system architecture

The developed neural system in the study is constructed as a three-layer feedforward neural network. It is inspired by the divergence-convergence architecture of insects' olfactory system and is composed of a sensory layer containing 10 neurons (first layer or L_1), hidden layer containing 60 neurons (second layer or L_2), and 10 motor neurons (third layer or L_3) (Fig. 1).

In Fig. 1 one of the motor neurons is shown. The sensory layer is activated by stimuli and their activities are modelled using a probabilistic approach. Specifically, the probability of firing of neurons is defined as the probability of one spike in each time bin that is represented as '1'. Hence, for each probability of firing, a spike train is constructed as ones and zeros such that the frequency of occurrence of ones are close to the probability of firing. The levels of stimulus intensity are presented as different probabilities of firing of the activated neurons in the sensory layer. Each stimulus input triggers spiking of a random 50% neurons of the sensory layer and sending information as spikes in time bins each equal to 10 ms.

The sensory layer and hidden layer are connected according to a connectivity rate (C_1). The connectivity rate is defined as the probability of connecting a neuron in the hidden layer into neurons of the sensory layer. The activity of the neurons in the hidden layer is modelled as an *Integrate and Fire neuron* (Eq. 1) constrained by electrophysiological data of honeybee's olfactory system [42] is represented in Table 1. The hidden layer is connected into the motor neurons layer (L_3) represented as connectivity rate (C_2) where their activity is also modelled as integrate and fire neuron.

$$C\frac{dV}{dt} = -g_{leak}*(V - V_{rest}) + I(t); dt = 0.01 \quad (1)$$

where I(t) is the current into neuron in a time bin 't'.

g_{leak} and V denote membrane conductance and membrane potential of L_2 and L_3 neurons, respectively.

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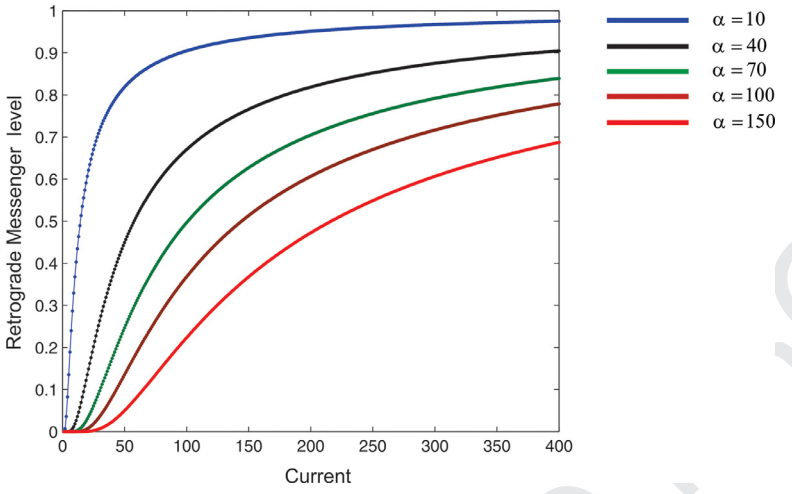

Fig. 2. The production of retrograde messenger in post-synaptic neuron (third layer) induced by total current from pre-synaptic neurons (second layer). Different model parameters (α values) determine the level of a produced retrograde signal at a given current.

The current into L_2 neurons and L_3 neurons are modeled as Eq. (2)

$$\dot{I} = -I(t)/\tau_I + \sum_{t_p} \delta(t - t_p); \qquad \tau_I = 30 \text{ ms} \tag{2}$$

where $I(t)$ denotes current into a postsynaptic neuron in time bin 't'. where $\delta(t - t_p)$ is the Dirac function that step-increases the variable I.

$\sum_{t_p} \delta(t - t_p)$ is the sum of the received spikes as input in a given time bin. The input intensity depends on both firing rate of pre-synaptic neurons, connectivity rate of layers and probability of neurotransmitter release in each pre-synaptic neuron. t_p is the time bin in which a spike is received. The total amount of current that a neuron in L_3 receives from connected neurons of L_2 at the end of each time bin (t) triggers the post-synaptic neuron to produce retrograde messenger (Eq. 3). α determines the level of produced and received retrograde messenger for a given level of current into post-synaptic neuron (Fig. 2).

$$RM(t) = \exp\left(-\alpha / I^{tot}\right) \tag{3}$$

where I^{tot} denotes total current into postsynaptic neurons at the beginning of time bin 't'.

In this study, in all simulations $\alpha = 120$ is used.

To model the effect of retrograde messenger produced in post-synaptic neurons (L_3) and received by pre-synaptic neurons (L_2) we considered different retrograde messengers with slow to fast effect on neurotransmitter release machinery by τ_{RM} values (Eq. 4).

$$RM_{ef}(t) = RM \frac{t}{\tau_{RM}} \exp\left(\frac{-t}{\tau_{RM}}\right) \quad ; \tau_{RM} = [10 \quad 200] \tag{4}$$

where RM in the right hand of Eq. 4 is the total amount of received retrograde messenger by a L_2 neurons at the end of each time bin.

Low τ_{RM} values induce fast effect on release machinery and fast decay of effect as well. High τ_{RM} values induce slow effect and slow decay of activity of release machinery (Fig. 3). Fig. 3 shows the increase and decay of retrograde messenger's effect on presynaptic neuron triggered at time bin equal to 1. In the simulations where RM may produce in a sequence of time bins, RM_{ef} may increase over time.

2.2. Synapse dynamics

The spiking activity of each neuron in L_2 may result in neurotransmitter release into the cleft that consequently leads to influx of current into the postsynaptic site (L_3) (Eq. 2).

