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Synaptic plasticity induced transition of spike propagation in neuronal networks

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A B S T R A C T

We investigate the impact of short-term plasticity on spike propagation in neuronal networks. We shown that for different combinations of the synaptic rise and decay time, neurons in the network exhibit a variety of different spike propagation transitions as the parameter related to the short-term plasticity increases. We establish the criteria for the existence and stability of simple and composite traveling waves, and we verify the analytical results by means of numerical simulations. Interestingly, we discover that the coexistence of simple and composite traveling waves, as well as the coexistence of stable and unstable waves is possible, provided only the short-term plasticity is properly set.

1. Introduction

A common experimental paradigm for the study of propagation of neuronal spikes is to record activity in vitro by means of a thin brain slice preparation [1,2]. The spikes emitted by different neurons in the network form the evolution of spatiotemporal waves, which are believed to be involved in the encoding of sensory stimulation [3–5]. Many theoretical investigations have made for dynamics of the spatiotemporal waves in neuronal networks. In particular, Bressloff studied the existence and stability of traveling waves in a one-dimensional network of integrate-and-fire neurons with synaptic coupling [4]. Neuronal field models have also been used extensively to study propagation phenomena [6–9]. In a continuous neuronal network, for example, the existence and stability of traveling pulse solutions are investigated in a set of integro-differential equations that describe activity in a spatially extended neuronal population with synaptic connection [7]. The effects of the range of shortcuts in the dynamic model of neural networks was explored, and some interesting results have been obtained [10,11]. Moreover, mathematical and computational models for the propagation of activity in coupled neurons with excitatory synapses were simulated and analyzed in Ref. [12], where it is shown that the velocity scales as a power law with the strength of synaptic coupling, and the exponent is dependent only on the rise phase of the synapse.

Recently, Tonnelier [13] examined the ability of spiking neural networks to propagate a spatiotemporal sequence of spikes. Furthermore, the influence of synaptic coupling and stochastic perturbations on the propagation of spike sequences was also investigated. Despite the vibrancy of this field of research and many fascinating discoveries that were reported in the preceding seminal works, the relationship between the short-term plasticity β, the synaptic rise time τ_r

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and the synaptic decay time τ_d has not been examined. This paper aims to fill this gap and to study this important open problem.

In spiking neural networks, the information is encoded in a firing sequence, t_i^f, which is the spiking time of neuron i. In what follows, we only consider the first firing time of each neuron.

We consider a spatially structured network, where the dynamics of membrane potential of every neuron, $v_i(t)$ is given by the following equation [9],

$$\frac{dv_i}{dt} = -v_i + I_i + I_{\text{app}}, \tag{1}$$

where I_i and I_{app} are the total synaptic current of neuron i and the external current, respectively. The neuron fires a spike when the membrane potential reaches a threshold v [14], and after the spike the membrane potential is reset to $v_r < v$. In this work, we set $v = 1$ without loss of generality.

Due to its important role on learning and the development of nervous system, long term plasticity has attached much attention [15]. Recently, another form of synaptic plasticity–short-term plasticity has also become the focus of nervous scientists, because it is associated with neuronal transmission of information and information processing [16,17]. Early studies showed that [18], low frequency stimulation of brain rhythms and short-term plasticity are linked.

Here we study one-spike propagation and consider only short-term modifications. Facilitation and depression are pre-synaptic processes that modify the synaptic efficiency. Let s be a variable that monitors synaptic efficiency, $\alpha(t)$ is set to describe a pre-synaptic spike that induces a postsynaptic current. Hence, the total synaptic current of neuron i is given as follows,

$$I_{i,s}(t) = g_{syn} s_i(t) \sum_{j=1}^{N} w_{i,j} \alpha(t - t_j^f), \tag{2}$$

where g_{syn} is the total synaptic conductance and $w_{i,j}$ is the strength of the synaptic connection from neuron j to neuron i. For convenience, we define $w_{i,j} = w(|i-j|), w_j = w_{i,i-j}$, and weights are normalized so that $\sum_j |w_j| = 1$. In addition, $s_i(t)$ is a depression for $\beta < 1$ or facilitation for $\beta > 1$, which is initially 1 and evolves as

$$s_i \to \beta s_i. \tag{3}$$

When a spike is received, it follows,

$$\frac{ds_i}{dt} = \frac{1 - s_i}{\tau_s} \tag{4}$$

at another time. The time constant τ_s is at a time scale significantly larger than any other one related to the first spike propagation. This leads to

$$\frac{ds_i}{dt} \to 0. \tag{5}$$

Therefore, during the propagation, we neglect the relaxation of s_i after the arrival of the traveling wave, and take it as a constant during each time interval. To efficiently control the shape of the postsynaptic current, we consider the normalized piecewise linear function $\alpha(t)$ as follows,

$$\alpha(t) = \frac{2}{\tau_r + \tau_d} \begin{cases} t/\tau_r & 0 \leqslant t \leqslant \tau_r \\ 1 + (\tau_r - t)/\tau_d & \tau_r \leqslant t \leqslant \tau_r + \tau_d \\ 0 & \text{otherwise} \end{cases} \tag{6}$$

where τ_r is the synaptic rise time, and τ_d is the synaptic decay time.

As the reset current of neuron i, we use $I_{app} = (v_r - 1)\delta(t - t_i^f)$, where δ is the Dirac function. Integrating Eq. (1) yields:

$$v_i(t) = \eta(t - t_i^f) + g_{syn} \sum_{j=1}^{N} \beta^{N-j+1} w_j \epsilon(t - t_{i-j}^f), \tag{7}$$

where $\eta(t) = (v_r - 1)e^{-t}\Theta(t)$ is the reset pulse, the function $\Theta(t)$ is the Heaviside step function, and

$$\epsilon(t) = \int_0^t \alpha(s) e^{-(t-s)} ds \Theta(t) \tag{8}$$

which is the solution of the equation

$$\epsilon'(t) + \epsilon(t) = \alpha(t), \quad \epsilon(0) = 0. \tag{9}$$

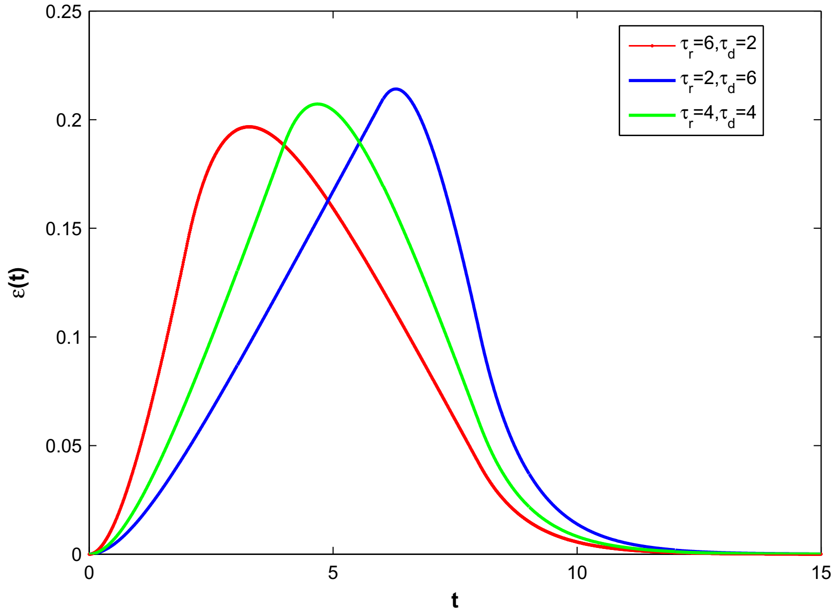

Fig. 1. Postsynaptic potential $\epsilon(t)$ for different combinations of the synaptic rise time τ_r and the synaptic decay time τ_d (see legend).

