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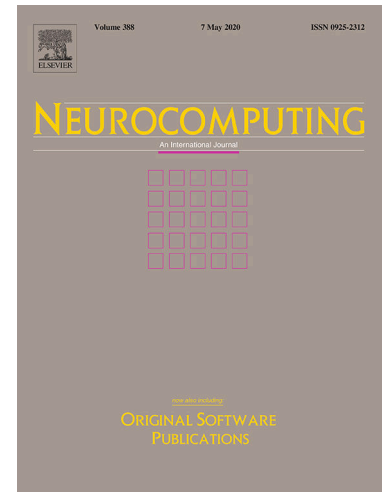
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PII: S0925-2312(20)30939-5
DOI: <https://doi.org/10.1016/j.neucom.2020.05.088>
Reference: NEUCOM 22407

To appear in: *Neurocomputing*

Received Date: 13 February 2020
Accepted Date: 29 May 2020



Please cite this article as: H. Tan, L. Wang, Interaction of neuronal and network mechanisms on firing propagation in a feedforward network, *Neurocomputing* (2020), doi: <https://doi.org/10.1016/j.neucom.2020.05.088>

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Interaction of neuronal and network mechanisms on firing propagation in a feedforward network

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ARTICLE INFO

Keywords:

Feedforward network
Neuronal diversity
Spiking propagation
Izhikevich neuron

ABSTRACT

The mammalian brain has enormously complex neuronal diversity and a highly modular structure. The propagation of information in the modular brain network can be modeled by a feedforward network (FFN). Although studies in this area have yielded many important results, neuronal diversity has rarely been considered. In the current work, we investigate the complex interactions between the intrinsic properties of neurons and the FFN structure in the propagation of spiking activity. Here, four typical types of cortical neurons reproduced by the Izhikevich neuron model are introduced. A homogeneous FFN composed of a single type of excitatory neuron (regular spiking, mixed model, or tonic bursting) can propagate spiking activity. However, an FFN with fast spiking neurons does not propagate spiking activity. By modifying the network structure and synaptic weights, the spiking propagation of the homogeneous FFNs can vary from synchronous transmission (with a high firing rate) to asynchronous transmission (with a low firing rate). Among the homogeneous FFNs, both the firing rate and the synchrony of the FFN with tonic bursting neurons are the highest, but those of the FFN with regular spiking neurons is lowest, even when implementing the same FFN structure. For the FFN with mixed neuronal types, interestingly, the spiking propagation is very sensitive to the composition of the four types of neurons. By introducing fast spiking neurons into the homogeneous FFN composed of excitatory neurons, spiking propagation can be modified from synchronous to asynchronous. Similarly, changing the proportion of any of the types of neuron affects the spiking propagation, even for very small changes. The underlying mechanism of these observed results has also been discussed.

1. Introduction

Neurons convert a stimulus from the external environment or signals from upstream neurons into a train of action potentials (spikes), which are believed to be the fundamental process in the realization of brain function. The brain is the most complex organ in the human body, consisting of approximately 100 billion neurons. In the brain, neurons exhibit great diversity in their shapes and functions [1, 2]. Triggered with an external stimulus, different neurons respond with different firing patterns. Based on the firing patterns observed by intracellular recordings, neurons in the mammalian brain can be divided into various types [3, 4]. Regular spiking, tonic bursting and fast spiking neurons are typical neurons that were discovered in in vivo physiology and laminar network anatomy experiments [3, 5]. In the subiculum, different pyramidal neurons can generate regular spiking and bursting spiking patterns [6]. Neuronal diversity contributes to the emergent properties of neural networks and, consequently, plays an important role in information processing in the nervous system [7, 8, 9]. Therefore, studies about the activities of the neuronal network of a brain region should take into account intrinsic behavioral diversity both within and between neuron types.

Moreover, the nervous system is a highly modular structure [10]. Information processing in the nervous system is related to different functional groups of neurons, by which

the information is transferred from one group to its downstream connected groups [11]. Thus, conditions under which spiking activity can be propagated among the neuronal groups are a crucial issue for information processing in the modular brain. In the last decade, a multilayer feedforward network (FFN) has been introduced to exploit the issue.

Multilayer FFNs, which provide important insights into the mechanisms of cortical computation, can mimic the properties of the propagation of spiking activity. Each layer of the network is related to a functional group of neurons, in which neurons in one group receive inputs from many neurons in the previous group, and thus the information is transmitted from one group to the next [11]. Recently, several computational studies have identified two dynamic activity modes that support the propagation of rate coding and temporal coding in the FFN [12, 13, 14]. When neurons in the first layer are subject to white noise, firing rate can be propagated in an FFN by the synchronized firings of Hodgkin-Huxley (HH) neurons [15, 16]. When weak signals are input to the neurons in layer 1, successive layers are able to propagate and amplify the signals while the neurons are subject to intrinsic or external noise above a certain level [17, 18]. Current computational studies also reveal that the propagation of spiking activities in an FFN depends on the interlayer connection probability, synaptic intensity, noise, and input signals [15, 16, 19, 20, 21]. Nevertheless, the diversity of neurons is rarely considered in studies of FFNs. Thus, it is not yet clear that the behaviors of spiking activity propagating within an FFN consider the intrinsic electrical properties of different neuronal types.