The neurons in L_2 has an initial release probability that can be decreased or increased through neuronal activity and different stimuli representation conditions that occur by the synaptic dynamics model developed in this study. In this model, it is assumed that presynaptic neurons are equipped with release machinery with an activity threshold ($\boldsymbol{\theta}$) that determines either decrease or increase in neurotransmitter release probability that is calculated at the end of each time bin. Two parameters, $\boldsymbol{K}$ and $\boldsymbol{M}$, are used in order to modify the decrease or increase of the release probability, respectively. If the level of induced activity of release machinery in each time bin gets a lower value compared to the threshold (θ) (Eq. 5) then the system increases the previous release probability (Eq. 6); otherwise, it leads to the decrease in the neurotransmitter release

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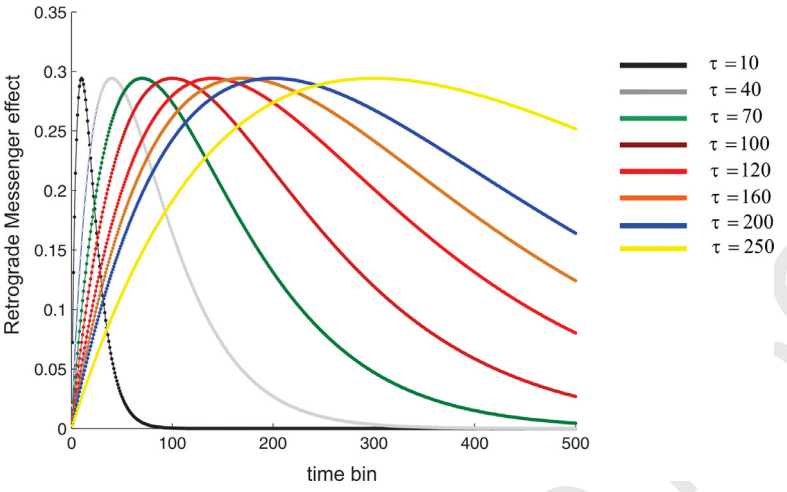

Fig. 3. The effects of diffused retrograde signalling from a post-synaptic neuron on activity of pre-synaptic neurons. This activity acts as a part of the 'controller' to determine probability of neurotransmitter release into a post-synaptic neuron. Different parameter values ($\boldsymbol{\tau}$) determine the biophysical features of retrograde signal like diffusion into a pre-synaptic neuron and induced activity inside a pre-synaptic neuron. Higher $\boldsymbol{\tau}$ values demonstrate retrograde signalling that are slowly diffused and act on pre-synaptic neurons.

Table 2
Summary of notations.

L_{1-3}	layers in feedforward neural network
r_{1-2}	connectivity rates of layers
$I(t)$	current into postsynaptic neuron
δ	Dirac function
t_p	time of receiving a spike
$\sum I$	total current into I&F neuron
$RM(t)$	retrograde messenger concentration
$RM_{ef}\ (t)$	induced changes in presynaptic neuron by RM
α	parameter of retrograde messenger production
τ_{RM}	parameter of diffusion of retrograde messenger
θ	threshold of RM_{ef} to increase or decrease P_{rel}
K, M	parameters of release probability
$E(t)$	error function
P_{rel}	release probability

probability expressed as Eq. 7. The difference between release machinery and the threshold can be expressed as 'error (E)' . For the sake of simplicity in implementing the model, release probability is calculated and updated as a difference equation at the beginning of each time bin.

$$E(t) = RM_{ef}(t) - \theta;\ \ \theta = [0.5\ \ 10] \tag{5}$$

$$\text{If } E(t) < 0 \quad P_{rel}^{t+1} = P_{rel}^{t} + M.(E(t))^2 \tag{6}$$

$$\text{If } E(t) > 0 \quad P_{rel}^{t+1} = P_{rel}^{t} - K.(E(t))^2 \tag{7}$$

$\boldsymbol{K}$ and $\boldsymbol{M}$ determine the rate of increase or decrease in release probability in the successive time bin. Initial release probability in all simulations is set to 0.95.

Using the changes of release probability expressed as Eqs. 5 to 7 some simulations are run in order to study the role of model parameters in different conditions. Summary of notations defined and used in the model is resented in Table 2.

2.3. Robustness of the system

The developed neural system demonstrates both sparse and burst spiking. To study how model parameter values ensure burst spiking activities in high level of stimulation (as L_1 neurons firing rate equal to 0.7), $\boldsymbol{K}$ and $\boldsymbol{M}$ values are set to 0.2 and 0.1, respectively. Then the stimulation level is lowered and the optimal values of θ and τ_{RM} are investigated to keep the L_3 firing rate at high levels. To obtain sparse spiking activities in high level of stimulation (as L_1 neurons firing rate equal to

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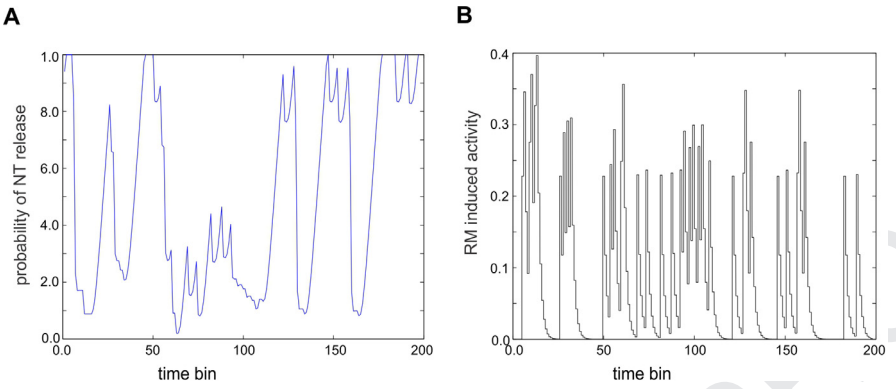