In view of $\alpha(t)$ set in this paper, $\epsilon(t)$ has the following form:

$$\epsilon(t) = \frac{2}{\tau_r + \tau_d} \begin{cases} 0 & t < 0 \\ (e^{-t} + t - 1)/\tau_r & t \leqslant \tau_r \\ 1 + \frac{\tau_r - t + 1}{\tau_d} + \frac{1}{\tau_r} e^{-t} - (\frac{1}{\tau_r} + \frac{1}{\tau_d}) e^{\tau_r - t} & \tau_r \leqslant t \leqslant \tau_r + \tau_d \\ (\frac{1}{\tau_r} + \frac{e^{\tau_r + \tau_d}}{\tau_d} - \frac{e^{\tau_r}}{\tau_r} + \frac{e^{\tau_r}}{\tau_d}) e^{-t} & \text{otherwise} \end{cases} \tag{10}$$

Fig. 1 gives the general shape of $\epsilon(t)$, it should be noted that no matter whatever the values of the synaptic time constants τ_r and τ_d, the postsynaptic potential $\epsilon(t)$ always increases from 0 to a maximum value (rise phase), and then decreases to a nonzero minimum over a relative long time span (decay phase).

2. Existence and stability of traveling waves

Firstly, it is of interest to discuss briefly the conditions for the existence of traveling waves. The spike sequence propagation in the neuronal network and the firing times of the neurons are given by,

$$t^f_{pi+k} = \frac{pi + k}{c} + \delta_k, \tag{11}$$

where $c > 0$ is the velocity of the wave, p is the length of the sequence, and i is the index of the i th repetition of the sequences. Moreover, $k \in \{0, \ldots, p-1\}$ is the label of the successive neurons in the sequence, and δ_k are the propagated inter-spike intervals, where $\delta_0 = 0$. As in Ref. [11], the traveling waves are divided into the simple and composite waves, respectively. The composite waves are characterized by the propagation that can be thought of as the superimposition of several simple waves, which propagate with the same velocity but with different time shifts. It is noted that in the present letter we consider only the first spike of each neuron. Hence, all the indexes used (i, p, k) are related to a spatial location and do not describe the successive spikes of a neuron.

2.1. Existence of traveling waves

Intuitively, the propagated sequence of a simple traveling wave is composed of a single neuron. In particular, it can be descried that as $\delta_k = 0$, for $\forall k \in \{0, \ldots, p-1\}$ or equivalently $p = 1$ in Eq. (11), the simple traveling wave can occur. Otherwise, the composite traveling wave can appear. Based on Eq. (7), it is found that the traveling wave solutions satisfy the following Eqs. (12)–(14):

$$V_k(\xi_k) = \eta(\xi_k) + g_{syn} \sum_{j=1}^{N} \beta^{N-j+1} w_j \epsilon\left(\xi_k + \frac{j}{c} + \delta_k - \tilde{\delta}_{k-j}\right), \tag{12}$$

where $\xi_k = t - t^f_{pi}$ and $\tilde{\delta}_j$ denotes the periodic extension of period p of δ_j. It requires the threshold condition $V_k(0) = 1, (k = 0, \ldots, p-1)$, which yields

$$g_{syn}\sum_{j=1}^{N}\beta^{N-j+1}w_j\epsilon\left(\frac{j}{c}+\delta_k-\tilde{\delta}_{k-j}\right)=1, \tag{13}$$

and also the causality criterion follows,

$$V_k(\xi_k) < 1, \quad \text{for } \xi_k < 0, \ k = 0, \ldots, p-1. \tag{14}$$

A necessary condition that satisfies criterion (14) is

$$\sum_{j=1}^{N}\beta^{N-j+1}w_j\epsilon'\left(\frac{j}{c}+\delta_k-\tilde{\delta}_{k-j}\right)>0. \tag{15}$$

To gain some insight into the analytical relationship of the wave speed and other parameters given in the studied equations, we firstly consider a simple network, where each neuron connects only to one other presynaptic neuron, namely $N = 1$. In fact, in this network, only simple traveling waves can exist, which we prove in the next section. For simplicity, we set $w_1 = 1$. Hence, we have:

$$\epsilon\left(\frac{1}{c}\right)=\frac{1}{\beta g_{syn}}. \tag{16}$$

In order to obtain the expression of the velocity based on Eq. (16), we can see the series expansion of Lambert W function that is proposed in Ref. [19]. The wave speed c can be obtained by solving the following equation:

$$x + e^{-x} = \mu, \quad 1/c \leqslant \tau_r, \tag{17}$$

where

$$\mu = 1 + \frac{\tau_r(\tau_r+\tau_d)}{2\beta g_{syn}}. \tag{18}$$

Therefore we have

$$c = \frac{1}{W_0(-e^{-\mu})+\mu}, \quad \tau_r^{-1} \leqslant c, \tag{19}$$

where W_k denotes the kth branch of the Lambert W function. Using the series expansion of W_0 near the branch point $z = e^{-1}$, we have

$$W_0(z) = -1 + \sqrt{2(ez+1)} - \frac{2}{3}(ez+1) + O(ez+1). \tag{20}$$

So based on Eq. (19), a large value of g_{syn} is necessary to get the asymptotic behavior of the wave speed, which is

$$c = \sqrt{\frac{\beta g_{syn}}{\tau_r(\tau_r+\tau_d)}} - \frac{1}{6} + O\left(1/\sqrt{\beta g_{syn}}\right). \tag{21}$$

For $N > 1$, as long as the value of g_{syn} is large enough, it is expected that we can find the large speed value, i.e. $1/c \ll 1$, where the simple traveling waves can be obtained. Substituting the Taylor series of $\epsilon(t)$,

$$\epsilon(t) = \epsilon(0) + \epsilon'(0)t + \varepsilon''(0)\frac{t^2}{2} + O(t^3), \tag{22}$$

into Eq. (13), and using

$$\epsilon(0) = \epsilon'(0) = 0, \ \ \epsilon''(0) = \frac{2}{\tau_r(\tau_r+\tau_d)}, \tag{23}$$

we can obtain,

$$c^2 \sim \frac{g_{syn}}{\tau_r(\tau_r+\tau_d)}\sum_{i=1}^{N}\beta^{N-i+1}i^2 w_i. \tag{24}$$

However, it can be observed that as $N > 1$, g_{syn} and c are relatively small, analytical conditions on the existence of traveling waves can not be obtained. Hence, we will discuss them in the later sections to show their complexity by means of some numerical examples.