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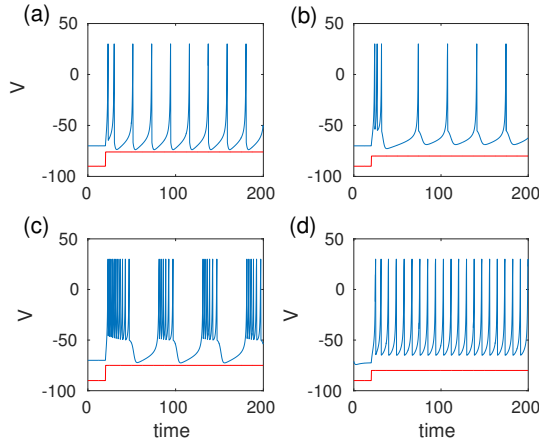


Figure 1: Four typical cortical neuron spiking patterns reproduced by the Izhikevich neuron model. Blue lines show the membrane potential and red lines represent the step of DC stimulus. The spiking patterns of excitatory neurons are related to (a) regular spiking [$a=0.04$; $b=0.2$; $c=-65$; $d=10$], (b) mixed model [$a=0.02$; $b=0.2$; $c=-55$; $d=4.5$] and (c) tonic bursting [$a=0.02$; $b=0.2$; $c=-50$; $d=2$]. The spiking pattern of inhibitory neuron is related to (d) fast spiking [$a=0.15$; $b=0.17$; $c=-65$; $d=2$].

As mentioned earlier, neuronal diversity plays a crucial role in information processing in the nervous system. In the mammalian brain, the diversity of neuronal and nonneuronal cell types guarantees the execution of high-order cognitive, sensory, and motor behaviors [22]. Networks with diverse neuronal types offer superior decoding ability compared with homogeneous networks [23]. In a hybrid coupled neural network, it was shown that different types of population spiking patterns can emerge [24] and strongly synchronized population spiking events lead to complete activity cessation [25], by changing the types of connections in the network. It has also been found that increasing the diversity of intrinsic neuronal types can enhance the encoding performance of neuronal populations [26]. Andrew Bogaard et al. found that the response of a neuronal network is strongly affected by intrinsic neuronal properties and that the introduction of a small number of cells with different excitability properties can profoundly influence the spatiotemporal activity of the neural network [27].

Considering the importance of neuronal diversity in the nervous system, the effect of the intrinsic electrical properties of different neuronal types on the propagation of spiking activity in an FFN is addressed in the current work. This paper is organized as follows. In Sec. 2, the neuronal model, the FFN connections and the simulation methods are introduced. Simulation results are shown in Sec. 3. The conclusions and discussion are presented in Sec. 4.

2. Model and method

Incorporating the biological dynamics of Hodgkin-Huxley neuron and the computational efficiency of integration and

firing neuron, Eugene M. Izhikevich developed a simple spiking neuron model and its dynamical equations are given as [28],

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I^{ext}, \quad (1)$$

$$\frac{du}{dt} = a(bv - u). \quad (2)$$

with the auxiliary after spike resetting:

$$\text{if } v \geq 30mV, \text{ then } \begin{cases} v \leftarrow c, \\ u \leftarrow u + d. \end{cases} \quad (3)$$

here, v is the membrane potential and u is a membrane recovery variable representing ionic currents of inactivation Na^+ and activation K^+ . The variable I^{ext} is external stimulus. This model is computationally efficient enough to simulate behaviors of thousands of neurons and the patterns of all known types of cortical neurons with the choice of parameters a , b , c , and d . The most typical spiking patterns of the cortical neurons reproduced by the Izhikevich model are given in Fig. 1. Injected with a step of DC current, most cortical neurons, namely the regular spiking neurons, fire spikes with short interspike period and then the period increases, as in Fig. 1 (a). Fig. 1 (b) shows the firing pattern of a stereotypical burst of spikes followed by repetitive single spikes, which can be observed in intrinsic bursting neurons of mammalian neocortex [3]. Some neurons, eg. the pyramidal neurons in layer II/III [29], generate repetitive high frequency bursts of spikes referred to tonic bursting, as in Fig. 1 (c). Fast spiking neurons, as shown in Fig. 1 (d), are always inhibitory in mammalian neocortex and fire periodic action potentials with high frequency. It is noted that those four typical spiking patterns of the cortical neurons are chosen in the following studies. The fast spiking neuron is inhibitory, but others are all excitatory. The values of parameters a , b , c , and d are give in the caption of Fig. 1.

In the current study, a 10-layer feed-forward network is constructed and each layer contains 200 Izhikevich neurons. There are no connections among the neurons in the same layer. Each neuron receives synaptic inputs randomly from neurons in the previous layer. The interlayer connection probability P_{layers} is set as a free parameter. The dynamics of the multilayer network can be described by,

$$\frac{dv_{l,i}}{dt} = 0.04v_{l,i}^2 + 5v_{l,i} + 140 - u_{l,i} + I_{l,i}^{ext} + I_{l,i}^{syn} + \xi_{l,i}(t), \quad (4)$$

$$\frac{du_{l,i}}{dt} = a(bv_{l,i} - u_{l,i}). \quad (5)$$

where, $v_{l,i}$ and $u_{l,i}$ are the membrane potential and the recovery variable of the i th neuron in layer l , respectively. $I_{l,i}^{ext}$ is treated as a sub-threshold base current only subjected to the neuron in first layer ($I_{1,i}^{ext}=0.6$ and $I_{2\sim10,i}^{ext}=0$). The Gaussian white noise $\xi_{l,i}(t)$ is delivered only to layer 1 and satisfies $\langle \xi_{l,i}(t) \rangle = 0$ and $\langle \xi_{l,i_m}(t_1)\xi_{l,i_n}(t_2) \rangle = 2D_l\delta_{m,n}\delta(t_1-t_2)$. D_l is the noise intensity of layer l ($D_1=4$ and $D_{2\sim10}=0$). It noted