Fig. 4. Closed-loop based dynamics of neurotransmitter release probability and induced release machinery activity in a pre-synaptic neuron by diffused retrograde messenger from post-synaptic neuron at threshold (θ) equal to 1. The change in release probability as a result of increase in release machinery activity affects current into post-synaptic neurons. Consequently, the change of current into post-synaptic neurons alters release machinery activity that change release probability over time. For all simulations in this figure ***K*** and ***M*** values are used as 0.02 and 0.2, respectively. $\boldsymbol{\tau}$ is set to 5 in the simulation.

0.2), ***K*** and ***M*** values are set to 0.2 and 0.1, respectively. Then the stimulation level is increased and the optimal values of θ and τ_{RM} are investigated to keep the L_3 firing rate at low levels (Fig. 9).

2.4. Computational complexity of the system

The proposed neural system incorporates a bio-inspired synaptic mechanism to show robustness to environmental changes that is modeled as different stimulation into L_1 neurons and is expressed as L_1 firing rate. It is expected that such simplified mechanisms do not increase running time of the algorithm remarkably when network size is increased. For this purpose, the running time of the algorithm in different network sizes and corresponding connection numbers are measured (K and M values are set to 0.2 and 0.1, $\theta = 4$ and $\tau_{RM} = 50$) (Fig. 10). Further, the running time is measured for both the Integrated and Fire neuron and Izhikevich neuron model [41].

2.5. Simulations

The stimulation of the neural system from the environment is modeled as randomly selected 50% neurons in L_1 in each algorithm's run. Firing rate of L_1 neurons is modeled as a probabilistic approach described in the method. L_2 neurons are activated as Integrate and Fire neurons and their spiking patterns in each time bin are integrated and used to stimulate L_3 neurons (motor neurons). L_3 neurons' activity is modeled as Integrate and Fire neurons and the average of their activities in each time bin is collected and the mean is presented. 500 times run of algorithm is used to calculate mean firing rate of L_3 neurons in all simulations. Connectivity rate of layers is also modeled as a probabilistic approach where each rate value is considered as probability of connecting of L_1 to L_2 or L_2 to L_3. In each algorithm run (and fix connectivity rate) new connectivity matrix of layers are constructed. In all simulations 200 seconds stimulation of L_1 neurons is applied as time window time to collect data. In each second 100 time bins is considered to measure average neurons activity (spikes).

3. Results

The main aim of this study is to model a closed loop synaptic mechanism in postsynaptic neurons in a feedforward network that enables them to control neurotransmitter release from presynaptic neurons in response to different levels of input intensities. In our neural system, spiking activity of L_3 depends strongly on input from L_1 andthe parameter values. Moreover, connectivity of layers plays an important role in transferring information from L_1 to L_3. Therefore, it is important to study changes in firing rate of L_3 in different conditions and parameter values. The neurotransmitter release from L_2 to L_3 in the model depends on K and M values that determine change in probability of neurotransmitter release in each time bin and threshold of the release machinery (θ). Therefore, the dynamic of release machinery (RM induced activity) and its impact on probability of neurotransmitter release can be studied. Fig. 4A,B demonstrates the relationship between change of release probability and activity of release machinery in 200 time bins of stimulation of L_2 neurons for $\theta = 2$. In this simulation, ***K*** is set to 0.01and ***M*** is set to 0.2. The threshold (θ) determines the tendency of pre-synaptic neuron to increase or decrease in release probability in each time bin. High threshold values leads to an increase in release probability over stimulation time.

To study the role of different ***K*** and ***M*** values in firing rate of L_3 neurons, threshold values (θ) equal to 1 to 4 are studied to measure firing rate of L_3 neurons (Fig. 5A-D). These simulations show that for all threshold values low ***K*** and high ***M*** values lead to higher firing rate of L_3 neurons. In addition, an increase in θ value results in an increase in firing rate of L_3 neurons. In these simulations τ isset to 10 and firing rate of L_1 neurons is set to 0.9. In order to study the role of different

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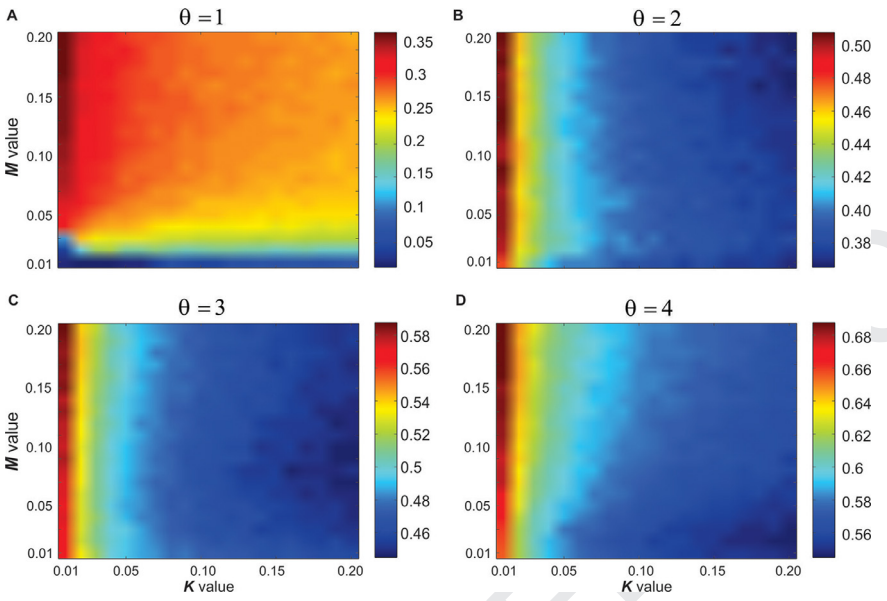