2.2. Stability of traveling waves

In order to discuss the stability conditions of the traveling waves, we suppose that the firing times of neurons are perturbed as follows,

$$\tilde{t}^f_{pi+k} = (pi + k)/c + \delta_k + \mu_{pi+k}, \tag{25}$$

where asymptotic stability of the traveling waves can be expressed as,

$$\lim_{j\to\infty} \mu_j = 0. \tag{26}$$

And then, the perturbed traveling wave solutions should satisfy

$$\tilde{v}_{pi+k}(t) = v_{pi+k}(t) - g_{syn}\sum_{j=1}^{N}\beta^{N-j+1}w_j\mu_{pi+k-j}\epsilon'(t - t^f_{pi+k-j}). \tag{27}$$

Now, we expand Eq. (27) to the first order in $\tilde{t}^f_{i-j}$ and get the threshold condition at $\tilde{t}^f_i$, which can lead to:

$$\sum_{j=1}^{N}\beta^{N-j+1}(\mu_i - \mu_{i-j})w_j\epsilon'\left(\frac{j}{c}\right) = 0. \tag{28}$$

Eq. (28) defines a map that has a general solution of the form $\mu_{pi+k} = \lambda_1^{i+1}\cdots\lambda_k^{i+1}\lambda_{k+1}^{i}\cdots\lambda_p^{i}$. Hence, it is obvious that the asymptotic stability holds if

$$\left|\prod_{l=1}^{p}\lambda_l\right| < 1. \tag{29}$$

In particular, for the simple traveling wave, we have $p = 1, \mu_i = \lambda^i$. Recall that since $\lambda = 1$ is a solution of Eq. (28), the characteristic equation can be obtained in the polynomial form:

$$P(\lambda) = (\lambda - 1)\sum_{i=0}^{N-1}b_i\lambda^i = 0, \tag{30}$$

where

$$b_i = \sum_{k=N-i}^{N}\beta^{i+1}w_k\epsilon'\left(\frac{k}{c}\right). \tag{31}$$

We know that the simple wave is asymptotically stable if and only if $P(\lambda)$ is Schur stable, namely all roots of $P(\lambda)$ lie in the interior of the unit circle. Furthermore, a simple sufficient condition for Schur stability is $b_{N-1} > b_{N-2} > \cdots > b_0 > 0$, which can give

$$\epsilon'(i/c) > 0. \tag{32}$$

Since $\epsilon'(i/c) = 0$, we have

$$i/c = \ln\frac{(\tau_r + \tau_d)e^{\tau_r} + \tau_d}{\tau_r}, \quad i = 0, \ldots, N. \tag{33}$$

This implies that the simple wave is stable if the following condition is satisfied,

$$\frac{N}{c} < \ln\frac{(\tau_r + \tau_d)e^{\tau_r} + \tau_d}{\tau_r}. \tag{34}$$

As a result, stable simple waves exist when g_{syn} and the wave speed are sufficiently large so that the arriving times of the presynaptic spike, $t^f_i = i/c$, occur in the rise part of the postsynaptic potential, where $\epsilon'(i/c) > 0$. It should be noted that this is the same as the conditions of stability for the neuronal network without short-term plasticity [11].

3. Transitions between simple and composite waves

For other combinations of the studied parameters, it can be expected that the composite waves can appear for suitable combinations of the parameter values. Furthermore, transitions between the simple waves and composite waves can occur as the key parameters are varied. In particular, it is known that 2-composite waves propagate (namely, there exist two interspike intervals, and we set them as $1/c \pm \delta$) if there exist two subthreshold time courses of the membrane potentials V_1 and V_2 such that

$$V_1(\xi_1) = \eta(\xi_1) + g_{syn}\sum_{j=1}^{N}\beta^{N-j+1}w_j\epsilon\left(\xi_1 + \frac{j}{c} - s_j\right) = 1, \tag{35}$$

$$V_2(\xi_2) = \eta(\xi_2) + g_{syn}\sum_{j=1}^{N}\beta^{N-j+1}w_j\epsilon\left(\xi_2 + \frac{j}{c} + s_j\right) = 1, \tag{36}$$

where two parameters c and δ are obtained from the threshold crossing conditions, which are given as follows,

$$g_{syn}\sum_{j=1}^{N}\beta^{N-j+1}w_j\epsilon\left(\frac{j}{c} \pm s_j\right) = 1, \tag{37}$$

where $s_j = \delta$ if j is even and $s_j = 0$ if j is odd.

For $N = 1$, from Eq. (37) we get $\epsilon(1/c - \delta) = \epsilon(1/c + \delta) = 1/g_{syn}$. According to the quality of the postsynaptic potential shown in Fig. 1, it is known that $\epsilon'(1/c + \delta) < 0$. Hence, there exist some ξ_2, which can satisfy the following equation,

$$V_2(\xi_2) = \eta(\xi_2) + g_{syn}\epsilon(\xi_2 + 1/c + \delta) > 1 \quad \text{for} \quad \xi_2 < 0, \tag{38}$$

which obeys the causality criterion of Eq. (14). Hence, it is clear that 2-composite waves are not possible for this case.

For $N = 2$, similarly we need consider the solutions of the following equation,

$$\beta^2 w_1\epsilon(1/c \pm \delta) + \beta w_2\epsilon(2/c) = 1/g_{syn}. \tag{39}$$

From the shape of the postsynaptic potential as depicted in Fig. 1, we have $\epsilon'(1/c - \delta) > 0$ and $\epsilon'(1/c + \delta) < 0$. During the decaying period, since $\epsilon(t)$ is monotonously decreasing, we have $\epsilon'(2/c) < 0$. Resultantly,

$$V_2'(0) = \beta^2 w_1\epsilon'(1/c + \delta) + \beta w_2\epsilon'(2/c) < 0, \tag{40}$$

which is inadmissible according to Eq. (15).

For $N = 3$, the solution of the 2-composite wave should simultaneously satisfy the following relations,

$$f(1/c, \delta) = \beta^3 w_1\epsilon(1/c - \delta) + \beta^2 w_2\epsilon(2/c) + \beta w_3\epsilon(3/c - \delta) - 1/g_{syn} \tag{41}$$

$$g(1/c, \delta) = \beta^3 w_1\epsilon(1/c + \delta) + \beta^2 w_2\epsilon(2/c) + \beta w_3\epsilon(3/c + \delta) - 1/g_{syn} \tag{42}$$

$$V_1(\xi) < 1, \; V_2(\xi) < 1, \quad \text{for} \;\; \xi < 0. \tag{43}$$

Moreover, the stability of the 2-composite wave is determined by:

$$\begin{aligned} &a_{12}\lambda_1\lambda_2^2 + a_{11}\lambda_1\lambda_2 + a_{01}\lambda_2 + a_{00} = 0 \\ &b_{21}\lambda_1^2\lambda_2 + b_{11}\lambda_1\lambda_2 + b_{10}\lambda_1 + b_{00} = 0 \end{aligned} \tag{44}$$

where

$$\begin{aligned} a_{12} &= \beta^3 w_1\epsilon'(1/c - \delta) + \beta^2 w_2\epsilon'(2/c) + \beta w_3\epsilon'(3/c - \delta) \\ a_{11} &= -\beta^3 w_1\epsilon'(1/c - \delta) \\ a_{01} &= -\beta^2 w_2\epsilon'(2/c) \\ a_{00} &= -\beta w_3\epsilon'(3/c - \delta). \end{aligned} \tag{45}$$

Here b_{ij} are obtained from a_{ji} by replacing δ by $-\delta$. The 2-composite wave is asymptotically stable if every pair of roots $(\lambda_1, \lambda_2, \lambda_3)$ of Eq. (44) satisfies $|\lambda_1\lambda_2\lambda_3| < 1$. From Eqs. (41)–(43), it is known that we can not analytically obtain the conditions of the 2-composite wave in the studied parameter space, and transitions between the simple and composite waves can also not be shown as the parameters vary. Thus, we can numerically verify the existence and stability of the 2-composite wave if there exist some parameter values, which can meet Eqs. (41)–(43). It should be noted that, in these parameters if $\delta = 0$, the traveling wave is a simple wave. In what follows, since $\epsilon(t)$ is a piecewise function about τ_r and τ_d, we will study three characteristic cases: (1) $\tau_r > \tau_d$; (2) $\tau_r = \tau_d$; (3) $\tau_r < \tau_d$. We set $g_{syn} = 8.4$, $w_i = 1/3$ and $i = 1, 2, 3$ unless stated otherwise.