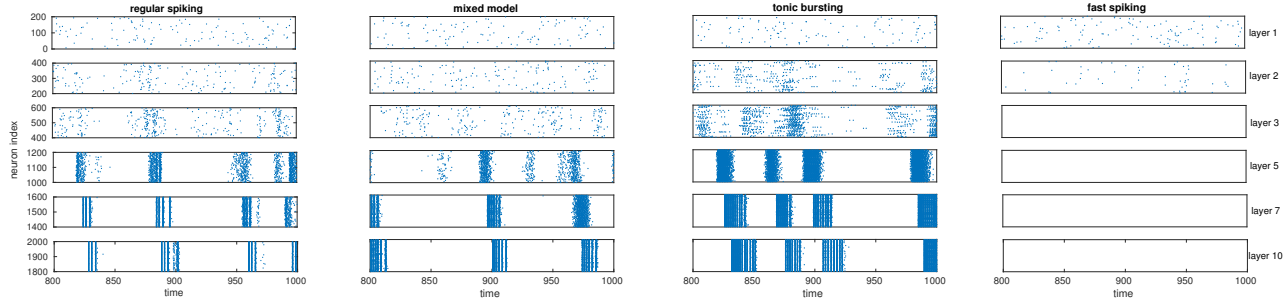


Figure 2: Raster plots showing the spiking propagation in the homogeneous FFN composed of a single type of excitatory neuron (regular spiking neuron, mixed model neuron, tonic bursting neuron, and fast spiking neuron). The parameter values are as follows: $g_{syn}=0.2$, $P_{layers}=0.05$.

that the sub-threshold base current I_{ext} can be set as zero, which is only used to make action potential generation easier with the noise in the first layer. Thus, noise is present only to make the neurons in the first layer to produce random action potentials.

The synaptic current $I_{l,i}^{syn}(t)$ between neurons in the neighbor layers is described as follow,

$$I_{l,i}^{syn}(t) = \frac{-1}{M} \sum_{j=1}^M g_{syn} \alpha(t - t_{l-1,j}) (V_{i,j} - V_{syn}), \quad (6)$$

with

$$\alpha(t) = (t/\tau) \exp(-t/\tau). \quad (7)$$

where, M is the number of neurons in layer $(l-1)$ connected to the (l, i) th neuron. g_{syn} is synaptic weight. $\tau=2$ ms is the rising time of synaptic input, also known as synaptic time constant. $t_{l-1,j}$ represent the firing of j th pre-synaptic neuron in layer $(l-1)$ coupled with (l, i) th neuron. V_{syn} is synaptic reversal potential determining the type of synapse (if the synapse is excitatory synapses, $V_{syn}=0.0$; if it is inhibitory, $V_{syn} = -80.0$).

It is noted that the base current and noise are only injected into the neurons in the first layer. The layer 10 is considered as the output layer. The noise intensity of the first layer is set as $D_1=4$ and that of other layers is set as zeros. The connection of neurons between two adjacent layers is random with the probability P_{layers} . Differential equations above are solved by the Euler method and the Gaussian white noise is generated by the algorithm introduced by Fox et al. [30].

Here, two important aspects of the feedforward neural network were considered: (i) the firing rate r_l of each layer, which is an average of all fires of all neurons in layer l . (ii) synchronization index of each layer K_l , which is an average cross-correlation of firing time of neurons. The synchronization index K_l is defined as averaging a pair coherence $K_{l,i,j}(\gamma)$ between neuron i and j over all neural pair in l th layer,

$$K_l = \frac{1}{M(M-1)} \sum_{i=1}^M \sum_{j=1, j \neq i}^M K_{l,i,j}(\gamma), \quad (8)$$

where,

$$K_{l,i,j}(\gamma) = \frac{\sum_{m=1}^k X(m)Y(m)}{\sqrt{\sum_{m=1}^k X(m) \sum_{m=1}^k Y(m)}}. \quad (9)$$

$K_{l,i,j}(\gamma)$ is measured by the cross correlation of spike trains at zero time lag within a time bin γ . The simulation time span T_{span} is divided into k bins of $\gamma=1$ ms. The spike train of neurons i and j are given by $X(m) = 0$ or 1 and $Y(m) = 0$ or 1 ($m = 1, \dots, k$), where 1 denotes a spike occurring in the bin and 0 otherwise.

3. Simulation results

Since the basic neuronal dynamics and the FFN structure have been introduced, we first study the spiking activities propagating in the FFN with a single type of neuron and then investigate the propagation in the FFN with a mixture of neuronal types.