Fig. 5. The firing rate of motor neurons for different ***K*** and ***M*** parameter values and τequal to 10. Figures **A** to **D** show firing rate for different ***K*** and ***M*** values and different thresholds of the controller. Higher threshold values cause a higher firing rate of motor neurons. The low threshold value decreases release probability and results in a decrease in current into motor neurons. In all conditions, lower ***K*** values and high ***M*** values lead to an increase in the average firing rate of motor neurons.

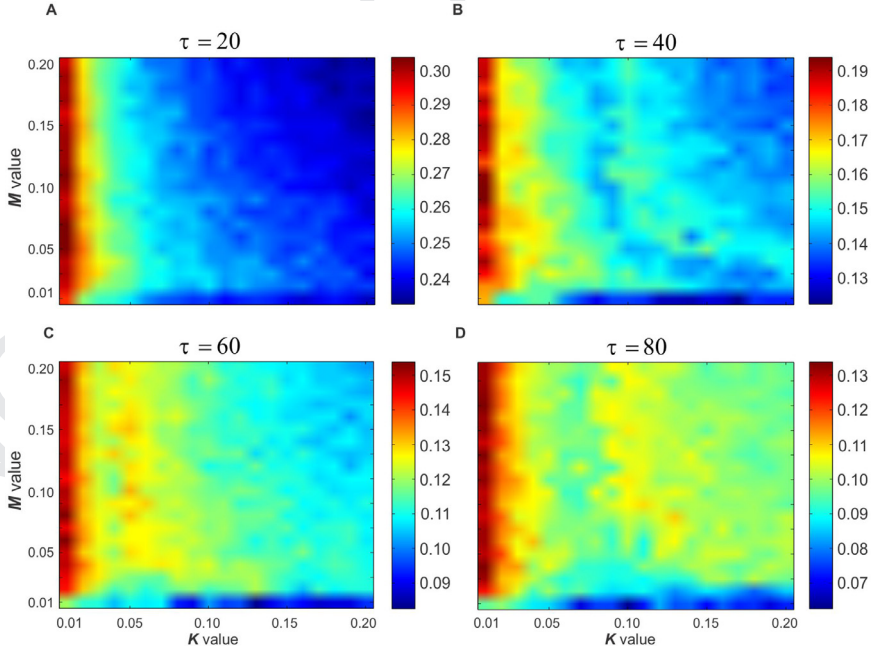

Fig. 6. Average firing rate of the motor neurons for different ***K*** and ***M*** parameter values for $\boldsymbol{\theta} = 2$. To study the effect of incremental $\boldsymbol{\tau}$ values on the firing rate of the motor neurons $\boldsymbol{\tau}$ equal to 20, 40, 60 and 80 are used (**A to D**). The simulations show that an increase in $\boldsymbol{\tau}$ value leads to decrease in firing rate of motor neurons for all pairs of ***K*** and ***M***.

τ values in the process of firing rate of L_3 neurons, simulations are run for $\theta = 2$ and τ_{RM}= 10 to 80. Simulations show decrease in ***K*** value and increase in ***M*** value lead to an increase in firing rate of L_3 neurons. Moreover, an increase in τ_{RM} values decreases the firing rate of L_3 neurons (Fig. 6A-D).

These results suggest that investigating the role of different θ and τ values in the firing rate of L_3 neurons. Fig. 7 shows the simulations for $\boldsymbol{K}$ = 0.01 and $\boldsymbol{M}$ = 0.2 values. Fig. 7A,B shows the results for connectivity between L_3 and L_2 equal to 0.4. Fig. 7C,D shows the results for connectivity between L_3 and L_2 equal to 0.9. As the firing rate of L_1 neurons may change

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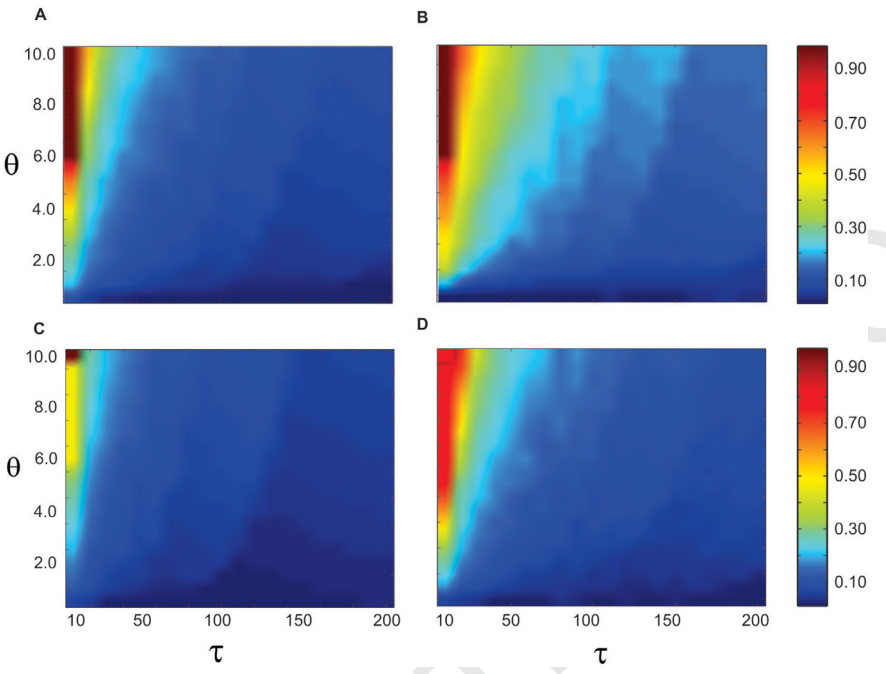

