Research Article

Weak Quasiperiodic Signal Propagation through Multilayer Feed-Forward Hodgkin–Huxley Neuronal Network

Yuangen Yao, Bowen Gong, Daxiang Lu, and Rong Gui

College of Science, Huazhong Agricultural University, Wuhan 430070, Hubei, China

Correspondence should be addressed to Yuangen Yao; yyg@mail.hzau.edu.cn

Received 27 December 2019; Revised 11 June 2020; Accepted 22 June 2020; Published 13 July 2020

Copyright © 2020 Yuangen Yao et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Quasiperiodic signal is ubiquitous and entrenched in neuronal networks, and thus taking it into consideration is necessary. The Wiener process with the intensity of $\sigma$ is used here to model randomly fluctuated phase in external weak quasiperiodic signal. The departure from the normal periodicity can be governed by the parameter $\sigma$. Then, the effects of randomly fluctuated phase of signal and time-periodic coupling intensity of synaptic junctions between neurons on propagation of weak quasiperiodic signal through feed-forward Hodgkin–Huxley network are explored in detail. Increasing $\sigma$ makes more neurons fire simultaneously, and better synchronous state is observed. Consequently, the external weak quasiperiodic signal introduced into all neurons in the first layer can be effectively transmitted through the whole feed-forward network via synchronization mechanism. In the case of time-periodic synaptic coupling intensity, when oscillatory frequency of synaptic coupling intensity is equal precisely to average frequency of external quasiperiodic signal, the propagation of weak quasiperiodic signal is optimal. Additionally, rapid oscillation of synaptic coupling intensity hinders or even kills the propagation of quasiperiodic signal to great depths of neuronal network, provided $\sigma$ is not large enough.

1. Introduction

Nervous system, as a very complex network, is comprised of the huge amounts of elementary elements named neurons [1]. Information gathered from sensory neurons propagates along links of neuronal network and then flows into the central nervous system. A sustained hot issue in computational science is to reveal how information can be encoded and propagated in the complex neuronal network [1, 2]. To do this, there are many network models presented for understanding of signal transmission in neuronal network, wherein multilayer feed-forward neuronal network (FFNN) has been largely used because it is suitable for accounting for experimental findings [3]. Wang and co-authors firstly adopted this model to study propagation of firing rate and found that synchronous firings can be gradually built up, and synchronous firings developed gradually contribute to transmission of periodic signal [3]. Based on the same theoretic model, Yi and Lang also explored thoroughly the effects of noise, connection probability between two neighboring layers, and the ratio of inhibitory connections on the propagation of firing rate [4]. They found that noise with increasing intensity enhances firing rate and accelerates establishment of synchronization by virtue of mechanism of stochastic resonance [4]. Via synchronization mechanism, firing rate can transmit successfully through the whole network if the connection probability between nearest layers is over certain a threshold [4]. The synchronization is built up more quickly for high connection probability, while firing rate and synchronization may be reduced as inhibitory connection increases gradually because inhibitory connection can counteract excitatory input [4]. Moreover, Lu et al. investigated the effect of background noise on transmission of an excitatory postsynaptic current signal (EPSC) in a 5-layer FFNN and found that there exists an optimal intensity of background noise, which can accelerate the speed of transmission of subthreshold postsynaptic signal and simultaneously can maintain the fidelity between system’s response and subthreshold EPSC signal [5]. In addition, the effects of synaptic weight and characteristic time on the...
signal propagation are explored based on a 10-layer FFNN of Hindmarsh–Rose (HR) neurons, and it was found that increasing synaptic weight is beneficial to propagation of weak spike train and synchronization formation [6]. Autapse-induced wave emitting and propagation in a chain-like FFNN of HR neurons was also observed, and excitation of autapse, as a pacemaker, can regulate collective behaviors of neurons [7]. Additionally, the effects of differential operational modes of coincidence detector and temporal integrator on signal propagation through multilayer FFNN were studied [8]. It was found that synchronization greatly contributes to propagation of rate signals with fidelity, and coincidence detectors precede temporal integrators in propagating rate signals [8]. Double coherence resonance phenomenon induced by correlated synaptic input and noise was observed in noisy FFNN [9]. Particularly, provided that intensity of intrinsic noise and signal frequency are appropriately adjusted, noisy FFNN can amplify weak signals, which is afferent to the input layer (i.e., first layer) [10]. Therefore, weak signal propagation can be optimized by the intensity of intrinsic noise, forcing frequency, and interlayer link density [10].