3.1. Spiking activity propagation in an FFN with a single neuronal type

In the current section, we explore the effects of different neurons and network topology on activity patterns in homogeneous networks composed of only one neuronal type. The raster plots shown in Fig. 2, reveal that the spiking activities can be propagated in an FFN with appropriate synaptic weights g_{syn} and interlayer connection probability P_{layers} . Since Gaussian white noise is input to layer 1 neurons, each neuron fires spikes randomly. For an FFN constructed with regular spiking neurons, mixed model neurons and tonic bursting neurons, the spikes that fire in layer 2 and layer 3 always do so randomly, but the number of spikes is greater than in layer 1, which implies that the firing rate also increases in those layers. We can observe a tendency of synchrony and the formation of blurry spike columns in layer 3. These properties are clearer for tonic bursting neurons than for the other two types of neurons. As the spikes continue to propagate, such as to layer 5 in Fig. 2, several distinct columns of spikes start to form. As spiking activity further propagates, synchronous firing is established in the deepest layer. The raster plots also indicate that the widths of the synchronous

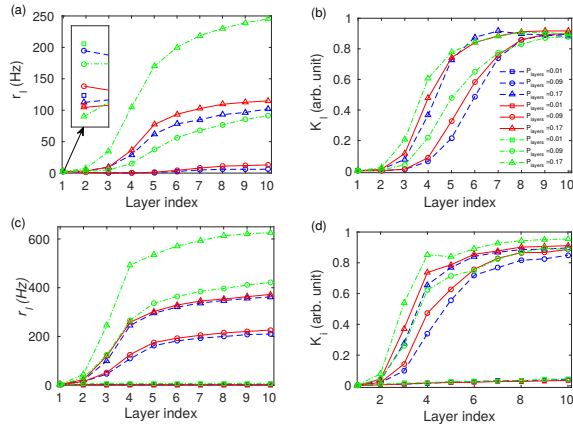


Figure 3: Firing rate [(a),(c)] and synchronization index [(b),(d)] versus layer l for different interlayer connection probabilities P_{layers} . The blue dashed lines indicate the results from FFNs with regular spiking neurons; the solid red lines indicate the results from FFNs with mixed model neurons; and the green dash-dot lines indicate the results from FFNs with tonic bursting neurons. $P_{layers}=0.01$ are marked with \square ; $P_{layers}=0.09$ are marked with \circ ; $P_{layers}=0.17$ are marked with \triangle . Synaptic weight: $g_{syn}=0.1$ for (a) and (b); $g_{syn}=0.3$ for (c) and (d). The inset plot in (a) is an enlarged plot of the firing rate of the first layer.

firing columns for the tonic bursting neurons are the largest among the different neural types.

However, for the FFN constructed by fast spiking neurons [right-hand-most column, Fig. 2], fewer spikes are produced in layer 2 than in layer 1, and the neurons do not fire spikes at all in layer 3. That is, the spiking activities cannot be propagated through the FFN when it consists only of fast spiking neurons. Such results can be attributed to the inhibitory synaptic connections among the spiking neurons.

For the three types of excitatory neurons (regular spiking neurons, mixed model neurons and tonic bursting neurons), the propagation of the spiking activity could be modeled in the FFN with proper parameters. It would be interesting to understand how the network structure and connections affect the spiking activity of the FFN for the three types of excitatory neurons. Thus, the firing rate r_l and synchronization index K_l for different synaptic weights g_{syn} and interlayer connection probabilities P_{layers} were calculated. Stronger synaptic weights and higher interlayer connection probabilities were shown to better facilitate synchronous spiking propagation and enhance the firing rate. When the synaptic weights are weak, spikes cannot be propagated by FFNs with low interlayer connection probabilities. As shown in Fig. 3 (a) ($g_{syn}=0.1$), the FFNs with interlayer connection probability $P_{layers}=0.01$ do not propagate the randomly generated spikes that were induced in layer 1 [as indicated by the unconnected square markers in the inset plot]. The synchronization is meaningless for a zero firing rate, so no lines of synchronization for $P_{layers}=0.01$ can be plotted in Fig. 3 (b).

Increasing the interlayer connection probability P_{layers} to 0.09, the spike activities can be propagated within the

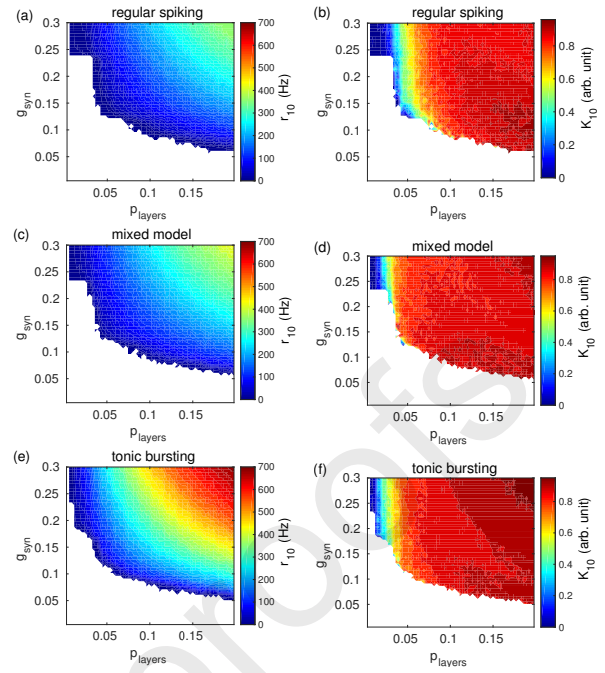


Figure 4: Color maps show the firing rate r_l and the synchronization index K_l in layer 10 versus synaptic weight g_{syn} and interlayer connection probability P_{layers} . The results are plotted for regular spiking neurons in (a) and (b), mixed model neurons in (c) and (d) and tonic bursting neurons in (e) and (f).