Fig. 7. Average firing rate of motor neurons for different $\boldsymbol{\theta}$ and $\boldsymbol{\tau}$ values. For each pair of $\boldsymbol{\theta}$ and $\boldsymbol{\tau}$ value, an average firing rate of the motor neurons for $\boldsymbol{K}$ equal to 0.01 and $\boldsymbol{M}$ equal to 0.2 is calculated. In figure **A** and **B** connectivity between second layer and the motor neurons is set to 0.9 and in figure **C** and **D** it is set to 0.3. The firing rate of the first layer is set to 0.4 (**A, C**) and 0.8 (**B, D**). In all simulations, lower $\boldsymbol{\tau}$ and higher $\boldsymbol{\theta}$ higher values increase the firing rate of the motor neurons.

in different stimulus presentation, different firing rate of L_1 neurons is also studied. For this purpose, $\boldsymbol{K}=0.01$ and $\boldsymbol{M}=0.2$ values are used for different θ values are used in the simulation for connectivity rate between L_3 and L_2 equal to 0.9 (Fig. 8A) and equal to 0.2 (Fig. 8B). For each connectivity rate, average firing rate of a L_3 neuron (>0) is calculated (Fig. 8C,D). These results show the possibility of controlling spiking activity of L_3 neurons by change in threshold value of L_2 neurons.

Fig. 9A,B shows the robustness of the system to different levels of stimulation to observe sparse and burst spiking by a change in θ and τ_{RM}.The results demonstrate that a gradual increase in τ_{RM} and decrease in θ leads to keep firing rate of L_1 neurons at low levels (sparse spiking) when incremental levels of stimulations are presented to the system. To obtain burst spiking in decremented changes in stimulation level, θ values are decreased and τ_{RM} values are increased. Fig. 10A,B demonstrates the impact of network size and number of connections in the network on time of running the model (Fig. 10C,D). The results show that the model using Integrate and Fire model works faster than the model using Izhikevich neuron model. The results also show the impact of size on running time for both model neurons.

4. Discussion

Exploring the mechanisms that enable animals' neural systems to detect and encode stimuli in an environment plays an important role in understanding information processing in the brain.

Biological neurons are characterized by their different firing rate in response to stimuli according to stimulus intensity. Some neurons show burst spiking, while others show sparse spiking activity. Understanding the neural mechanism of spiking of different neurons in the brain plays a critical role in understanding the encoding and decoding mechanisms and applying them in artificial neural systems. It is likely that some neurons rely on some dendritic mechanisms like controlling of neurotransmitter release by retrograde signalling to control the flow of activation signals from presynaptic neurons. However, neurons have no direct control on spiking activities of their inputs (the spiking of presynaptic neurons), though they may indirectly control the flow of information into their dendrites. Such mechanisms give the capability to control fluctuations in neuronal population activities triggered by stimuli in the environment. Specially, the role of retrograde signals from postsynaptic to presynaptic neurons to change the probability of neurotransmitter release of presynaptic neurons is relatively well-known. Such changes in neurotransmitter release as a function of presynaptic neurons' activities can help prevent wasting neural metabolic energy to produce, release and uptake of neurotransmitters through neuronal communication.

There are other simulation method that model neurotransmitter release based on spike timing [33], based on parameters influencing high calcium microdomains [3]. The role of interaction of fast retrograde signalling with Hebbian Plasticity to generate high encoding feedforward neural system has been theoretically studied [12]. In this work, a feedforward neural

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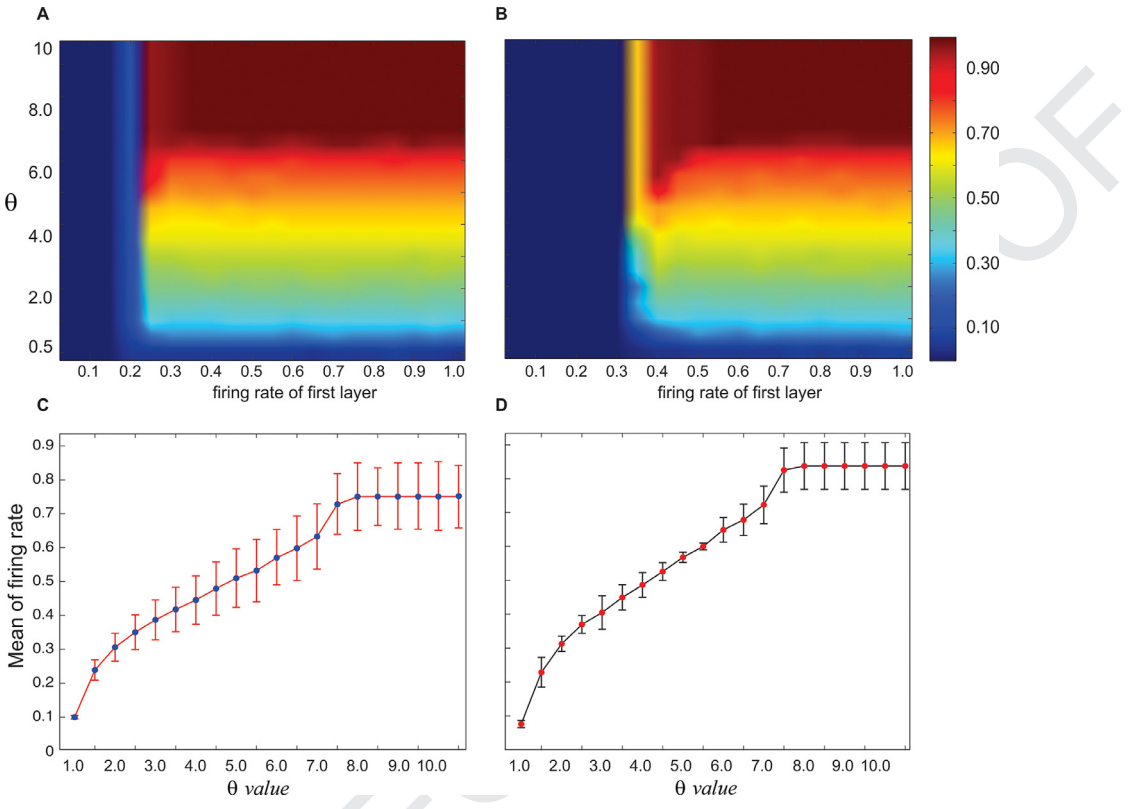

