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Properties of the transmission of pulse sequences in a bistable chain of unidirectionally coupled neurons

Yo Horikawa*, Hiroyuki Kitajima

Faculty of Engineering, Kagawa University, Takamatsu 761-0396, Japan

A R T I C L E I N F O

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A B S T R A C T

We study the propagation of pulse sequences in a chain of neurons with sigmoidal input–output relations. The propagating speeds of pulse fronts depend on the widths of the preceding pulses and adjacent pulse fronts interact attractively. Sequences of pulse widths are then modulated through transmission. Equations for changes in pulse width sequences are derived with a kinematical model of propagating pulse fronts. The transmission of pulse width sequences in the chain is expressed as a linear system with additive noise. The gain of the system function increases exponentially with the number of neurons in a high-frequency region. The power spectrum of variations in pulse widths due to spatiotemporal noise also increases in the same manner. Further, the interaction between pulse fronts keeps the coherence and mutual information of initial and transmitted pulse sequences. Results of an experiment on an analog circuit confirm these properties.

1. Introduction

Coupled nonlinear dynamical systems have received much attention in various fields, e.g. in the dynamics of neuronal networks, immune networks and ecological systems [11,21,38,47]. A ring neural network, which is a ring of unidirectionally coupled neurons with sigmoidal input–output relations, is an example of a typical coupled system. It was proposed as a simple model of neural networks to generate spontaneous oscillations [2]. It has been studied in the field of recurrent neural networks [3,24] and mathematically as an example of a cyclic feedback system [17], and its various properties have been derived. When the strength of coupling is larger than a critical value, the network is globally bistable if the number of inhibitory (negative) couplings is even; in contrast, it has a stable periodic solution and oscillates if the number of inhibitory couplings is odd. In the former bistable networks, it has been shown that delays cause various spatiotemporal patterns [22,56] and long-lasting transient oscillations [4,5,46]. The latter oscillations are qualitatively the same as those obtained with a ring oscillator, which is a ring of inverters and buffers, and this type of network is widely used as a variable-frequency oscillator in digital circuits [23].

It has recently been shown that the duration of transient oscillations in bistable ring neural networks increases exponentially with the number of neurons, even in the absence of delays [29,30,37]. Such exponential dependence of transient time on system size is of wide interest since systems never reach their asymptotically stable states within a practical period of time, and thus their transient states can play a more important role than the stable states. This phenomenon has been found in one-dimensional reaction-diffusion equation models describing phase transition, in which the motion of unstable fronts or kink patterns is extremely slow and the duration of these patterns increases exponentially with domain lengths [9,13,28,36]. Further, it has been shown that such extremely slow motion of various patterns exists in several high-dimensional reaction-diffusion systems related to phase separation and coarsening in binary alloys, the exit problem for diffusion in a potential well, and spike patterns in an activator–inhibitor model for morphogenesis; this slow motion is referred to as metastable dynamics ([54,55], and references therein). It has also been found in more complicated systems and patterns, e.g. transient chaos in coupled map lattices [34] and a reaction-diffusion model [53], and transient patterns in some neural network models [6,19,51,58].

The transient oscillations in ring neural networks are traveling waves rotating in the networks, and the mechanism of exponential increases in their duration has been described with a kinematical model [30]. There is an interaction between the multiple traveling fronts in the network, the strength of which decreases exponentially with their distances, i.e. the number of neurons between them. The interaction is attractive, and it increases the speeds of the fronts as distances to the forward fronts decrease. As a result, adjacent fronts with small distances collide one by one, and the network finally reaches a bistable steady state so that the oscillation ceases. However, the oscillation

* Corresponding author. Tel.: +81 87 864 2211; fax: +81 87 864 2262.
E-mail address: horikawa@eng.kagawa-u.ac.jp (Y. Horikawa).

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lasts an exponentially long time due to the exponentially small interaction. It was also shown that spatiotemporal noise of intermediate strength increases the duration of transient oscillations due to the nonlinearity in the interaction, while spatial randomness reduces the increasing rate from an exponential to a polynomial order of the number of neurons [32]. The interaction between traveling waves and spatiotemporal noise has also been shown to cause a correlation in a series of periods in oscillations in networks of a ring oscillator type [31].

It is known that similar kinematics exist in the propagation of a spike train in a nerve fiber; this phenomenon is referred to as the dispersion relation [43,49]. The speeds of spikes decrease in the relative refractory period after the passage of the previous spikes, during which time the nerve membrane is in the process of recovering to the resting state and its excitability is reduced. In contrast to a ring neural network, the interaction between nerve spikes is repulsive and periodic nerve spike trains are stable. It has been shown that the interspike intervals of a spike train smooth during propagation and that the nerve fibers work as a low-pass filter [25,26].

Concerning signal transmission as spike propagation in a nerve fiber, an open chain of unidirectionally coupled neurons with the same sigmoidal input–output relations as a ring neural network can work as a transmission line of binary signals. Computer simulation can show that stimuli given at one end of the chain are magnified to one of the bistable states of the neurons, depending on their signs. A pulse sequence is then generated, being propagated in the chain and transmitted to the other end. The propagation of waves in such synaptically coupled neurons has been observed in activity patterns in neural tissue. It has then been studied with ion channel models in which synaptic couplings are involved instead of diffusive couplings [12,20,52]. The existence and stability of these traveling waves and their properties have also been derived by integro-differential equations with nonlocal spatiotemporal interaction for firing rate models [1,10,15] and integrate-and-fire models [8,14]. Further, arrays of coupled bistable elements have also been studied from the perspective of stochastic resonance in spatially extended systems [16,40,42,50]. It has then been shown that stochastic resonance in the form of the noise-sustained propagation of signals and waves occurs in diffusively coupled diode resonators [41], one-way coupled bistable systems [57], two-way coupled bistable oscillators [36] and a cascade of two-state threshold elements [7]. In a chain of neurons, it is expected that the interaction between pulse fronts as well as spatiotemporal noise causes characteristic changes in a pulse sequence during propagation. These changes result in the modulation of signals encoded in a pulse sequence, similar to that occurring in a nerve fiber.