FFN with a very low firing rate. However, the corresponding synchronization index K_l increases layer by layer and finally saturates, as shown in Fig. 3 (b). This reveals the importance of network connections, in that the firing activities synchronously propagate within FFNs with even very low firing rates. The firing rates of bursting neurons increase rapidly and to much larger levels than those of the other two types of neurons. By further increasing the interlayer connection probability ($P_{layers}=0.17$), the propagated firing rates and the corresponding synchronization indexes are increased for all types of excitatory neurons. When the synaptic weights are strong, as shown in Fig. 3 (c) and (d), the spiking activities can be propagated within FFNs with low interlayer connection probabilities ($P_{layers}=0.01$), although with very low firing rates. The corresponding synchronicity is also very poor throughout the entire network. These results reveal that the spiking activities asynchronously propagate in networks with low firing rates. Increasing the interlayer connection probability enhances the firing rate and synchronicity propagation. The firing rate and synchronization of FFNs consisting of tonic bursting neurons are obviously larger than those of FFNs consisting of the other two types of excitatory neurons.

To systematically show the influence of network properties in the propagation of neural activity in FFNs with different types of neurons, color maps of firing rate and synchronization index are shown in Fig. 4. As the synaptic weight g_{syn} and interlayer connection probability P_{layers} change, the

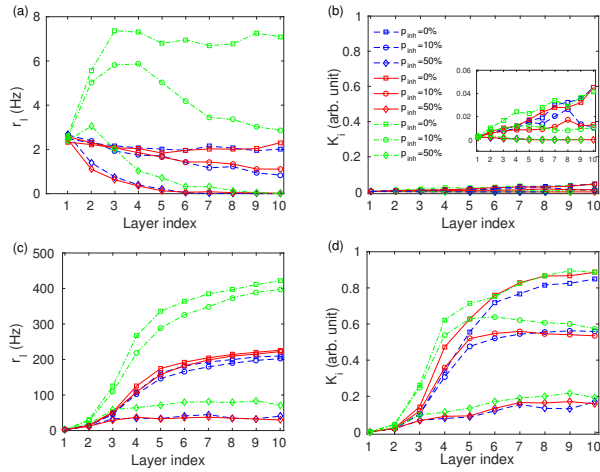


Figure 5: Firing rate r_l [(a),(c)] and synchronization index K_l [(b),(d)] versus layer l after introducing inhibitory fast spiking neurons to homogeneous excitatory FFNs. The different line styles indicate the results from FFNs with different types of neurons: regular spiking neurons (blue dashed lines), mixed model neurons (red solid lines) and tonic bursting neurons (green dashed-dotted lines). Different markers indicate different proportions of fast spiking neurons introduced: 0% (\square), 10% (\circ) and 50% (\diamond). The interlayer connection probability is set to 0.01 (upper panels) and 0.09 (bottom panels). The synaptic weight is 0.3 for all panels.

FFNs exhibit different behaviors of spiking activity propagation. In the region with low synaptic weight g_{syn} and interlayer connection probability P_{layers} [the blank areas of Fig. 4], the firing rate of layer 10 is zero, which means that the spiking activity cannot be propagated for these parameters. Consequently, the corresponding synchronization indexes of those areas cannot be calculated because there is no spike propagation in this layer. For FFNs with large synaptic weights g_{syn} and interlayer connection probabilities P_{layers} , both the firing rate and synchronization index are very high. This reveals that FFNs with such parameters can propagate the spiking activity synchronously and at a high firing rate. When the interlayer connection probability is low, FFNs with strong synaptic weight can propagate spiking activity at a low firing rate. The corresponding synchronization index is also very low. That is, FFNs can desynchronize the propagation of neural activity in this case. It is also interesting that the spiking activities synchronously propagate on FFNs with low firing rates when the synaptic weights are relatively small but the interlayer connection probability is relatively large. For FFNs constructed with any of the three types of excitatory neurons, these results are similar to each other. However, the ranges of the firing rates are different: the propagated firing rates of tonic bursting neuron FFNs are largest (r_{10} greater than 600 Hz), but those of regular spiking neuron FFNs are smallest (r_{10} less than 350 Hz). Moreover, as the FFN neuronal type changes from regular spiking to mixed model and finally to tonic bursting, the area of low synchronization index is reduced.

3.2. Spiking activity propagation in FFNs with multiple neuronal types

To further understand the effect of different neuronal types on the propagation of spiking activity in an FFN, we first introduce fast spiking neurons to homogeneous excitatory FFNs and then mix the four kinds of typical spiking neurons into a single FFN.

3.2.1. Introduction of fast spiking neurons to homogeneous excitatory FFNs

In this section, the synaptic weighting is chosen as $g_{syn}=0.3$, and the neural network is allowed to transmit spiking activity synchronously and asynchronously by changing the interlayer connection probability P_{layers} for homogeneous FFNs composed of the three excitatory neuron types. The fast spiking inhibitory neurons are randomly introduced into each layer with probability P_{inh} .