Fig. 8. The firing rate of the motor neurons vs. the firing rate of the first layer and different $\boldsymbol{\theta}$ values at the connectivity rate between the second layer and the motor neurons are equal to 0.9 (**A**) and connectivity is equal to 0.3 (**B**).**C**. Mean of the firing rate of motor neurons vs. different $\boldsymbol{\theta}$ values over firing rate of the first layer between 0.2 and 1.0 for connectivity is equal to 0.9 (**C**) and over 0.35 and 1.0 for connectivity is equal to 0.3 (**D**). The simulations show that different levels of motor neurons spiking rate the systems can be controlled by change in $\boldsymbol{\theta}$ value. $\boldsymbol{K}$ value and $\boldsymbol{M}$ value used in the simulations is equal to 0.01 and 0.2, respectively. $\boldsymbol{\tau}$ equal to 10 is used in all simulations.

network is presented that is able to detect stimuli. The synaptic mechanism that is modelled in the synapses between motor neuron and presynaptic neurons enables the motor neuron to control the levels of input they receive over time. The controlling system acts as a closed-loop system that includes the production of different kinds of retrograde messengers in a postsynaptic neuron in response to influx current and their effect on neurotransmitter release from a presynaptic neuron. In our work, we presented a retrograde signaling based hypothetical mechanism for controlling neurotransmitter release in bio-inspired neural networks constrained by neurobiological data from insects' memory systems. Such changes in neurotransmitter release influence the current into a postsynaptic neuron in each successive time bin. The amount of produced retrograde messenger in response to a given current in a time bin is determined by α parameter. In this study a moderate α value equal to 120 is used in all simulations. However, by changing α values, one can study the role of changes in firing rate of the neural system. Different retrograde messengers have a different rate of diffusion into presynaptic neurons and different speed of affecting the release machinery of the presynaptic neurons.

To our knowledge, this is the first work to model controlling of neurotransmitter release in sparse and burst spiking neurons robust to stimulation changes by a retrograde signalling based closed loop. The role of retrograde signaling from postsynaptic neurons into presynaptic neurons on release probability is known; however, the mechanisms of retrograde signalling's effect on cellular level and at different time scales are not fully known. Inspired by these observations, we developed a neural network model that can be applied in artificial systems including cognitive robotics where spiking neural networks are used to construct simple sensory-perception loops. Although variation in biophysical characteristics of neurons that induce sparse and burst spiking modes and their functional importance are under research, we assumed that retrograde signaling can play a critical role in controlling release probability (and so controlling functional spiking) when the neural system exist in dynamic environment with fluctuating stimulations. Moreover, this assumption and simplified controller developed in this study allows using a bio-inspired neural mechanism in artificial systems in the future.

In this work, in order to exhibit any spiking mode, electrical properties of presynaptic neurons are not affected. Instead, at the synaptic level, the probability of neurotransmitter release changes as a closed loop that modifies 'functional spiking of neurons', which is defined as spikes that trigger neurotransmitter release into the synaptic cleft. This work proposes novel experimental studies on the cellular mechanisms of neural adaptation to changes in stimulation of neurons in short term scale. This helps develop efficient artificial neural systems that exhibit different spiking patterns and able to shift from