Weak signal detection and transmission have been widely investigated both in experiment and theory based on various neuron models [11–17]. Voltage-sensitive ion channels embedded in cell membranes are indispensable for biological signal transduction, which play vital roles in the formation of nerve action potentials and synaptic transmission [14]. Polypeptide alamethicin-promoted formation of ion channels in lipid bilayer is highly dependent on transmembrane potential [14]. Based on a simplest biological system of parallel voltage-dependent ion channels formed by peptide alamethicin, noise-induced enhancement of signal transduction can be experimentally observed at the subcellular level [14]. Higher organisms, such as crayfish, have evolved to be capable of detecting weak signal via stochastic resonance generated even in individual neuron by optimizing endogenous sources of noise [15]. Furthermore, noise-assisted improvement in behavioral and/or functional performance, such as behavioral responses to weak sensory inputs with human brain, can also be confirmed experimentally [18, 19]. Theoretically, Yilmaz and co-workers investigated in detail the effects of coupling strength and delay time of electrical autapse on weak periodic signal detection in stochastic Hodgkin–Huxley neuron [20]. In addition, our previous studies showed that bounded noises [21–23], autapse with time-periodic coupling intensity [24], and electromagnetic fluctuation [25] significantly influence signal detection and transmission in single neuron. Although many research studies have contributed to signal detection and transmission, it is worth reminding that these studies are limited to periodic signal. Given that real-world external signals in real complex neuronal networks are more likely to be irregular and the phase of signal may vary randomly with time due to stochastic fluctuation in medium or interface where signal travels through [26], investigation transmission of quasiperiodic signal with stochastic phase fluctuation is more realistic from this perspective. In addition, stochastic disturbance of phase has been shown to reduce the threshold of neuron firing and thus to optimize information transmission [22].

On the other hand, synaptic coupling intensity is thought to be constant in most previous studies. However, synapses are plastic rather than constant. Neurons have the capacity of modifying the strength of synaptic connections through various different forms and mechanisms of synaptic plasticity [27–31]. Moreover, the range of temporal scale of synaptic plasticity is from milliseconds to hours, days, and even longer [28]. Therefore, synaptic plasticity can be roughly classified into two categories: short-term synaptic plasticity and long-term synaptic plasticity according to lasting time. Numerous forms of short-term synaptic plasticity, whose time scale is from milliseconds to several minutes, have been widely observed in species ranging from simple invertebrates to mammals [28, 31]. Additionally, short-term synaptic plasticity has been thought to play significant role in short-term adaptations to transient changes in behavioral states and sensory inputs [28, 31], while long-term synaptic plasticity plays important roles in the formation of specific brain network characteristics during learning and memory processes, as well as in clinical recovery after brain damage [27, 29, 32]. Theoretically, synaptic plasticity can be roughly characterized by a time-periodic coupling intensity. Furthermore, resonant phenomena, enhancement of temporal coherence, and spatial synchronization induced by time-periodic coupling intensity of plastic synapses can be observed theoretically [33–35]. Particularly, our previous study confirmed numerically that autapse with time-periodic coupling intensity can effectively improve the efficiency and time precision of signal transmission and simultaneously improve the adaptive capacity of neurons [24]. However, whether the results obtained from single neuron can be extended to more realistic and biological multilayer FFNN of Hodgkin–Huxley neurons is still unclear.

Therefore, the present paper aims to study this problem. To do this, a 10-layer FFNN of Hodgkin–Huxley neurons is constructed firstly. Then, external weak quasiperiodic signals are afferent to each neuron in input layer (i.e., the first layer) of FFNN, and the Fourier coefficient $Q$ is calculated to measure the correlation between quasiperiodic signals imposed on input layer and collective temporal activities of neurons in other layers of FFNN. By observing the change of $Q$ with control parameters, weak quasiperiodic signal propagation through FFNN is thoroughly investigated. Lastly, the effects of synaptic plasticity on weak quasiperiodic signal propagation through FFNN can be taken into account by introducing time-periodic coupling intensity.