4. Numerical results

4.1. Case $\tau_r > \tau_d$

We firstly consider $\tau_r = 6$ and $\tau_d = 2$. Based on Eqs. (41)–(43), the results presented in Fig. 2 indicate the variations of $1/c$ and δ as the short-term plasticity β changes, which shows the existence of simple as well as composite waves in some parameter regions. In particular, as $\beta \in (0.923, 0.94)$, two simple waves can coexist and they are unstable. This results from the roots $(\lambda_1, \lambda_2, \lambda_3)$ of Eq. (30), which can not satisfy $|\lambda_1\lambda_2\lambda_3| < 1$. For a good understanding, taking $\beta = 0.93$ ($\beta \in (0.923, 0.94)$), we get two simple waves with the velocities $1/c_1 = 2.357$ and $1/c_2 = 2.083$. And then, from the piecewise function of $\epsilon(t)$, we get

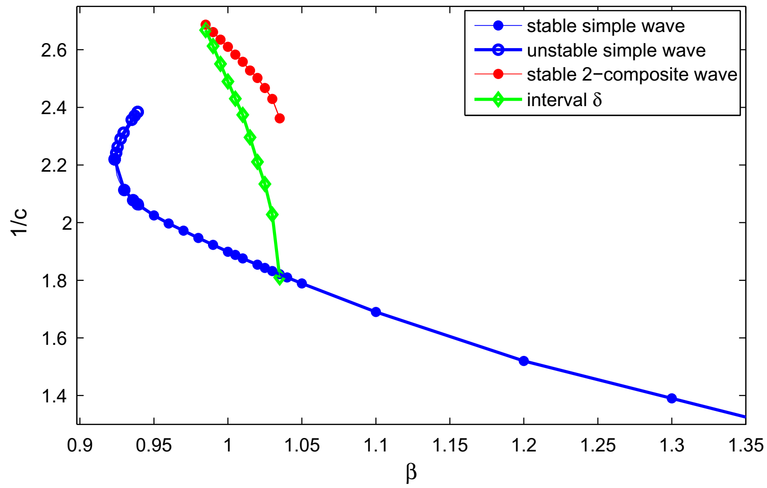

Fig. 2. Transition of the propagation modes induced by the short-term plasticity β as $\tau_r = 6$ and $\tau_d = 2$.

$$\epsilon'(t) = \begin{cases} 0 & t < 0 \\ (1 - e^{-t})/24 & t \leqslant 6 \\ -1/8 - e^{-t}/24 + e^{6-t}/12 & 6 \leqslant t \leqslant 8 \\ (-1/24 - 1/8e^8 + e^6/6)e^{-t} & \text{otherwise} \end{cases} \tag{46}$$

Hence,

$$\epsilon'(1/c_1) = 0.0377, \ \ \epsilon'(2/c_1) = 0.0413, \ \ \epsilon'(3/c_1) = -0.0965 \tag{47}$$

$$\epsilon'(1/c_2) = 0.0365, \ \ \epsilon'(2/c_2) = 0.041, \ \ \epsilon'(3/c_2) = -0.0601. \tag{48}$$

Then, Eq. (30) becomes as the following form,

$$255\lambda^3 + 326\lambda^2 + 384\lambda - 965 = 0, \tag{49}$$

$$96\lambda^3 - 316\lambda^2 - 381\lambda + 601 = 0, \tag{50}$$

and the roots of Eqs. (49) and (50) are as follows,

$$\lambda_1 = 1.0, \ \ \lambda_2 = -1.1392 + 1.5769i, \ \ \lambda_3 = -1.1392 - 1.5769i, \tag{51}$$

$$\lambda_1 = 1.0, \ \ \lambda_2 = 3.8978, \ \ \lambda_3 = -1.6061, \tag{52}$$

where Eq. (49) with its eigenvalues (51) describes the case of $1/c_1 = 2.357$, while Eq. (50) with its eigenvalues (52) describes the case of $1/c_2 = 2.083$. It is obvious that $|\lambda_1\lambda_2\lambda_3| > 1$ for all cases. Thus, two simple waves are both unstable. However, if $\beta \in (0.94, 0.985)$, only one stable simple wave exists. In this case, we have

$$\ln\frac{(\tau_r + \tau_d)e^{\tau_r} + \tau_d}{\tau_r} = 6.288, \ \ N = 3. \tag{53}$$

Hence, if $1/c < 2.096$ as noted in Eq. (34), the wave is stable. For example, when $\beta = 0.94$, we have a simple wave with velocity of $1/c = 2.06$, and obviously $1/c = 2.06 < 2.096$. Hence, it is stable. Interestingly, if β goes beyond 0.985, the 2-composite wave will appear. Further investigations show that a sTable 2-composite wave and a stable simple wave can coexist when $\beta \in (0.985, 1.04)$. For example, when $\beta = 1$, a 2-composite wave with the velocities $1/c = 2.61$ and $\delta = 2.49$ occurs. From the Eq. (44), the following forms are obtained,

$$\epsilon'(1/c_1 - \delta) = 0.0047, \ \ \epsilon'(2/c_1) = 0.0414, \ \ \epsilon'(3/c_1 - \delta) = 0.0415, \tag{54}$$

$$\epsilon'(1/c_2 + \delta) = 0.0414, \ \ \epsilon'(2/c_2) = 0.0414, \ \ \epsilon'(3/c_2 + \delta) = -0.0101. \tag{55}$$

Hence, we have

$$876\lambda_1\lambda_2^2 - 47\lambda_1\lambda_2 - 414\lambda_2 - 415 = 0, \tag{56}$$

$$727\lambda_2\lambda_1^2 - 414\lambda_2\lambda_1 - 414\lambda_1 + 101 = 0, \tag{57}$$