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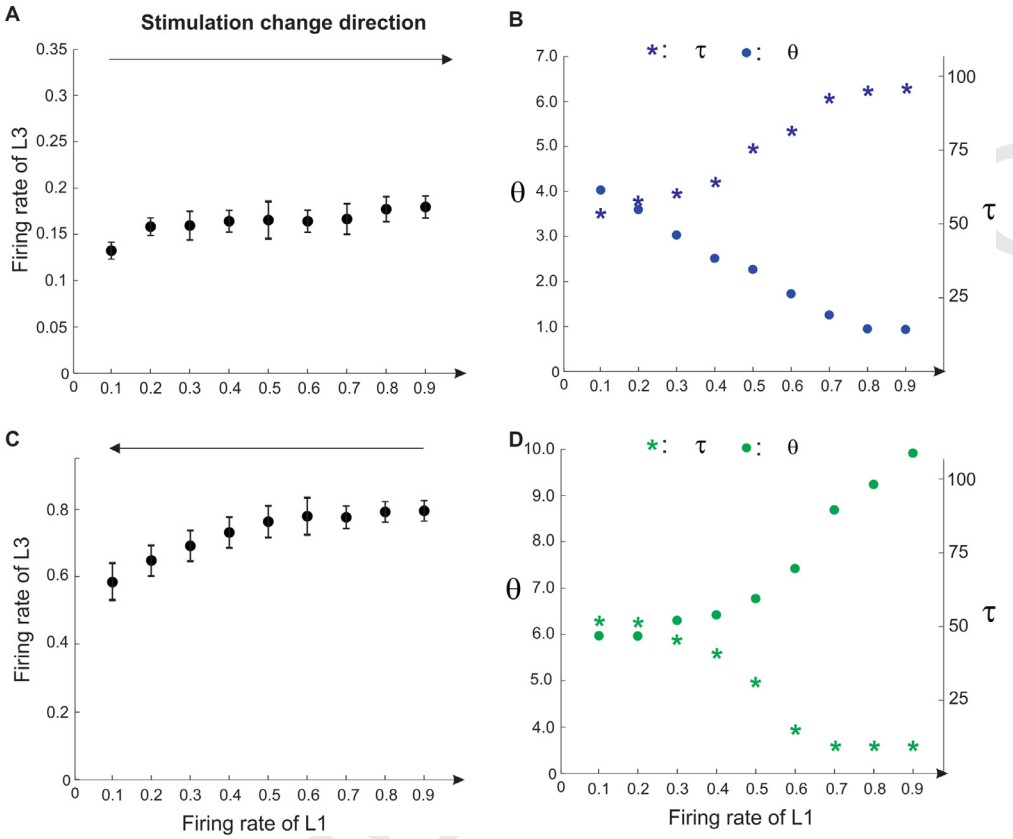

Fig. 9. Robustness of the systems in relation to changes in its stimulation by L_1 neurons (K and M value are set to 0.2). **A.** Sparse spiking activity of L_3 neurons by using optimal parameter conditions shown in **B.B.** Optimal parameter values to obtain minimum change in firing rate of sparse activity of L_3 neuron. At higher levels of stimulation (higher firing rate of L_1 neurons),τ should be increased while an increase in θ is required to keep L_1 firing rate at low values. For low stimulation as initial conditions, τ and θ values are set to 50 and 4, respectively. **C.** Burst activity of L_3 neurons for optimal parameter values shown in **D. D.** Optimal parameter values to obtain minimum change in burst activity of L_3 neuron. At lower levels of stimulation (lower firing rate of L_1 neurons, τ should be increased while a decrease in θ is required to keep L_1 firing rate at high values when stimulation is lowered. For high stimulation as initial conditions, τ and θ values are set to 10 and 10, respectively.

a spiking to a different mode. This simply occurs due to a change in two model parameters τ_{RM} and θ. Therefore, this synaptic closed loop allows for the development of Spiking Neural Networks with self control capabilities to be used in artificial systems including robotics.

The model exerts the biophysical features of retrograde messengers as different levels of τ_{RM} values. The results show that low τ_{RM} values leads to a higher firing rate of motor neurons due to a fast effect as well as a fast decay. But high τ_{RM} values lower firing rate as a consequence of accumulation of induced activity by retrograde messengers in pre-synaptic neurons. However, the neural system may benefits from high τ_{RM} values for long-term memory where the system needs to keep its high or low firing rate over a long time. Another parameter of the model that is involved in information processing of the developed neural system is the threshold of the release machinery (θ). In our model, an increase in threshold value leads to an increase in motor neuron's firing rate for a given ***M*** and ***K*** values and τ_{RM} value equal to 10. In general, high ***M*** and low ***K*** values result in higher motor neuron's firing rate. In the simulations, fixing threshold value and increasing τ_{RM} value resulted in a decrease of motor neurons firing rate. As the neural system showed robustness to fluctuation of firing rate of first layer neurons for a given θ value, Fig. 8 proposes a controlling mechanism of motor neurons' firing rate by changing θ values. If such a neural system is expected to show sparse spiking, it exerts lower θ values while high θ values equipped the neural system with burst spiking activity.

The theory that is presented here is on the mechanism of homeostatic regulation of neurotransmitter release as a probabilistic event by postsynaptic dendrites. It is based on hypothetical protein machinery or biochemical pathway that acts according to its activity level compared to its threshold of shifting increases or decreases in release probability. This study assigns an important role for a molecular mechanism in the neurons that are able to help modify synaptic information flow. Therefore, it proposes experimental investigations to test such hypothesis involved in dendritic computations.

Theoretical studies can help understand neuronal computations using novel models and simulations that can also be used in developing artificial spiking neural systems. One of the challenges in developing next generation of artificial systems (e.g.