2. Model and Simulation

As previously described [3, 4, 10], a 10-layer FFNN of Hodgkin–Huxley neurons is constructed (Figure 1). There is no link between neurons in the same layer, but each neuron randomly receives $N \times P$ synaptic inputs from the previous layer. Here $N$ and $P$ are the number of neurons in each layer and connection probability between nearest layers, respectively. Unless otherwise stated, $N$ and $P$ are set to 200 and 0.1,
respectively. The first and the last layers are considered as input and output layers, respectively. External quasiperiodic signals are only afferent to all neurons in the first layer.

Figure 1: A schematic of a 10-layer feed-forward network with $N = 200$ Hodgkin–Huxley neurons in each layer. There is no link between neurons at the same layer. Each neuron randomly receives $N \times P$ synaptic inputs from the previous layer. $P$ denotes connection probability between nearest layers. The first and the last layers are considered as input and output layers, respectively. External quasiperiodic signals are only afferent to all neurons in the first layer.

Table 1: Employed parameters and their values for the Hodgkin–Huxley neuron model [3, 4].

| Symbol | Definition | Value and units |
|--------|------------|-----------------|
| $C_m$  | Capacitance of membrane | 1 $\mu$F/cm$^2$ |
| $V_K$  | Potassium reversal potential | $-77$ mV |
| $V_{Na}$ | Sodium reversal potential | $50$ mV |
| $g_L$  | Leakage reversal potential | $-54.4$ mV |
| $gK$   | Potassium channel conductance | $36$ mS/cm$^2$ |
| $gNa$  | Sodium channel conductance | $120$ mS/cm$^2$ |
| $gL$   | Leakage conductance | $0.3$ mS/cm$^2$ |

The synaptic current $I_{ij}^{syn}(t)$, which is from layer $j-1$ and received by neuron $i$ in layer $j$ at time $t$, is represented by an alpha function and yields [3, 4] $I_{ij}^{syn}(t) = - (1/M) \sum_{k=1}^{M} W_{ij}^{syn}(t) = (1/M) \sum_{k=1}^{M} \epsilon_{ij}^{syn}(t - T_{kj}) \sin(\omega t), \quad t \geq T_{kj}$.

Here, $T_{kj}$ denotes Heaviside step function. $T_{kj}$ stands for the firing time (i.e., starting time of synaptic interaction) of the $k$-th neuron in layer $j-1$ coupled with neuron $i$ in layer $j$. $M$ represents the number of neurons in layer $j-1$ coupled with the $i$-th neuron in layer $j$. All synaptic inputs are thought to be excitatory through choosing an appropriate synaptic reversal potential of $V_{syn} = 0$ mV [3, 4]. $\tau$ stands for duration of synaptic interaction and is set to $2$ ms [3, 4].

Here, we consider synaptic coupling intensity to be time-periodic, and it can be roughly characterized by the following equation [24, 35, 37]: $\epsilon_{ij}^{syn} = \epsilon_0 [1 + \sin(\omega t \tau)]$. Here, $\epsilon_0$ indicates the amplitude of synaptic coupling intensity and is set to $0.6$ throughout this paper [3, 4]. $n$ indicates that the frequency of synaptic coupling intensity is $n$ times of the average frequency $\omega$ of the external quasiperiodic signal. In particular, if $n$ is equal to $0$, then synapses are constant.

In equation (1), $\xi_i(t) = A \sin[\omega t + \sigma W(t)]$ denotes external quasiperiodic signals with an amplitude $A$ and an average frequency $\omega$ [22, 38]. Note that external quasiperiodic signals $\xi_i(t)$ are only afferent to all neurons in the input layer (i.e., the first layer). Moreover, we select specific $A = 2.8$ and $\omega = 2\pi f = 300\pi$ to ensure that the periodic dynamics of individual neurons are governed by more biologically realistic Hodgkin–Huxley equation [3, 4, 36]:

\[
\frac{dV_{ij}}{dt} = \left[ -g_K n_h^4 (V_{ij} - V_K) + g_{Na} m_i^3 h_i (V_{ij} - V_{Na}) \right] + g_L (V_{ij} - V_L) + I_0 + I_{ij}^{syn}(t) + \xi_i(t),
\]

(1)

where $V_{ij}$, $m_i$, $h_i$, and $n_i$ denote membrane potential, the activation and inactivation variables of the sodium current, and activation variable of the potassium current for the $i$-th neuron in the $j$-th layer. $I_0$ characterizes external stimulus current and is set to $1 \mu$A/cm$^2$ throughout this paper [3, 4]. All parameter values used throughout this paper are listed in Table 1.