Fig. 5 gives the firing rates and synchronization indexes of homogeneous FFNs with different proportions of fast spiking inhibitory neurons. When the interlayer connection probability is low [such as $P_{layers}=0.01$ in Fig. 5 (a) and (b)], the spiking activity asynchronously propagates within FFNs with a low firing rate. Once fast spiking inhibitory neuron is introduced, the firing rate is decreased. When the proportion of fast spiking neurons is sufficiently large, the propagation of spiking activity within the FFN is blocked. Homogeneous FFNs composed of regular firing neurons are more likely to be blocked by introducing fast firing neurons.

When the interlayer connection probability is high, the spiking activity synchronously propagates within the FFNs at high firing rates in the absence of fast spiking neurons [see lines $P_{inh} = 0\%$ in Fig. 5 (c) and (d)]. As the number of introduced fast spiking inhibitory neurons increases, both the firing rate and the synchronization index decrease. That is, the firing rate propagated within the FFN can be effectively regulated by changing the proportion of fast spiking inhibitory neurons. For example, the firing rate of the output layer (layer 10) is approximately 422 Hz without fast spiking neurons but can be greatly reduced by changing the neurons to the fast spiking variety, as shown in Fig. 5 (c). Moreover, the propagation within the FFN will also be adjusted from synchronous transmission to asynchronous transmission by the introduction of fast spiking neurons, as shown in Fig. 5 (d).

The color maps in Fig. 6 illustrate the firing rates and synchronization indexes of layer 10 as a function of both the proportion P_{inh} of introduced fast spiking inhibitory neurons and the interlayer connection probability P_{layers} of the FFN. When the interlayer connection probability is very small [the blank areas of the color maps in Fig. 6], the spiking activity cannot be propagated to the deep layers of the FFN. Thus, there is no firing rate or synchronization index for the parameters in the blank areas. By increasing the interlayer connection probability, the spiking activity can propagate within the FFN. Both the firing rate and the synchronization index increase with the interlayer connection probability. However, the firing rate and the synchronization index decrease when

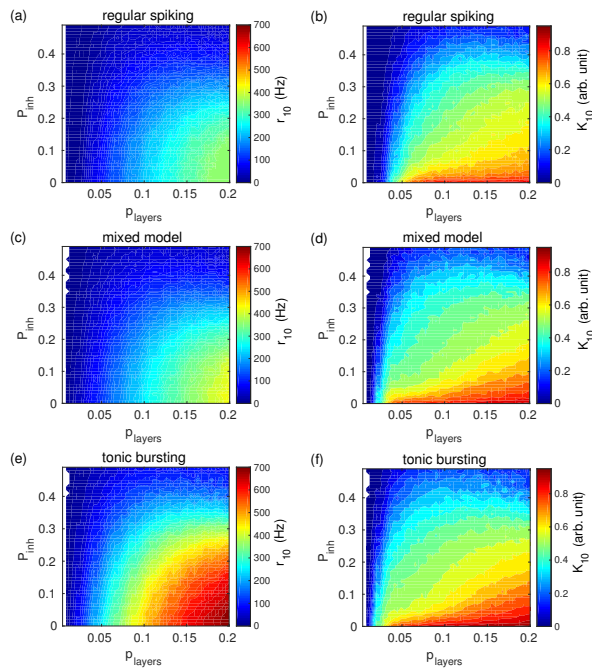


Figure 6: Color maps show the firing rate r_l and the synchronization index K_l of layer 10 versus both the proportion P_{inh} of introduced fast spiking inhibitory neurons and the interlayer connection probability P_{layers} . The results are plotted for regular spiking neurons in (a) and (b), mixed model neurons in (c) and (d) and tonic bursting neurons in (e) and (f).

the proportion of introduced fast spiking inhibitory neurons increases. Obviously, to achieve synchronous propagation of the spiking activity, a higher interlayer connection probability and a smaller proportion of introduced fast-spiking neurons are required. To achieve asynchronous transmission, a smaller interlayer connection probability and a larger proportion of introduced fast-spiking neurons are required. The FFNs with tonic bursting neurons exhibit higher firing rates than those with mixed model neurons and regular spiking neurons after introducing the same proportion of fast firing neurons.

3.2.2. Mixture of the four types of typical spiking neurons in a FFN

In this section, we mixed the four types of typical spiking neurons in an FFN. Here, all four types of neurons are randomly distributed in each layer of the FFN. The probability of fast spiking neurons P_f is set to a constant 10% in each layer. The proportion of mixed model neurons P_m in each layer varies: 0%, 10%, 30%, and 50%. The proportion of tonic spiking neurons P_t is related with the proportion of regular spiking neurons P_r as follows: $P_r = 1 - P_m - P_t - P_f$.