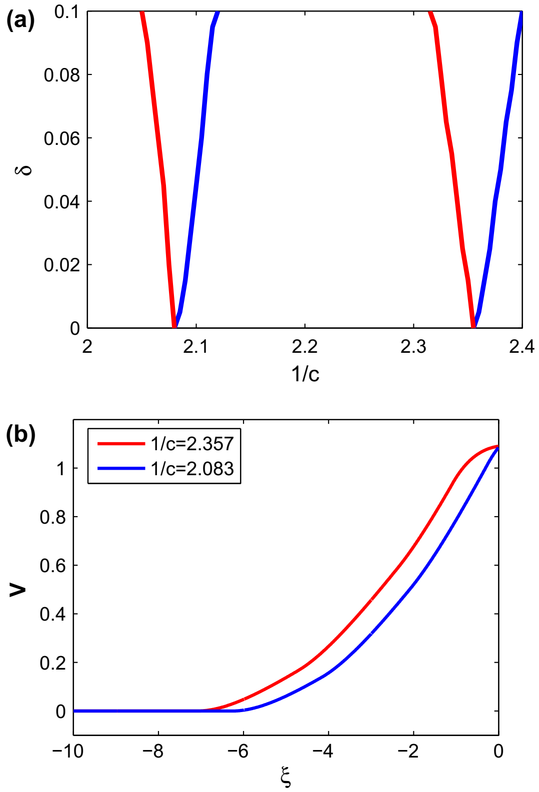

Fig. 3. (a) Plot of the level curves $f(1/c,\delta)=0$ (blue) and $g(1/c,\delta)=0$ (red) when $\tau_r=6,\tau_d=2$ and $\beta=0.93$. Here, it is shown that there are only two intersection points, both of which represent the simple waves. (b) The membrane potentials of the two simple unstable waves. One is with the velocity $c=1/2.357$, the other is with the velocity $c=1/2.083$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and the roots of Eqs. (56) and (57) are

$$\lambda_{11}=1.0,\quad \lambda_{12}=\frac{26685462}{233485501}+\frac{626}{233485501\sqrt{6807092739}},\quad \lambda_{13}=\frac{26685462}{233485501}-\frac{626}{233485501\sqrt{6807092739}};\tag{58}$$

$$\lambda_{21}=1.0,\quad \lambda_{22}=-\frac{10372609}{6053160}+\frac{77}{6053160\sqrt{6807092739}},\quad \lambda_{23}=-\frac{10372609}{6053160}-\frac{77}{6053160\sqrt{6807092739}}.\tag{59}$$

Therefore, $|\lambda_{i1}\lambda_{i2}\lambda_{i3}|<1\ (i=1,2)$. Hence, 2-composite waves in this interval of β are stable. As β further increases to 1.04, the 2-composite wave will disappear, leaving only one stable simple wave with the velocity $1/c<2.096$.

For more details on the impact of the short-term plasticity β on the occurrences of waves, we can choose some typical short-term plasticity values β. Firstly, we choose $\beta=0.93$. Fig. 3 shows the plot of the level curves $f(\delta,1/c)=0$ and $g(\delta,1/c)=0$. It can be observed that there are only two intersections, where two simple unstable waves can appear. For $\beta=1$, the results in Fig. 4 illustrate that only two intersections are acceptable with the conditions $1/c>\delta$, $V'(0)>0$ being required. The upper intersection point denoted by black dot implies the sTable 2-composite traveling wave. Whereas, the lower one denotes the stable simple traveling wave. In addition, the speed of the 2-composite wave is $1/c=2.61$ with $\delta=2.49$, and the velocity of the simple wave is $1/c=1.899$ as illustrated in Fig. 4(a). Furthermore, the coexistence of a stable simple wave together with a stable composite wave in the network can be clearly seen in Fig. 5. For $\beta=1.05>1.04$, only one stable simple wave is shown in Fig. 6. Hence, these results supplement nicely those presented in Fig. 2.

4.2. Case $\tau_r=\tau_d$

In this subsection, we consider $\tau_r=\tau_d=4$. Similar to the above studies, the variations of $1/c$ and δ are shown in Fig. 7 as the short-term plasticity β is varied. It is shown that the 2-composite wave can exist as $\beta\in(0.897,0.918)$. More interestingly, it is found that in this interval, two simple waves can also coexist. However, the wave with high velocity is unstable and the one with lower velocity is stable. We take $\beta=0.91$ as an example. By calculations, we find that there are two simple waves, with the velocity of $1/c_1=2.23, 1/c_2=2.04$. From the piecewise function $\epsilon(t)$, we can get,

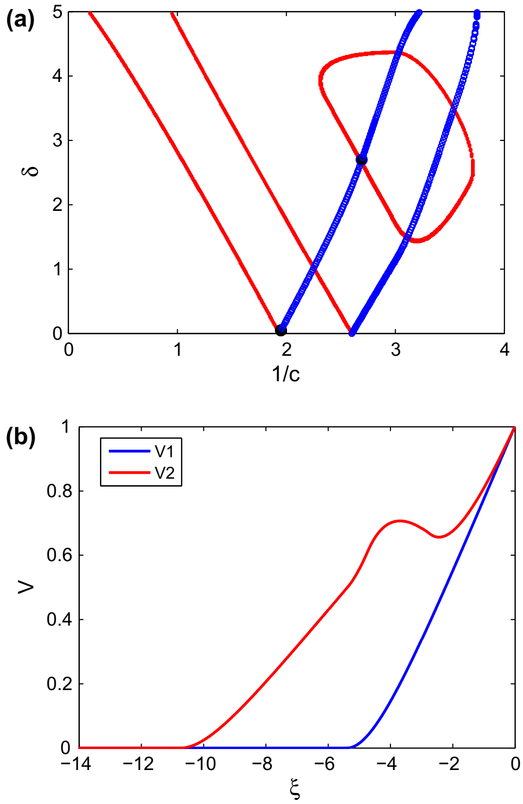

Fig. 4. (a) Plot of the level curves $f(1/c, \delta) = 0$ (blue) and $g(1/c, \delta) = 0$ (red) when $\beta = 1$. Two black dots are admissible, where the upper one denotes the sTable 2-composite wave and the bottom one denotes the stable simple wave. The other intersections can not satisfy the causality criterion given by Eq. (36). (b) $V1$ and $V2$ of the 2-composite wave described by the upper black dot. It can be observed that they do satisfy the causality criterion given by Eq. (36). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

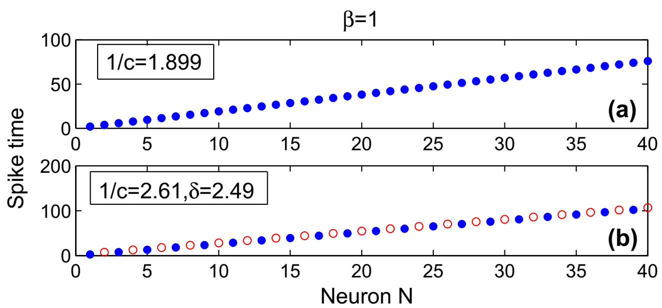

Fig. 5. Bistability between (a) simple wave with the velocity $c = 1/1.899$ and (b) 2-composite wave with the velocity $c = 1/2.61$ and $\delta = 2.49$ in the network. The dots represent the firing times of neurons. In (a) a simple wave propagates, and in (b) different initial conditions lead to the propagation of one 2-composite wave. The parameters are: $\tau_r = 6$, $\tau_d = 2$ and $\beta = 1$.

$$\epsilon'(t) = \begin{cases} 0 & t < 0 \\ (1 - e^{-t})/16 & t \leqslant 6 \\ -1/16 - e^{-t}/16 + e^{4-t}/8 & 6 \leqslant t \leqslant 8 \\ -e^{-t}/16 - e^{8-t}/16 + e^{4-t}/8 & \text{otherwise} \end{cases} \tag{60}$$

