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Effects of asymmetry in an output function on the pinning of rotating waves in a ring neural oscillator with asymmetric bidirectional coupling and self-coupling

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ABSTRACT

Effects of asymmetry in a sigmoidal output function of neurons on rotating waves in a ring of neurons with asymmetric bidirectional coupling and self-coupling were studied. Propagation of wave fronts in rotating waves failed, i.e., the pinning of rotating waves occurred not only when self-coupling was excitatory but also when self-coupling was inhibitory, in which there were unsaturated neurons at wave fronts. Conditions for the pinning of wave fronts were derived by using a piecewise linear output function. The pinning conditions depended on whether bidirectional coupling was excitatory or inhibitory in the presence of asymmetry in an output function.

1. Introduction

A ring of coupled neurons with sigmoidal input–output relations, which is referred to as a ring neural network, has attracted much attention. A sigmoidal neuron is a firing rate model of a neuron or neural assembly [1–3] and it is widely used in artificial neural networks. A ring of unidirectionally coupled sigmoidal neurons can show stable oscillations when the number of inhibitory connections is odd [4]. The oscillations of the states of neurons are due to a rotating wave propagating in a ring. Such a ring is qualitatively the same as a ring oscillator, which is a closed loop of inverters and buffers, and this type of a network is widely used as a variable-frequency oscillator [5]. Although the structure of a ring neural network is simple, its properties have been studied as a basic model of a recurrent neural network [6,7] and mathematically as a cyclic feedback system [8]. The formation of spatiotemporal patterns in one-dimensional and two-dimensional arrays of piecewise linear neurons with local coupling and their application to signal processing have been studied as a cellular neural network [9–14]. Further, a lot of work has been carried out on effects of delays on spatiotemporal patterns in a ring of sigmoidal neurons, e.g., see references in [15]. Although most of their studies are restricted to rings of small numbers (from two to six), studies on rings of general (not specific) numbers of neurons have been carried out [16–18]. It has been shown that delays cause long-lasting rotating waves and oscillations in a ring of unidirectionally coupled neurons [19–21]. It has also been shown that transient rotating waves in a ring with unidirectional coupling are dynamically metastable even in the absence of delays, i.e. their duration increases exponentially with the number of neurons [22]. Effects of inertial terms [23], spatiotemporal noise and asymmetry in a sigmoidal output function of neurons [24] on metastable dynamical transient rotating waves in a ring of unidirectionally coupled neurons have then been studied.

Such propagating waves in rings of coupled systems have drawn a lot of interest in various fields and have been widely studied. The existence and stability of traveling waves in lattice dynamical systems and coupled map lattices have been studied extensively and we just mention some review papers [25–27]. Concerning neural networks, rings of synaptically coupled spiking neurons have been employed as models of central pattern generators in the central nervous system, e.g., for early work [28,29]. Then, a lot of work has been carried out on rings of various kinds of neuron models, e.g., see references in [15,30]. Discrete-time dynamics of ring neural networks has also been studied [31,32]. Further, wave propagation in a large population of neurons in the brain, e.g., the cortex, hippocampus and thalamus, have been examined by neural field models, which are described by

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integro-differential equations with sigmoidal functions of neural activity; for review [33,34]. Apart from the nervous system and neural networks, studies on traveling waves as splay-phase synchronized oscillations in rings of coupled nonlinear oscillators (van der Pol oscillators) date back to [35–37]. Then, a lot of work on rings of coupled various kinds of oscillators has been carried out in electronics, physics and biology; for recent work, e.g., overdamped Duffing oscillators [38,39], the Stuart–Landau oscillators [40–42] and delayed-feedback optoelectronic oscillators [43]. For example, rings of chaotic oscillators have been examined in relation to chaos synchronization. Then, not only periodic rotating waves but also quasiperiodic, chaotic and hyperchaotic rotating waves have been observed in rings of unidirectionally coupled Chua's circuits [44–48], Lorenz systems [44,46,47,49–52] and Duffing oscillators [53]. Transient chaotic rotating waves have also observed in rings of unidirectionally coupled Bonhoeffer–van der Pol oscillators [54] and Lorenz systems [55]. Long-lasting metastable dynamical transient rotating waves, which emerge in a ring of unidirectionally coupled sigmoidal neurons as mentioned above, have been found in rings of unidirectionally coupled various systems: overdamped Duffing oscillators [56], cubic maps [57], parametric oscillators [58], Lorenz systems [55] and Bonhoeffer–van der Pol models [30]. For practical applications, these metastable dynamical rotating waves have been reported in a ring of ferromagnetic cores [59] and a generalized repressilator model, which is one of genetic regulatory networks [60,61], as well as traffic jams in a car-following model for a traffic flow problem [62].

In this paper, we consider a ring of sigmoidal neurons with asymmetric bidirectional coupling and self-coupling as well as asymmetry in an output function. We then study conditions for the pinning (propagation failure) of wave fronts, which seem not to have been examined. A ring with unidirectional coupling is special structure and bidirectional coupling and self-coupling are generally included in neural networks. When bidirectional coupling or self-coupling exists, the pinning of rotating waves can occur, i.e. the propagation of their wave fronts fails and rotating waves change into steady states. Such pinning of wave propagation is commonly seen in spatially discrete coupled systems [63–68].