In this study, we considered signal transmission in an open chain of unidirectionally coupled neurons in the presence of spatiotemporal noise. We derived a kinematical model of the propagation of pulse fronts (edges) occurring in the same way as in a ring neural network. Adjacent pulse fronts interact attractively through the pulse widths in addition to fluctuations due to noise. Propagating pulse sequences are unstable due to the attractive interaction, and pulses tend to collide and disappear. However, pulses can propagate without disappearance over an exponentially large number of neurons since the interaction decreases exponentially with the pulse width. We then formulated the transmission of a pulse width sequence as a linear system with additive noise. Both the gain in the transfer function of the system and the power spectrum of variations due to noise increase exponentially with the number of neurons in high-frequency regions. Further, the interaction between pulse fronts prevents the coherence and mutual information of input and output pulse width sequences from decreasing through transmission due to noise.

The rest of the paper is organized as follows. In Section 2, a model of a chain of neurons is explained and its behavior is shown with a computer simulation. In Section 3, a kinematical model of the propagation of pulse fronts is derived, and changes in pulse widths during propagation are expressed with this model. Properties of changes in a pulse sequence are shown in Section 4. The transfer function of transmission, the power spectrum of variations due to noise, and the coherence and mutual information of initial and transmitted pulse sequences are derived. It is also qualitatively explained that the mean pulse width increases logarithmically with the number of neurons due to the disappearance of pulses, and this explanation is confirmed by computer simulation. Further, the method and results of an experiment with an analog circuit of the chain is shown in Section 5. Finally, our conclusion and discussion are given in Section 6.

2. Chain of neurons

We consider a chain of unidirectionally coupled neurons with sigmoidal input–output relations and a signaling problem on it. A model equation is

$$\begin{aligned}
&\mathrm{d}x_1(t)/dt = -x_1(t)+s(t)\\
&\mathrm{d}x_n(t)/dt = -x_n(t)+f(x_{n-1}(t))+\sigma_x w_n(t) \quad (2 \le n \le N)\\
&f(x) = \tanh(gx)(|g|>1)\\
&E\{w_n(t)\}=0, \quad E\{w_n(t)w_{n'}(t')\} = \delta_{nn'}\cdot\delta(t-t')
\end{aligned} \tag{1}$$

where x_n is the state of the nth neuron, N the number of neurons, $f(x)$ the output function of neurons of sigmoidal form and g the output gain. Neurons are unidirectionally coupled in a chain and the output of each neuron is transmitted to the next neuron. Gaussian white noise $w_n(t)$ with the strength σ_x is also added to each neuron independently. This model of a chain of neurons is regarded as a noisy signal transmission line. When a stimulus $s(t)$ is added to the first neuron, it is transmitted from neurons to neurons. When a small constant stimulus $s(t)=s_0(|s_0|\ll 1)$ is added, its absolute value is amplified since the absolute value of the output gain is larger than unity ($|g|>1$). It approaches one of the stable steady states $\pm xp(xp=f(x_p)>0)$ through transmission depending on the sign of s_0 and g. The absolute value of the steady states increases to unity as the gain increases ($|xp|\to 1$ for $|g|\to\infty$). In the following we consider excitatory couplings (positive gains), i.e. $g>1$. It should be noted that obtained results are applicable to chains of neurons with negative gains ($g<-1$). In fact, chains of neurons with negative gains are transformed to those with positive gains by changing the signs of the states of alternate neurons, e.g. $x_{2m}\to -x_{2m}$.

Let a stimulus $s(t)$ be the following periodic binary rectangular pulses with variations in pulse widths.

$$\begin{aligned}
s(t) &= -x_p<0 \quad (t_{2k-1}(0)<t<t_{2k}(0)) \quad (k\ge 0,\ t_{-1}(0)=-\infty)\\
&= x_p>0 \quad (t_{2k}(0)<t<t_{2k+1}(0))\\
T_j(0) &= t_j(0)-t_{j-1}(0) = m(T)+\sigma_T w_j \quad (j\ge 1, \quad \sigma_T \ll m(T))\\
E\{w_j\} &= 0, \quad E\{w_j w_{j'}\} = \delta_{j,j'}
\end{aligned} \tag{2}$$

where we assume that the stimulus is fixed to $s=-x_p$ for $t<t_0(0)$, and the states of all neurons in the chain are also set to be $-x_p$ for $t<t_0(0)$, which is the negative steady state (resting state) of the chain. The first change in the stimulus to $s=x_p$ occurs at $t=t_0(0)$ and then the stimulus changes its sign at t_j alternately. The temporal width of the jth pulse in the stimulus, i.e. an interval $t_j(0)-t_{j-1}(0)$ between the $j-1$st and jth changes in the sign of the stimulus is denoted by $T_j(0)$. The mean of the pulse widths is $m(T)$