Thus

$$\epsilon'(1/c_1) = 0.0558, \quad \epsilon'(2/c_1) = 0.0157, \quad \epsilon'(3/c_1) = -0.0541; \tag{61}$$

$$\epsilon'(1/c_2) = 0.0520, \quad \epsilon'(2/c_2) = 0.0607, \quad \epsilon'(3/c_2) = -0.0301. \tag{62}$$

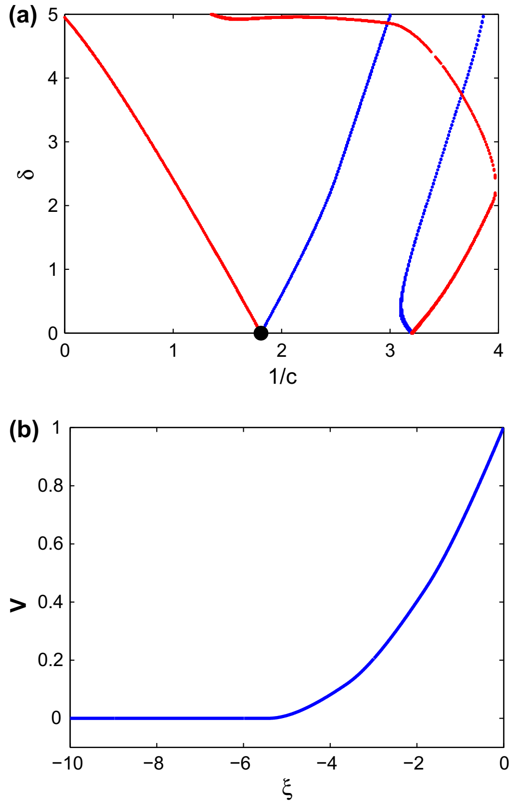

Fig. 6. (a) Plot of the level curves $f(1/c, \delta) = 0$ (blue) and $g(1/c, \delta) = 0$ (red) as $\tau_r = 6, \tau_d = 2$ and $\beta = 1.05$. Only the black dot on the bottom is admissible, which denotes a stable simple wave. The other intersections on the upper are invalid because the causality criterion is not satisfied or $1/c < \delta$ is not realized. (b) Membrane potential of the simple wave at the black dot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

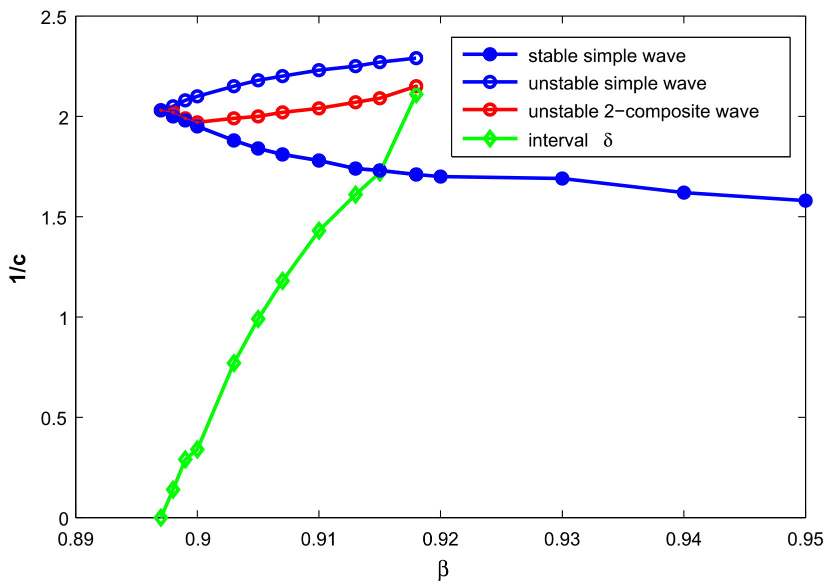

Fig. 7. Transition of the propagation modes induced by the short-term plasticity β as $\tau_r = \tau_d = 4$.

Hence, we can get the following formulas from Eq. (30),

$$64\lambda^3 - 462\lambda^2 - 143\lambda + 541 = 0; \tag{63}$$

$$682\lambda^3 - 431\lambda^2 - 552\lambda + 301 = 0; \tag{64}$$

whose roots are:

$$\lambda_1 = 1.0, \;\; \lambda_2 = 7.3663, \;\; \lambda_3 = -1.1475; \tag{65}$$

$$\lambda_1 = 1.0, \;\; \lambda_2 = -0.8734, \;\; \lambda_3 = 0.5053; \tag{66}$$

in which Eq. (63) describes the unstable case of $1/c_1 = 2.23$ where $|\lambda_1\lambda_2\lambda_3| > 1$, while Eq. (64) describes the stable case of $1/c_2 = 1.78$ where $|\lambda_1\lambda_2\lambda_3| < 1$.

For the 2-composite wave, we have,

$$\epsilon'(1/c_1 - \delta) = 0.0285558, \;\; \epsilon'(2/c_1) = 0.0518, \;\; \epsilon'(3/c_1 - \delta) = -0.0004; \tag{67}$$

$$\epsilon'(1/c_2 + \delta) = 0.0606, \;\; \epsilon'(2/c_2) = 0.0518, \;\; \epsilon'(3/c_2 + \delta) = -0.0589. \tag{68}$$

Based on Eq. (44), it can yield,

$$703\lambda_1\lambda_2^2 - 236\lambda_1\lambda_2 - 471\lambda_2 + 4 = 0, \tag{69}$$

$$384\lambda_2\lambda_1^2 - 502\lambda_2\lambda_1 - 471\lambda_1 + 589 = 0, \tag{70}$$

of which the roots are,

$$\lambda_{11} = 1.0, \;\; \lambda_{12} = \frac{1450424}{4305875} + \frac{4}{4305875\sqrt{127414059361}}, \;\; \lambda_{13} = \frac{1450424}{4305875} - \frac{4}{4305875\sqrt{127414059361}}; \tag{71}$$

$$\lambda_{21} = 1.0, \;\; \lambda_{22} = -\frac{1566769}{967680} + \frac{1}{967680\sqrt{127414059361}}, \;\; \lambda_{23} = -\frac{1566769}{967680} - \frac{1}{967680\sqrt{127414059361}}. \tag{72}$$

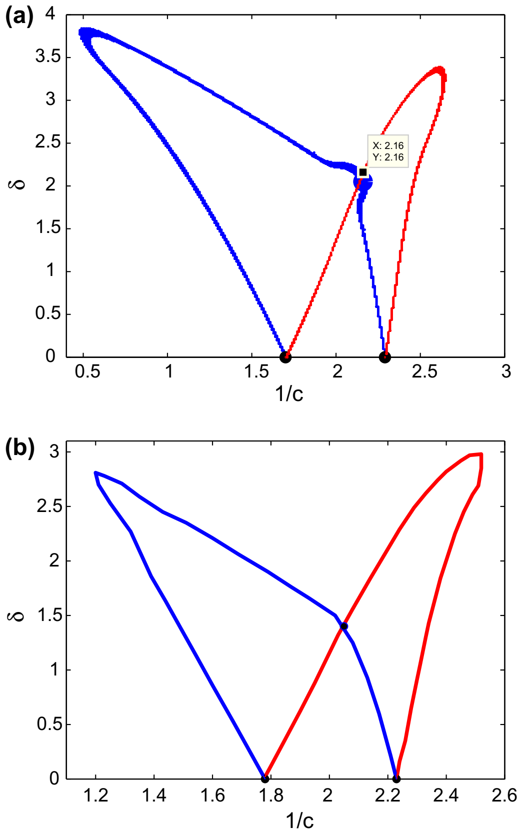

Fig. 8. (a) Plot of the level curves $f(1/c, \delta) = 0$ (blue) and $g(1/c, \delta) = 0$ (red) when $\tau_r = \tau_d = 4$ and $\beta = 0.897$, where $1/c = \delta = 2.16$. The acceptable intersections are emphasized by black dots, the upper one denotes the stable 2-composite wave, the other two lower ones denote two unstable simple waves. (b) Plot of the level curves $f(1/c, \delta) = 0$ (blue) and $g(1/c, \delta) = 0$ (red) when $\tau_r = \tau_d = 4$ and $\beta = 0.91$. The upper one denotes the stable 2-composite wave with $1/c = 2.04$, $\delta = 1.43$, the other two lower ones denote two stable simple waves, where one with the velocity $1/c = 1.78$, the other one with the velocity $1/c = 2.23$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