The dynamical equations for gating variables of $m_i$, $h_i$, and $n_i$ are given below [3, 4, 36]:

\[
\frac{dy_{ij}(t)}{dt} = \alpha_{y} [1 - y_{ij}(t)] - \beta_{y} y_{ij}(t), \quad y_{ij} = m_i, h_i, n_i.
\]

(2)

The nonlinear functions of $\alpha_{y}$ and $\beta_{y}$ are expressed as [3, 4, 36]

\[
\alpha_m = \frac{0.1 (V_{ij} + 40)}{1 - \exp(-(V_{ij} + 40)/10)}.
\]

(3a)

\[
\beta_m = 4 \exp\left(-\frac{V_{ij} + 65}{18}\right).
\]

(3b)

\[
\alpha_h = 0.07 \exp\left(-\frac{V_{ij} + 65}{20}\right).
\]

(3c)

\[
\beta_h = \frac{1}{1 + \exp(-(V_{ij} + 35)/10)}.
\]

(3d)

\[
\alpha_n = \frac{0.01 (V_{ij} + 55)}{1 - \exp(-(V_{ij} + 55)/10)}.
\]

(3e)
signal is too weak to evoke a spike by itself (Figure 2). In other words, the quasiperiodic signal is subthreshold (i.e., weak). Moreover, $W(t)$ represents the Wiener process with the intensity of $\sigma$. The departure from the normal periodicity can be governed by the parameter $\sigma$. If $\sigma$ is equal to 0, signals are normal periodic signals (Figure 3). The time evolution of $W(t)$ is obtained in our numerical simulations by the following formula [22, 39]:

$$W(t) = W(t-\Delta t) + \sqrt{-2\Delta t \ln(X_1)} \cos(2\pi X_2),$$

where $X_1$ and $X_2$ are two independent random numbers uniformly distributed on the unit interval. Euler’s method with a time step $\Delta t = 0.001 \text{ ms}$ is used to integrate equations of (1)–(4). The different initial values for variables do not result in any remarkable changes in main results.

In addition, we use Fourier coefficient $Q_j$ to measure the correlation between the input frequency $\omega$ and the collective temporal activities of all neurons in layer $j$. Its expression is defined as follows [8, 22, 23, 40, 41]:

$$Q_j = \sqrt{Q_{j, \text{sin}}^2 + Q_{j, \text{cos}}^2},$$

$$Q_{j, \text{sin}} = \frac{\omega}{\pi m} \int_{T_0}^{T_0 + 2\pi m/\omega} S_{j, \text{avg}}(t) \sin(\omega t) \, dt,$$

$$Q_{j, \text{cos}} = \frac{\omega}{\pi m} \int_{T_0}^{T_0 + 2\pi m/\omega} S_{j, \text{avg}}(t) \cos(\omega t) \, dt,$$

$$S_{j, \text{avg}}(t) = \frac{1}{N} \sum_{i=1}^{N} S_{ij}(t),$$

$$S_{ij}(t) = \begin{cases} 1, & \text{if } V_{ij}(t) > V_{\text{th}} = 0, \\ 0, & \text{if } V_{ij}(t) \leq V_{\text{th}} = 0. \end{cases}$$

Clearly, larger $Q_j$ indicates higher correlation between signals in input layer and collective temporal activities of the neurons in layer $j$ and thus means that more information is transported through particular angular frequency $\omega$. In other words, $Q_j$ can measure transmission efficiency of input signals. It is generally acknowledged that subthreshold oscillations cannot carry any information. Therefore, a spiking threshold of $V_{\text{th}} = 0$ is used to distinguish between the spikes and the subthreshold oscillations so that temporal activities of neuron $i$ in the layer $j$ are characterized by pulse train $S_{ij}(t)$ (Figure 4). Collective temporal activities of the layer $j$ are described by the averaged pulse train $S_{j, \text{avg}}(t)$. In addition, to eliminate the effect of initial values of variables, a sufficiently large $T_0 = 500 \text{ ms}$ is adopted, and $m = 500$ is used to ensure statistical validity.