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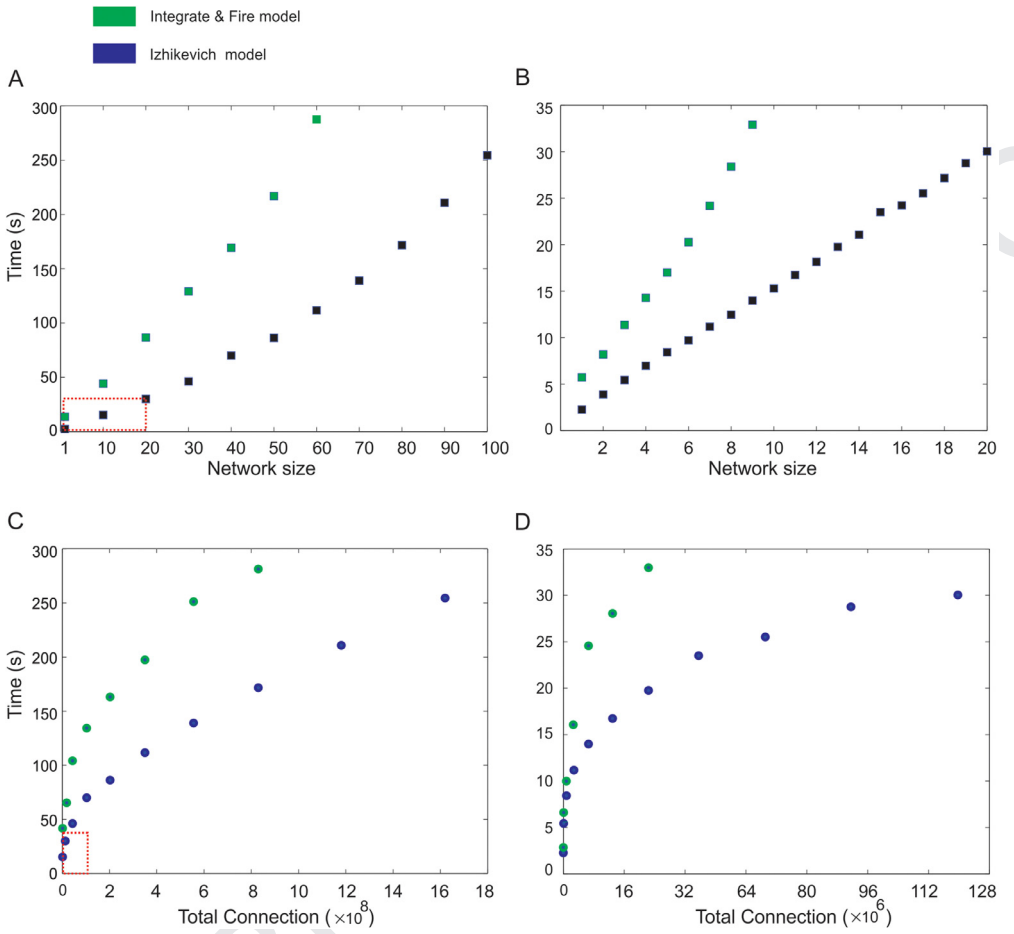

Fig. 10. Numerical results on the computational complexity of the model to study the impact of neuron model used in simulations. Integrate and fire vs. Izhikevich models are compared. The time of running algorithm for a given set of parameter values versus network size and network connections are shown in **(A, B)** and **(C, D),** respectively. Initial size of the network in all simulations is 10, 60 and 10 neurons in L_1, L_2, and L_3, respectively. The connectivity rate of L_1-L_2 and L_2-L_3 is set to 0.9 and 0.3, respectively. **A.** Network size is between 1 and 100 times initial size of the network and between 1 and 20 in **B**. Time of running program is measured versus total number of connection of layers for whole network size (**C**) and network size between 1 and 20 (**D**). The results show that compared to the Izhikevich model, the Integrate and Fire model can lead to a lower running time of the algorithm.

navigating robots) is how to implement the efficiency of animals' brain in encoding complex environments enriched with different kinds of stimuli that should be detected, encoded and stored in the neural networks [37]. Therefore, one fundamental step to generate new artificial systems would be to understand basic information processing in neural circuits underlying behavior (e.g. learning tasks). This includes understanding molecular, cellular, synaptic and network level mechanisms. This study is aimed to illustrate the potential of developing bio-inspired neural systems that are equipped with simplified synaptic communication in biological neurons. One challenge for developing a class of spiking neural networks is how to implement a simplified model of complicated cellular mechanisms in biological neurons. For this purpose, we propose to investigate the possibility of new classes of bio-inspired neural networks that are highly similar to biological neural systems.

The structural and physiological parameters in biological neural systems determine their capability to exhibit cognitive functions like learning and memory. The existence of different mechanisms of information processing strongly depends on the brain region and neuron type. Combining different mechanisms at different levels (molecular, synaptic, cellular and network)across different time scales of an event into models, may play an important role in exploring neural circuits of different cognitive capabilities of animals' brains. For example, neural systems may gain benefits from STDP and Hebbian mechanisms in combination with retrograde signalling based mechanisms. However, it is necessary to develop simulations using integrated mechanisms in different paradigms to explore the importance of such combined mechanisms. The work presented here can enhance our understanding of complex strategies that have been developed through evolution and used by the human and animal brain for information processing and intact behaviour.

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5. Conclusion

Brain-like artificial architectures using spiking neural networks (SNN) have many industrial applications including cognitive robotics [39]. To achieve this goal the main challenge is to understand morphological and electrophysiological variations observed in biological neural networks. Studying the cellular and synaptic mechanisms and function of sparse and burst neuronal activities play critical role in understanding how information is transformed in brains.

By exploring the role of neuronal architecture and information processing of different neural systems, biologically plausible brain-like artificial systems can be developed in future.

In this work some synaptic and cellular and network knowledge on biological systems are used to develop a feedforward neural system that is capable to control the functional activity of its neurons in different levels of environmental stimulation. Simplified mechanisms implemented in this work allow industrial application of the model and propose some possible mechanisms in neurons to investigate as well.

This work proposes novel experimental studies on the role of retrograde signaling in short time scale on the controlling of neurotransmitter release of presynaptic neurons by postsynaptic neurons. This work presents a cellular hypothesis on how neurons exhibit persistent sparse or burst spiking activity by changing their probability of neurotransmitter release in synapses.

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