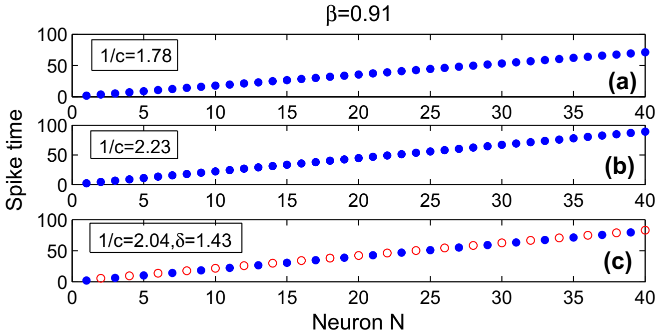

Fig. 9. Three modes of propagations, including two simple waves and one 2-composite wave when $\tau_r = \tau_d = 4$ and $\beta = 0.91$. (a) One simple wave with the velocity $c = 1/1.78$. (b) The other simple wave with the velocity $c = 1/2.23$. (c) One 2-composite wave with the velocity $c = 1/2.04$, $\delta = 1.43$, which is unstable.

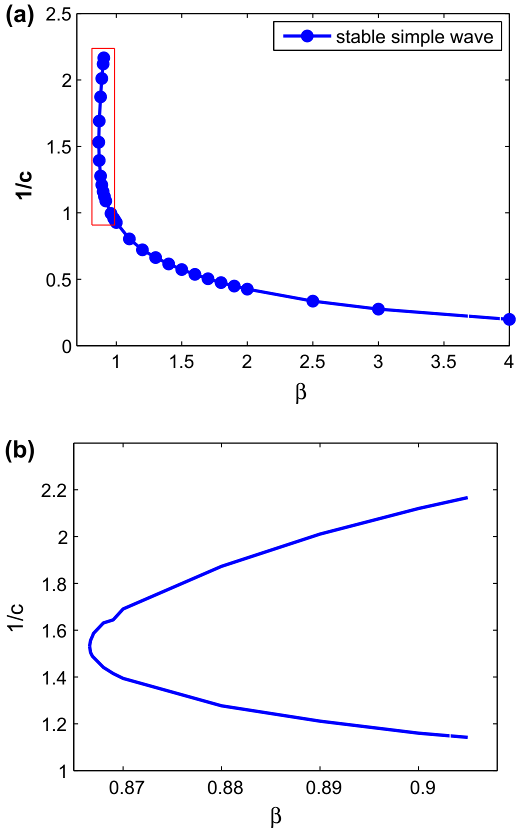

Fig. 10. (a) Transition of propagation modes induced by the short term plasticity β as $\tau_r = 2$ and $\tau_d = 6$. (b) A local amplification of (a), which clearly shows that in this interval, the studied network have two types of the simple waves.

Then $|\lambda_{i1}\lambda_{i2}\lambda_{i3}| = 1.3288 > 1$ $(i = 1, 2)$, which implies that the 2-composite waves in this interval of β are unstable. As $\beta > 0.918$, the upper branch will disappear, leaving only one acceptable branch, which denotes stable simple traveling waves.

For clarity, the results in Fig. 8(a) with $\beta = 0.897$ show that the upper intersection point is $1/c = \delta$, which implies that the 2-composite wave can appear from this moment because $1/c \geqslant \delta$. And, the lower two intersection points denote two simple waves since $\delta = 0$ (This can also be seen in Fig. 8(b)). Three modes of propagation, including two simple waves and one 2-composite can be seen in Fig. 9 as $\tau_r = \tau_d = 4$ and $\beta = 0.91$, where one simple wave has velocity $c = 1/1.78$, the other simple wave has velocity $c = 1/2.23$, and one 2-composite wave has the velocity $c = 1/2.04$ with $\delta = 1.43$.

It is noted that there are two transitions of propagation. One transition is from two modes of simple wave and one 2-composite wave to only one simple wave. The other transition is from unstable simple wave to stable simple wave. More importantly, Ref. [11] pointed out that a necessary condition for the existence of a stable composite wave is $\tau_r > \tau_d$. However, if the depression of synaptic plasticity is considered, unstable composite waves can be obtained even when $\tau_r = \tau_d$.

4.3. Case $\tau_r < \tau_d$

As the last case, we consider $\tau_r = 2$ and $\tau_d = 6$. As the β is increased, the variation of $1/c$ is illustrated in Fig. 10. It can be seen that when $\beta \in (0.867, 0.906)$, there are two stable simple waves. The reason is that the roots of Eq. (44) satisfy $|\Sigma\lambda_i| < 1$. For example, when $\beta = 0.905$, we get two simple waves with the velocity of $1/c_1 = 1.142$ and $1/c_2 = 2.167$. And, from the piecewise function $\epsilon(t)$, we have

$$\epsilon'(t) = \begin{cases} 0 & t < 0 \\ (1 - e^{-t})/8 & t \leqslant 2 \\ -1/24 - e^{-t}/8 + e^{2-t}/6 & 2 \leqslant t \leqslant 8 \\ -e^{-t}/8 - e^{8-t}/24 + e^{2-t}/6 & \text{otherwise} \end{cases} \tag{73}$$

Thus

$$\epsilon'(1/c_1) = 0.0851, \quad \epsilon'(2/c_1) = 0.0711, \quad \epsilon'(3/c_1) = -0.0057; \tag{74}$$

$$\epsilon'(1/c_2) = 0.0851, \quad \epsilon'(2/c_2) = -0.0272, \quad \epsilon'(3/c_2) = -0.04; \tag{75}$$