### 3. Main Results

#### 3.1. Effects of Stochastic Phase Fluctuation on Synchronization and Signal Propagation

Firstly, we investigate the effects of stochastic phase fluctuation on dynamical activity of single Hodgkin–Huxley neuron. As shown in Figure 4, larger stochastic phase fluctuation (i.e., larger $\sigma$) is more likely to inspire more spikes. Information is encoded in the spike trains with two encoding mechanisms of firing rate and spike timing. Given that the firing rate encodes information by the numbers of spikes in time bins [3], we speculate that stochastic phase fluctuation in weak quasiperiodic signal is more conducive to weak signal propagation through the whole FFNN. In addition, synchronization of temporal activities of neurons plays a vital role in signal propagation from a group of neurons to next groups. Therefore, the effects of stochastic phase fluctuation in quasiperiodic signals on synchronization are examined by plotting firing patterns for different layers of FFNN (Figure 5). Higher synchronization suggests that more neurons in the same layer fire spikes simultaneously. It is clear that for a given $\sigma = 0.5$ or 0.4, neurons in the first three layers of FFNN fire irregularly (Figure 5), but after the 4th layer, the synchronized firing states are gradually established, and the firing pattern can robustly propagate through the whole FFNN (Figure 5). By comparing raster plots of spikes for different $\sigma$, it is easily seen that quasiperiodic signal with stronger stochastic phase fluctuation (i.e., larger $\sigma$) evokes more spikes within the same time scale and thus is more beneficial to propagation of weak rhythmic activity by synchronization mechanism.

Further, in order to measure transmission efficiency of input signals, we calculate Fourier coefficient $Q_j$ of each layer for different $\sigma$ and then investigate the effects of different levels of stochastic phase fluctuation on the propagation of quasiperiodic signal propagation through FFNN. As depicted in Figure 6, if $\sigma$ is less than 0.4, $Q_j$ decreases monotonously to zero as the layer index $j$ increases gradually, which indicates that external weak quasiperiodic
signals, introduced to the neurons in the first layer, cannot be transmitted effectively towards deeper layers, or even die out (Figure 6). But if $\sigma$ is greater than certain value, such as 0.4, $Q_j$ increases monotonously with the increase of layer index $j$ and finally remains almost unchanged (Figure 6).

Therefore, external weak quasiperiodic signals introduced to all neurons in the input layer can be transmitted more effectively through the whole FFNN with the increasing stochastic phase fluctuation. Moreover, this result may also suggest that successive layers can progressively

**Figure 3:** Sampled time series of external quasiperiodic signal $A \sin[\omega t + \sigma W(t)]$ with an amplitude $A$ and an average frequency $\omega$. $W(t)$ represents the Wiener process with the intensity of $\sigma$. The departure from the normal periodicity can be governed by the parameter $\sigma$. If $\sigma$ is equal to 0, signals are normal periodic signals. From top to bottom, $\sigma$ takes values of 0, 0.1, 0.2, 0.3, 0.4, and 0.5, successively.

**Figure 4:** Sampled time series of membrane potential $V(t)$ and the corresponding pulse train $S(t)$ for single Hodgkin–Huxley neuron with constant external injected current $I_0 = 1 \mu A/cm^2$. From top to bottom, $\sigma$ takes values of 0.2, 0.4, and 0.5.
amplify the received signal from previous layers under the appropriate degree of stochastic phase fluctuation (Figure 6). There may exist a competition between signal amplification and attenuation, which results in the non-monotonic dependence of $Q_j$ on layer index $j$ when $\sigma$ is equal to 0.4 (Figure 6).

3.2. Effects of Time-Periodic Synaptic Coupling Intensity on Signal Propagation. Here, we consider synaptic coupling intensity to be time-periodic and then explore effects of time-periodic synaptic coupling intensity on signal propagation through FFNN. In order to provide an insight into the relationship between the oscillatory frequency of synaptic coupling intensity $\epsilon_{\text{syn}}$ and average frequency $\omega$ of weak quasiperiodic signals, the dependence of $Q_j$ of layer $j$ on frequency ratio $n$ is shown in Figure 7. It is obvious that the optimal oscillatory frequency of synaptic coupling intensity is obtained at $n = 1$. In other words, when oscillatory frequency of synaptic coupling intensity is equal precisely to average frequency of external quasiperiodic signals, FFNN works in the best state, and thus the maximum transmission efficiency can be achieved. If synaptic coupling intensity oscillates slowly, external weak quasiperiodic signals always propagate through the whole FFNN (Figure 7(a)), but transmission efficiency is much less than the optimal value. If synaptic coupling intensity oscillates rapidly, external weak quasiperiodic signals cannot propagate through deeper layers (Figure 7(a)). However, increasing stochastic phase fluctuation in quasiperiodic signals, such as $\sigma = 0.5$, can contribute to signal transmission towards deeper layers and even the whole FFNN (Figure 7(b)).
4. Conclusions