Given the above hybrid scheme of neuronal types, Fig. 7 shows the firing rate (upper panels) and synchronization index (lower panels) versus the layer index. It is clear that the propagation of spiking activity is sensitive to the composition of the four types of neurons in the FFN. In Fig. 7 (a) and (e), the probability of mixed model neurons P_m is set

to zero, which means that the FFN is composed of fast firing neurons, tonic bursting neurons, and regular firing neurons. Since the amount of fast spiking is set to a constant 10%, there is a greater proportion of tonic bursting neurons than regular firing neurons. As the proportion of tonic spiking neurons increases, the firing rates propagated within the FFN increase, even for a small percentage of tonic spiking neurons. Similarly, the firing rate of the FFN decreases as the proportion of regular spiking neurons increases. On the whole, regardless of the proportion of tonic bursting neurons or regular spiking neurons in the FFN network, the propagation of the firing rate within the FFN is between that of the FFN solely composed of tonic spiking and fast spiking neurons and that of the FFN solely composed of regular spiking and fast spiking neurons. Although the behaviors of the propagation of synchrony are not greatly affected by the increase in tonic spiking neurons, the synchrony of the early layers is enhanced, while that of the deep layers is weakened. Moreover, increasing the proportion of tonic bursting neurons in the mixed-neuron FFN does not yield a synchronization index higher than that of the FFN solely composed of tonic spiking and fast spiking neurons.

From the left column to the right column of Fig. 7, the proportion of mixed model neurons in the FFN is increased. Increasing the proportion of mixed model neurons has no notable effect on the behavior of the propagation of spiking activity within the FFN as the proportion of tonic spiking neurons increases. However, the range and magnitude of the firing rates substantially decrease as the proportion of mixed model neurons increases. It should be noted that an increase in the proportion of fast spiking neurons could decrease the firing rates and synchrony of the spiking activity propagation and regulate the spiking propagation from synchronous to asynchronous (these data are not explicitly shown here, but can be observed in Figs. 5 and 6.).

4. Conclusion and Discussion

The mammalian nervous system is a laminar structure containing many areas and neuronal types that form a complex neuronal network [31]. Information propagates within and across the many networks, which could be easily simulated through an FFN [11]. There are many anatomical pieces of evidence for the rationality of FFN, such as the sequential brainstem nuclei in sensory pathways or the cortical layers through which thalamic inputs from layer IV propagate [32]. In the last decade, several computational studies have addressed the issue of spiking activity propagation in FFNs and have identified the propagation of either asynchronous (rate code) or synchronous (temporal code) spiking [11, 14, 15]. Moreover, the brain has a great variety of neurons, which differ from each other dramatically in their patterns of action potentials. In cortex layers 2, 3 and 5 of adult rats, three types of neurons (regular spiking, burst spiking, and fast spiking) have been identified in the different layers [33]. However, the physiological fact of neuronal variety has not been considered in the research of information prop-

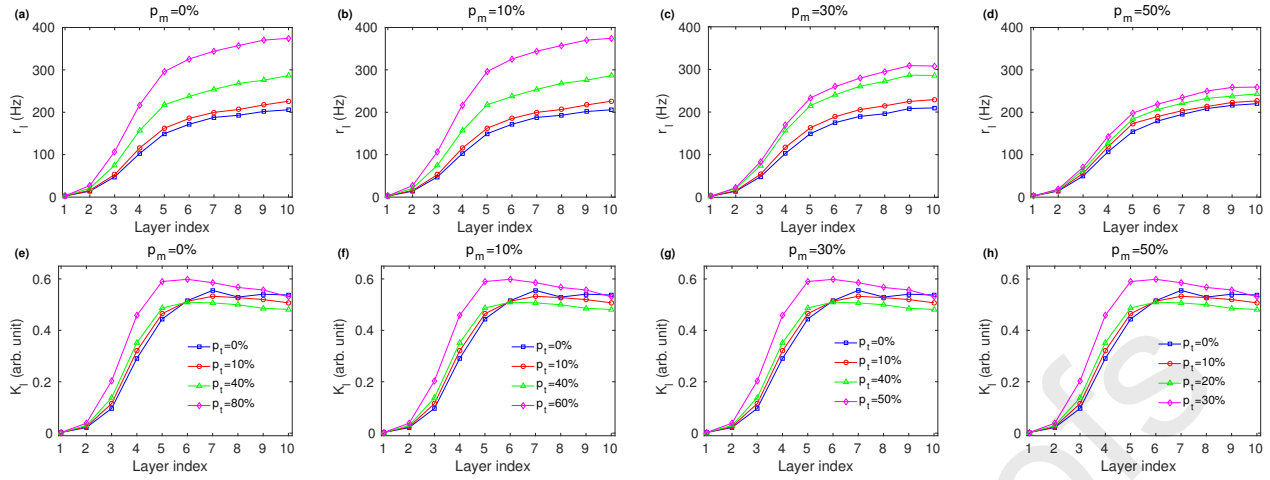


Figure 7: Firing rate r_i [(a),(b),(c),(d)] and synchronization index K_i [(e),(f),(g),(h)] versus layer i for heterogeneous FFNs with different mixtures of the four types of typical spiking neurons. In the FFNs with mixed neuronal types, the proportion of fast spiking neurons P_f in each layer is set to a constant 10%; the probability of mixed model neurons P_m in each layer is set to 0% [(a) and (e)], 10% [(b) and (f)], 30% [(c) and (g)], and 50% [(d) and (h)]; and the probability of regular spiking neurons P_r and the probability of tonic spiking neurons P_t are interrelated ($P_t=1-P_m-P_r-P_f$). The synaptic weight is 0.3.

agation within the FFN. The spiking activities transmitted through FFNs constructed with different types of neurons is still under debate. In the current work, we have addressed such issues and obtained some general results.