Eq. (30) gets the following forms,

$$1283\lambda^3 - 697\lambda^2 - 643\lambda + 57 = 0; \tag{76}$$

$$361\lambda^3 + 697\lambda^2 - 658\lambda - 400 = 0; \tag{77}$$

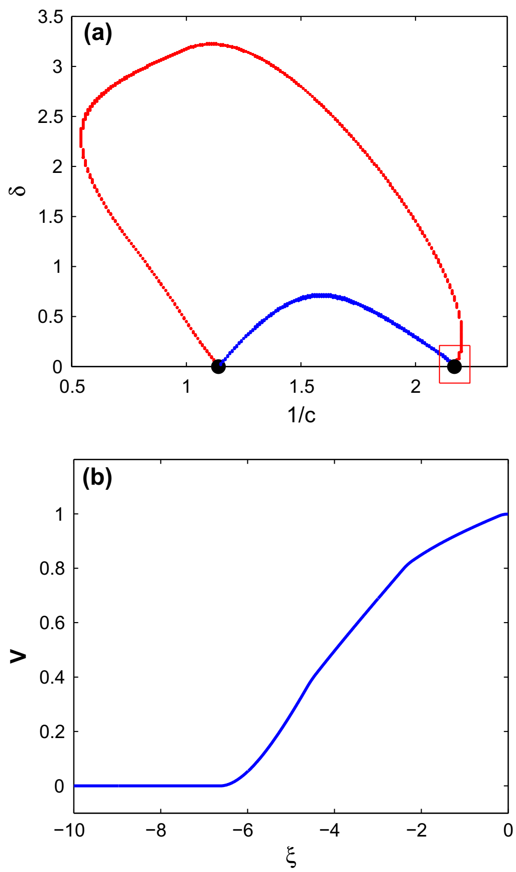

Fig. 11. (a) Plot of the level curves $f(1/c, \delta) = 0$ (blue) and $g(1/c, \delta) = 0$ (red) when $\tau_r = 2$, $\tau_d = 6$ and $\beta = 0.905$, where two intersections are permissible. (b) The membrane potential of the right black dot in the red box is revealed, which denotes that the intersection is acceptable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

their roots are,

$$\lambda_{11} = 1.0, \quad \lambda_{12} = -0.6728, \quad \lambda_{13} = 0.0085; \tag{78}$$
$$\lambda_{21} = 1.0, \quad \lambda_{22} = -0.5391, \quad \lambda_{23} = 0.0824; \tag{79}$$

where Eq. (76) describes the case of $1/c_1 = 1.142$, while Eq. (77) describes the case of $1/c_2 = 2.167$. For both cases, we can get $|\Sigma\lambda_{i1}\lambda_{i2}\lambda_{i3}| < 1$. Therefore, the two simple wave are both stable.

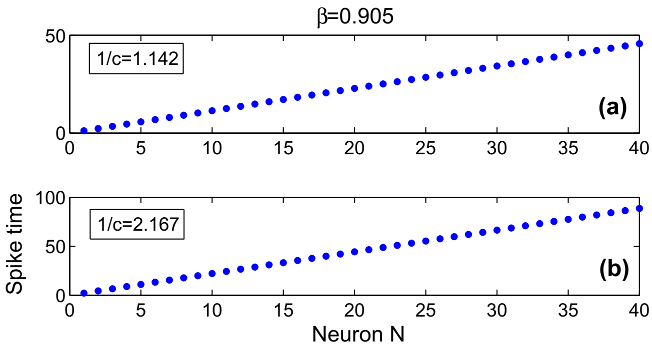

Fig. 12. Two different simple waves when $\tau_r = 2$, $\tau_d = 6$ and $\beta = 0.905$. (a) One simple wave with the velocity $c = 1/1.142$. (b) One simple wave with the velocity $c = 1/2.167$.

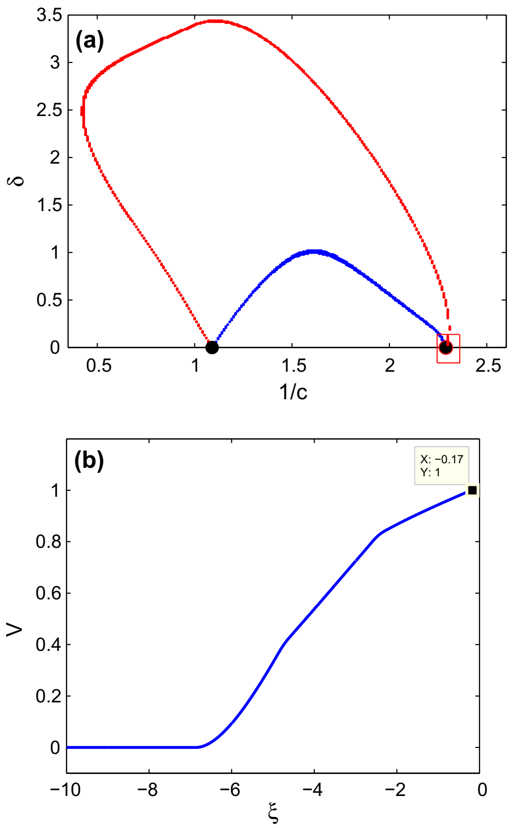

Fig. 13. (a) Plot of the level curves $f(1/c, \delta) = 0$ (blue) and $g(1/c, \delta) = 0$ (red) when $\tau_r = 2$, $\tau_d = 6$ and $\beta = 0.92$, where the black dot in the left is acceptable, which implies a simple wave. The right intersection point is unacceptable because its membrane potential can meet $V(\xi) = 1$, with $\xi < 0$. (b) The membrane potential of the intersection in the red box is shown. It reveals that it is inadmissible because $V(-0.17) = 1$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In addition, as given in Eq. (34), we have

$$\ln\frac{(\tau_r+\tau_d)e^{\tau_r}+\tau_d}{\tau_r}=3.5711,\quad N=3. \tag{80}$$

Hence, if $1/c < 1.19$, the simple wave is stable. As shown in Fig. 10, when $\beta > 0.906$, there is only one stable simple wave. Based this inference, it is concluded that as $\tau_r < \tau_d$, no composite wave can appear.

In particular, two simple waves with different velocities are exhibited as $\beta = 0.905$ in Fig. 11 (also see Fig. 12). However, it is shown in Fig. 13 that as $\beta = 0.92$, only one stable simple wave can be obtained.

5. Conclusion

In sum, we have investigated the propagation of spikes in neuronal networks incorporating short-term plasticity, and analyzed the existence and stability conditions of the traveling waves. Analytical conditions were derived for the existence and stability of the simple waves. In addition, it is shown that the simplest synaptic connection that support 2-composite traveling waves is a network, where each neuron must connect with at least three pre-synaptic neurons. By means of the theoretical analysis and numerical methods, transitions of the simple waves and composite waves have been studied for different combinations of synaptic rise and decay times in dependence on the neuronal short-term plasticity. Interestingly, we have found that for $\tau_r > \tau_d$ the stable and unstable simple waves can coexist, and then transit to a single stable simple wave. Furthermore, a stable simple wave and a composite wave can also coexist, and then transit to a single stable simple wave. For $\tau_r = \tau_d$, it is shown that a stable simple wave, an unstable simple wave and an unsTable 2-composite wave can all coexist, and then transit to a single stable simple wave as the short-term plasticity increases. Whereas for $\tau_r < \tau_d$, we have demonstrated that the transition from the coexistence of two simple waves to only a single simple wave is possible as the short-term plasticity increases. Short-term synaptic plasticity plays an essential role in the realizing neuronal normal functions. It can achieve reliable neural information transmission, adjust the balance between excitation and inhibition of cortex [19,20]. Short-term synaptic plasticity may participate in some high-level brain functions, such as attention, priming, sleep rhythm, learning and memory. In addition, since it is known that the propagation of spikes in neuronal networks is closely related to the processing of information, we hope that the presented results on the synaptic plasticity induced transition of spike propagation in neuronal networks can pave the way for new advances in this vibrant field of research.

Acknowledgments

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