Multilayer feed-forward neuronal network (FFNN) has been used as an ideal theoretical model to investigate the propagation of firing rate as well as weak signal transmission. But these previous studies focus exclusively on normal periodic signals and assume synaptic coupling intensity to be constant. However, real-world external signals in real complex neuronal networks are more likely to be irregular, and the phase of signal may vary randomly with time due to stochastic fluctuation in medium or interface where signal travels through. In addition, synapses are plastic rather than constant. Short-term synaptic plasticity has been widely observed in species ranging from simple invertebrates to mammals and has been deemed to play significant role in short-term adaptations to sensory inputs. Therefore, investigation transmission of quasiperiodic signal with stochastic phase fluctuation in weak quasiperiodic signal is more realistic under the circumstance of time-periodic synaptic coupling intensity rather than constant coupling intensity.

Based on the FFNN model, we study the effects of stochastic phase fluctuation and time-periodic synaptic coupling intensity on propagation of external weak quasiperiodic signals through multilayer FFNN by using the Fourier coefficient $Q_j$ for quantitatively characterizing the efficiency of signal transmission. For single Hodgkin–Huxley neuron, external weak quasiperiodic signal evokes more spikes than normal periodic signal. Therefore, stochastic phase fluctuation in weak quasiperiodic signal is more conducive to weak signal propagation. For the FFNN of Hodgkin–Huxley neurons, stochastic phase fluctuation in weak quasiperiodic signal can result in better synchronization of firing pattern in neuronal network. Consequently, weak quasiperiodic signals can transmit effectively through deeper layer of FFNN. Moreover, successive layer can progressively amplify received signal from previous layer. Stochastic phase fluctuation and hierarchical network structure both contribute to long-range transmission of signal through deep neuronal network. Further, the effects of time-periodic synaptic coupling intensity are studied. When oscillatory frequency of synaptic coupling intensity is equal precisely to average frequency of external quasiperiodic signals, the propagation of weak quasiperiodic signals through FFNN is optimal. If synaptic coupling intensity oscillates slowly, the successful propagation of weak quasiperiodic signals to deeper layers of FFNN can be observed, but transmission efficiency is much less than the optimal value. However, signal propagation may cease directly if synaptic coupling intensity oscillates rapidly. It should be pointed out that large stochastic phase fluctuation may result in serious loss of fidelity in the transmitted signal. Therefore, organisms may have the capacity to adjust the levels of stochastic phase fluctuation. We believe that the results presented here may shed some possible light on understanding long-range propagation mechanism of signals with imperfect rhythm through deep neuronal network.

Data Availability

No data were used to support this study.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

The authors thank Dr. Ming Yi (CUG), Dr. Lijian Yang (CCNU), and Dr. Dengguo Wei (HZAU) for their helpful suggestions on the project implementation and writing. This
study was supported by the National Natural Science Foundation of China (grant nos. 31601071 and 11804111).

References

[1] A. A. Faisal, L. P. J. Selen, and D. M. Wolpert, “Noise in the nervous system,” Nature Reviews Neuroscience, vol. 9, no. 4, pp. 292–303, 2008.

[2] A. Kumar, S. Rotter, and A. Aertsen, “Spiking activity propagation in neuronal networks: reconciling different perspectives on neural coding,” Nature Reviews Neuroscience, vol. 11, no. 9, pp. 615–627, 2010.

[3] S. Wang, W. Wang, and F. Liu, “Propagation of firing rate in a feed-forward neuronal network,” Physical Review Letters, vol. 96, no. 1, p. 18103, 2006.

[4] M. Yi and L. Yang, “Propagation of firing rate by synchronization and coherence of firing pattern in a feed-forward multilayer neuronal network,” Physical Review E, vol. 81, no. 6, p. 61924, 2010.

[5] L. Lu, Y. Jia, J. B. Kirunda et al., “Effects of noise and synaptic weight on propagation of subthreshold excitatory postsynaptic current signal in a feed-forward neural network,” Nonlinear Dynamics, vol. 95, no. 2, pp. 1673–1686, 2019.

[6] M. Ge, Y. Jia, J. B. Kirunda et al., “Propagation of firing rate by synchronization in a feed-forward multilayer Hindmarsh-Rose neural network,” Neurocomputing, vol. 320, pp. 60–68, 2018.