When a sigmoidal output function is symmetric and piecewise linear, conditions for the pinning of wave fronts in the presence of excitatory (positive) self-coupling have been derived [12,13]. Wave fronts are pinned when the strength of excitatory self-coupling is larger than asymmetry in the strength of bidirectional coupling. Excitatory self-coupling tends to keep the states of neurons unchanged. Then the stability of steady states increases and wave fronts are hard to propagate. It has also been shown that the pinning of rotating waves occurs even when self-coupling is inhibitory (negative) [15]. Wave fronts in rotating waves and their pinned states have neurons the sigmoidal output of which is not saturated, which correspond to steady states obtained for symmetric bidirectional coupling [10,12]. Inhibitory self-coupling tends to change the signs of the states of neurons and thus makes wave fronts propagate. However, the states of neurons at wave fronts become unsaturated so that pinning can occur.

Rotating waves, which are caused by qualitatively the same mechanism as those in a ring of coupled sigmoidal neurons and show metastable transient dynamics, have also been shown to emerge in a ring of synaptically coupled Bonhoeffer–van der Pol models [30], i.e., spiking neuron models. Adjacent neurons are coupled unidirectionally with slow inhibitory synapses. In its steady state, neurons in a firing state and a resting state are alternately located. The rotating waves take the form of propagating oscillations, in which successive two neurons are in the same states (resting–resting or firing–firing) and the location of the inconsistency propagates in the direction of coupling. The firing and resting states of a spiking neuron correspond to a positive and negative steady states of a sigmoidal neuron, respectively. The two states of a spiking neuron differ qualitatively and the difference can be modeled by asymmetry in the output of a sigmoidal neuron. Thus, effects of asymmetry in a sigmoidal neuron are of importance in order to study the pinning of rotating waves in rings of such spiking neurons with asymmetric bidirectional coupling and self-coupling.

We derived conditions for the pinning of wave fronts in the presence of asymmetry in a sigmoidal output function by using a piecewise linear output function. There were multiple separated pinned regions in a plane of the strengths of asymmetric bidirectional coupling and self-coupling, in which the numbers of unsaturated neurons at wave fronts were different with each other. Effects of asymmetry in an output function depended on whether bidirectional coupling was excitatory or inhibitory. When bidirectional coupling was excitatory, pinned regions shifted monotonically along the axis of the strength of asymmetric bidirectional coupling as asymmetry in an output function increased. Wave fronts were pinned when asymmetry in an output function was compensated with asymmetric bidirectional coupling. When bidirectional coupling was inhibitory, changes in pinned regions were more complicated and depended on the parity of the number of unsaturated neurons at wave fronts. When the number of unsaturated neurons at a wave front was odd, pinned regions shifted along the axis of the strength of asymmetric bidirectional coupling like the shifts for excitatory coupling, but in a different manner. When the number of unsaturated neurons was even, the size of pinned regions changed along the axis of the strength of self-coupling. Then rotating waves were still always pinned when bidirectional coupling was symmetric. Conditions for the pinning also changed when one of positive and negative steady states was unsaturated, in which only wave fronts with even numbers of unsaturated neurons existed.

In the rest of the paper, a model equation of a ring of sigmoidal neurons with asymmetric bidirectional coupling, self-coupling and an asymmetric sigmoidal output function is introduced in Section 2. The bifurcations of its steady states and limit cycles are explained and the patterns of rotating waves are shown. In Sections 3 and 4, rings with excitatory and inhibitory bidirectional coupling are dealt with, respectively. It is shown that there are wave fronts having neurons in unsaturated states when self-coupling is inhibitory. Then, conditions for the pinning of wave fronts are derived by using a piecewise linear output function. Finally, conclusion and future work are given in Section 5. In Appendix A, the existence and stability of steady solutions to associated linear differential equations for unsaturated neurons are shown.

2. A ring of sigmoidal neurons and rotating waves

We consider the following ring of sigmoidal neurons with asymmetric bidirectional coupling and self-coupling.

$$dx_n/dt = -x_n + \frac{c(1+d)}{2} f(gx_{n-1}) + \frac{c(1-d)}{2} f(gx_{n+1}) + sf(gx_n)$$
$$f(x) = \{1-\exp[-2x/(1-e^2)]\}/\{1/(1+e)+\exp[-2x/(1-e^2)]/(1-e)\}$$
$$(1 \le n \le N, \quad x_{n \pm N} = x_n, \quad g > 0, \quad d \ne 0, \quad -1 < e < 1) \tag{1}$$

where x_n is the state of the nth neuron, f is an output function of a neuron with an asymmetric shift e, g is an output gain, c is the strength of bidirectional coupling between adjacent neurons, d is asymmetry in bidirectional coupling, and s is the strength of self-coupling. A periodic boundary condition is imposed so that a total of N neurons make a closed loop. The asymptotic values of f at infinity of x are $f(x) \to 1+e$ (>0) ($x \to \infty$) and $f(x) \to -1+e$ (<0) ($x \to -\infty$), while $f(x) = \tanh(x)$ when $e=0$. The origin ($x_n=0$