Four typical cortical neuron spiking patterns reproduced by the Izhikevich neuron model were introduced in an FFN. The homogeneous FFNs constructed by each of three types of excitatory neurons (regular spiking neuron, mixed model neuron, and tonic bursting neuron) can propagate spiking activities. However, the FFN constructed solely of fast spiking neurons cannot propagate spiking activity to the deep layers due to the inhibitory connections between the neurons. By changing the network structure and connection strengths, the spiking propagation of homogeneous FFNs (for all three types of excitatory neurons) varies from synchronous transmission with a high firing rate to asynchronous transmission with a low firing rate. In the same FFN, the firing rates of tonic bursting neurons are largest and those of regular spiking neurons are smallest. Moreover, as the network structure and connection strengths change, the resulting range of firing rates of tonic spiking neurons is the widest. In the FFN with mixed neuronal types, the propagation of spiking activity is sensitive to the proportions of the four types of neurons in the network. After fast spiking neurons are introduced to the homogeneous excitatory neuron FFNs, the spiking could be regulated from synchronous to asynchronous. Similarly, changing the proportion of any of the types of neuron affects spiking propagation could be affected, even for very small changes.

The underlying mechanism of the observed results can be understood as follows. To activate the firing of action potentials in the FFN, a fast-rising synaptic stimulation is needed to depolarize the membrane potential to reach the threshold potential $V_{threshold}$ (for Izhikevich neurons, the threshold potential $V_{threshold}=30$ mV). When the synaptic input

signals from different presynaptic neurons arrive at the same time, the postsynaptic membrane potential can easily reach the threshold potential to generate action potentials. The neurons in the network operate as evidence detectors and are sensitive to the exact timing of synaptic inputs from multiple presynaptic neurons [15]. As the layer index increases, the temporal correlation of the multiple synaptic inputs received by the neurons increases. The neurons begin firing more action potentials, increasing the firing rate. Since all neurons in the same layer received presynaptic pulses with high temporal correlations, the neurons fire synchronously. When the connection probability between the layers is small, it is difficult for the neurons in the subsequent layers to receive strongly correlated synaptic inputs. Therefore, in the FFNs with small connection probabilities, the firing rate increases little as the layer index increases. In this case, the activities asynchronously propagate within the FFN with a low firing rate. The different intrinsic dynamics of the different types of neurons result in different action potential response behaviors and different synaptic outputs, even when injected with the same stimulus. For example, a fast spiking neuron responds to extremely high-frequency action potentials and outputs inhibitory synaptic signals, which prevent the depolarizing process and inhibit the formation of an action potential in the postsynaptic neuron. In this way, the FFN with different types of neurons shows different patterns of activity propagation. Changing the proportion of any of the neuron types in the network alters both the node dynamics and the synaptic signals within the FFN. Thus, spiking propagation is sensitive to the composition of neuronal types.

It is also interesting that there is a time lag between the synchronized firings of two neighboring layers, as shown in Fig. 2. These time lags are largely related to the time of depolarization of the membrane potential and the time of synaptic signal formation and transmission (such as the synaptic

time constant τ). If stable synchrony is well established, the time lag between the synchronous firings of two neighboring layers is almost unchanged during propagation. The propagation of the firing rate within the FFN is intrinsically related to the transmission of information received by the neurons. For information transmitted from upstream neurons or the external environment, such as multiple noisy oscillatory signals [34] or subthreshold signals with background noise [35, 36], neurons respond with action potentials at different firing rates and code the input signals in either rate mode (synchronous) or temporal mode (asynchronous) [11]. Either the asynchronous or synchronous spiking propagates through different layers with a time lag due to the properties of synaptic transition and neuronal response [14, 37].

In the current work, it was found that the firing rates that propagated within the FFN can be modulated by the connection properties of the network and the intrinsic dynamics of the different neuronal types. Moreover, we also observed that the firing rates that propagated within the FFN could vary from 2 Hz up to 700 Hz by changing these network and neuron parameters. In *in vivo* and *in vitro* experiments, a wide frequency range has been recorded at the cellular and network levels; the firing rates of different types of neurons in the brain were shown to range from 0 to 400 Hz [38, 39, 40], and extracellularly recorded local field potentials of the brain show that their oscillations could vary from <4 Hz to 600 Hz [41, 42, 43]. High-frequency firing neurons have the advantage of short conduction delays in the central nervous system [44]. Moreover, the excess Na^+ influx in myelinated axons and some fast synaptic transmission could optimize the high firing rate propagation [45, 46]. The broad frequency range is also beneficial to the coding process [44]. Although the role of high-frequency firing rates or neural oscillations in the nervous system is not well understood, the results in the current work reveal clues indicating that the high firing rate is related to the intrinsic dynamics of the neurons and the network structure.

Overall, characterizing and understanding the underlying mechanisms of neural information encoding and transmission across modular brain structures is one of the central problems in neuroscience. The current simulation results also reveal that neuronal diversity is also an important factor that affects neural coding and information transmission. Gjorgjieva et al. have reported similar results, showing that the presence of diverse ion channels and their dynamics endow single neurons the ability to switch the mode of information transmission in a neural network [47]. Thus, we believe that the results of the current work highlight the importance of the combined interactions of diverse intrinsic neuronal types in information transmission.

Acknowledgements

This work was supported by the Weigao Young Talent Launch Project.

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