[7] J. Ma, X. Song, J. Tang, and C. Wang, “Wave emitting and propagation induced by autapse in a forward feedback neuronal network,” Neurocomputing, vol. 167, pp. 378–389, 2015.

[8] L. Liu, F. Liu, D. Xu, and W. Wang, “Signal propagation through feedforward neuronal networks with different operational modes,” EPL (Europhysics Letters), vol. 85, no. 3, p. 38006, 2009.

[9] C. Men, J. Wang, Y.-M. Qin, B. Deng, K.-M. Tsang, and W.-L. Chan, “Propagation of spiking regularity and double coherence resonance in feedforward networks,” Chaos: An Interdisciplinary Journal of Nonlinear Science, vol. 22, no. 1, p. 013104, 2012.

[10] M. Ozer, M. Perc, M. Uzuntarla, and E. Kokkukaya, “Weak signal propagation through noisy feedforward neuronal networks,” NeuroReport, vol. 21, no. 5, pp. 338–343, 2010.

[11] C. Wang, J. Tang, and J. Ma, “Minireview on signal exchange between nonlinear circuits and neurons via field coupling,” The European Physical Journal Special Topics, vol. 228, no. 10, pp. 1907–1924, 2019.

[12] J. Ma, Z.-Q. Yang, L.-J. Yang, and J. Tang, “A physical view of computational neurodynamics,” Journal of Zhejiang University-Science A, vol. 20, no. 9, pp. 639–659, 2019.

[13] Z. Liu, C. Wang, G. Zhang, and Y. Zhang, “Synchronization between neural circuits connected by hybrid supranet,” International Journal of Modern Physics B, vol. 33, no. 16, Article ID 1950170, 2019.

[14] S. M. Bezrukov and I. Vodyanoy, “Noise-induced enhancement of signal transduction across voltage-dependent ion channels,” Nature, vol. 378, no. 6555, pp. 362–364, 1995.

[15] J. K. Douglass, L. Wilkens, E. Pantazelou, and F. Moss, “Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance,” Nature, vol. 365, no. 6444, pp. 337–340, 1993.

[16] K. Wiesenfeld and F. Moss, “Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDs,” Nature, vol. 373, no. 6509, pp. 33–36, 1995.

[17] M. D. McDonnell and L. M. Ward, “The benefits of noise in neural systems: bridging theory and experiment,” Nature Reviews Neuroscience, vol. 12, no. 7, pp. 415–425, 2011.

[18] K. Kitajo, D. Nozaki, and L. M. Ward, “Behavioral stochastic resonance within the human brain,” Physical Review Letters, vol. 90, no. 21, p. 218103, 2003.

[19] P. E. Greenwood, L. M. Ward, D. F. Russell, A. Neiman, and F. Moss, “Stochastic resonance enhances the electrosensory information available to paddlefish for prey capture,” Physical Review Letters, vol. 84, no. 20, pp. 4773–4776, 2000.

[20] E. Yilmaz and M. Ozer, “Delayed feedback and detection of weak periodic signals in a stochastic Hodgkin-Huxley neuron,” Physica A: Statistical Mechanics and Its Applications, vol. 421, pp. 455–462, 2015.

[21] Y. Yao and J. Ma, “Weak periodic signal detection by sine-Wiener-noise-induced resonance in the FitzHugh-Nagumo neuron,” Cognitive Neurodynamics, vol. 12, no. 3, pp. 343–349, 2018.

[22] Y. Yao, L. Yang, and C. Wang, “Subthreshold periodic signal detection by bounded noise-induced resonance in the FitzHugh-nagumo neuron,” Complexity, vol. 2018, Article ID 652650, 10 pages, 2018.

[23] Y. Yao, C. Ma, C. Wang, M. Yi, and R. Gui, “Detection of subthreshold periodic signal by multiplicative and additive cross-correlated sine-Wiener noises in the FitzHugh-Nagumo neuron,” Physica A: Statistical Mechanics and Its Applications, vol. 492, pp. 1247–1256, 2018.

[24] Y. Yao and J. Ma, “Signal transmission by autapse with constant or time-periodic coupling intensity in the FitzHugh-Nagumo neuron,” The European Physical Journal Special Topics, vol. 227, no. 7–9, pp. 757–766, 2018.

[25] Y. Yao, C. Su, and J. Xiong, “Enhancement of weak signal detection in the Hodgkin-Huxley neuron subjected to electromagnetic fluctuation,” Physica A: Statistical Mechanics and Its Applications, vol. 531, p. 121734, 2019.

[26] H. Markram, J. Lübke, and M. Frotscher, “Regulation of synaptic transmission in the dentate area of the anaesthetized rat,” Annual Review of Neuroscience, vol. 12, no. 1, pp. 159–189, 1989.

[27] M. S. Bassi, E. Iezzi, and L. Gilio, “Synaptic plasticity shapes brain connectivity: implications for network topology,” International Journal of Molecular Sciences, vol. 20, no. 24, p. 6193, 2019.

[28] A. Citri and R. C. Malenka, “Synaptic plasticity: multiple forms, functions, and mechanisms,” Neuropsychopharmacology, vol. 33, no. 1, pp. 18–41, 2008.

[29] M. Ozer, M. Perc, M. Uzuntarla, and E. Kokkukaya, “Weak signal propagation through noisy feedforward neuronal networks,” NeuroReport, vol. 21, no. 5, pp. 338–343, 2010.

[30] C. Wang, J. Tang, and J. Ma, “Minireview on signal exchange between nonlinear circuits and neurons via field coupling,” The European Physical Journal Special Topics, vol. 228, no. 10, pp. 1907–1924, 2019.

[31] J. Ma, Z.-Q. Yang, L.-J. Yang, and J. Tang, “A physical view of computational neurodynamics,” Journal of Zhejiang University-Science A, vol. 20, no. 9, pp. 639–659, 2019.

[32] Z. Liu, C. Wang, G. Zhang, and Y. Zhang, “Synchronization between neural circuits connected by hybrid supranet,” International Journal of Modern Physics B, vol. 33, no. 16, Article ID 1950170, 2019.

[33] S. M. Bezrukov and I. Vodyanoy, “Noise-induced enhancement of signal transduction across voltage-dependent ion channels,” Nature, vol. 378, no. 6555, pp. 362–364, 1995.

[34] J. K. Douglass, L. Wilkens, E. Pantazelou, and F. Moss, “Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance,” Nature, vol. 365, no. 6444, pp. 337–340, 1993.

[35] K. Wiesenfeld and F. Moss, “Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDs,” Nature, vol. 373, no. 6509, pp. 33–36, 1995.
[34] X. Lin, Y. Gong, and L. Wang, “Multiple coherence resonance induced by time-periodic coupling in stochastic Hodgkin-Huxley neuronal networks,” Chaos: An Interdisciplinary Journal of Nonlinear Science, vol. 21, no. 4, Article ID 043109, 2011.

[35] A. Birzu and K. Krischer, “Resonance tongues in a system of globally coupled FitzHugh-Nagumo oscillators with time-periodic coupling strength,” Chaos: An Interdisciplinary Journal of Nonlinear Science, vol. 20, no. 4, Article ID 043114, 2010.

[36] A. L. Hodgkin and A. F. Huxley, “A quantitative description of membrane current and its application to conduction and excitation in nerve,” The Journal of Physiology, vol. 117, no. 4, pp. 500–544, 1952.

[37] E. Yilmaz, V. Baysal, and M. Ozer, “Enhancement of temporal coherence via time-periodic coupling strength in a scale-free network of stochastic Hodgkin-Huxley neurons,” Physics Letters A, vol. 379, no. 26-27, pp. 1594–1599, 2015.

[38] D. Li, W. Xu, X. Yue, and Y. Lei, “Bounded noise enhanced stability and resonant activation,” Nonlinear Dynamics, vol. 70, no. 3, pp. 2237–2245, 2012.

[39] W. Guo, L.-C. Du, and D.-C. Mei, “Transitions induced by time delays and cross-correlated sine-Wiener noises in a tumor-immune system interplay,” Physica A: Statistical Mechanics and Its Applications, vol. 391, no. 4, pp. 1270–1280, 2012.

[40] L. Yang, W. Liu, and M. Yi, “Vibrational resonance induced by transition of phase-locking modes in excitable systems,” Physical Review E, vol. 86, no. 1, p. 16209, 2012.

[41] C. Yao and M. Zhan, “Signal transmission by vibrational resonance in one-way coupled bistable systems,” Physical Review E, vol. 81, no. 6, p. 61129, 2010.