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Effects of asymmetric coupling and self-coupling on metastable dynamical transient rotating waves in a ring of sigmoidal neurons

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HIGHLIGHTS

- Metastable dynamical transient rotating waves in a ring neural network are studied.
- A kinematical equation for a change in bump length of rotating waves is derived.
- Conditions for the stabilization and pinning of rotating waves are obtained.
- An exponential growth rate of the duration of transient rotating waves is obtained.
- The growth rate depends on the strength of asymmetric coupling and self-coupling.

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ABSTRACT

Transient rotating waves in a ring of sigmoidal neurons with asymmetric bidirectional coupling and self-coupling were studied. When a pair of stable steady states and an unstable traveling wave coexisted, rotating waves propagating in a ring were generated in transients. The pinning (propagation failure) of the traveling wave occurred in the presence of asymmetric coupling and self-coupling, and its conditions were obtained. A kinematical equation for the propagation of wave fronts of the traveling and rotating waves was then derived for a large output gain of neurons. The kinematical equation showed that the duration of transient rotating waves increases exponentially with the number of neurons as that in a ring of unidirectionally coupled neurons (metastable dynamical transients). However, the exponential growth rate depended on the asymmetry of bidirectional coupling and the strength of self-coupling. The rate was equal to the propagation time of the traveling wave (a reciprocal of the propagation speed), and it increased near pinned regions. Then transient rotating waves could show metastable dynamics (extremely long duration) even in a ring of a small number of neurons.

1. Introduction

Rings of coupled neurons (ring neural networks) have been of wide interest since they can generate various spatiotemporal patterns and oscillations despite their simple structure. Central pattern generators, which control rhythmic motion such as walking, flying and swimming, have been modeled by neural networks with closed loops, e.g., for early work (Friesen & Stent, 1977; Kling & Székely, 1968) and reviews (Friesen & Stent, 1978; Ijspeert, 2008; Pearson, 1993). A lot of work has been carried out on the synchronization and bifurcations of oscillations in rings of various kinds of neuron models, e.g., (Bazhenov, Huerta, Rabinovich, & Sejnowski, 1998; Bonnin, 2009; Enjieu Kadji, Chabi Orou, & Woafo, 2007; Ermentrout, 1985; Friesen & Stent, 1977; Grasman & Jansen, 1979; Kitajima, Yoshinaga, Aihara, & Kawakami, 2001; Kyprianidis & Stouboulos, 2003; Linkens, Taylor, & Duthie, 1976; Oprisan, 2010; Perlikowski, Yanchuk, Popovych, & Tass, 2010; Somers & Kopell, 1993; Still & Le Masson, 1999; Wang, Lu, & Chen, 2007; Wang, Lu, Chen, & Guo, 2006; Yanchuk & Wolfrum, 2008). Ring networks with identical neurons and coupling have been dealt with from the viewpoint of group theory due to their symmetry (Bressloff, Coombes, & de Souza, 1997; Buono, Golubitsky, & Palacios, 2000; Collins & Stewart, 1994; Golubitsky, Stewart, & Schaeffer, 1988). In this paper, a ring of coupled simple neuron models with sigmoidal input–output relations is considered. It has been shown that a ring of unidirectionally coupled sigmoidal neurons can show oscillations if it has an odd number of inhibitory coupling (Amari, 1978). Such a ring is qualitatively the same as a ring oscillator, which is a ring of inverters and buffers in wide use as a variable-frequency oscillator in digital circuits (Gutierrez, 1999). Although a ring of sigmoidal neurons is quite simple, its properties have been studied as a basic model of recurrent neural networks (Atiya & Baldi, 1989; Hirsh, 1989) and as a cyclic feedback

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system with monotone dynamics (Gedeon, 1998). Pattern formation in a ring of piecewise linear neurons and its application to signal processing have been studied as a cellular neural network (Chua & Yang, 1988; Crounse, Chua, Thiran, & Setti, 1996; Setti, Thiran, & Serpico, 1998; Thiran, 1997; Thiran, Crounse, Chua, & Hasler, 1995; Thiran, Setti, & Hasler, 1998). It has been shown that its discrete-time version has multiple periodic orbits (Blum & Wang, 1992; Pasemann, 1995). Effects of delays have also been extensively studied on a ring of sigmoidal neurons with delays. Various oscillations, spatiotemporal patterns and their bifurcations have been shown in the cases of unidirectional coupling (Guo & Huang, 2007b; Li & Wei, 2005b; Wei & Li, 2004; Wei & Velarde, 2004; Wei & Zhang, 2008), both unidirectional and self-coupling (Campbell, 1999; Campbell, Ruan, & Wei, 1999; Li & Wei, 2005a; Yuan & Li, 2010), bidirectional coupling (Bélair, Campbell, & van den Driessche, 1996; Marcus & Westervelt, 1989; Wu, 1998; Zou, Huang, & Chen, 2006; Zou, Huang, & Wang, 2010), both bidirectional and self-coupling (Campbell, Yuan, & Bungay, 2005; Guo, 2005; Guo & Huang, 2003, 2006, 2007a; Huang & Wu, 2003; Hu & Huang, 2009; Yuan & Campbell, 2004) and asymmetric coupling (Lin, Lemmert, & Volkmann, 2001; Xu, 2008; Yan, 2006; Zhang & Guo, 2003). Of particular interest are long-lasting transient oscillations in a ring of unidirectionally coupled sigmoidal neurons with delays (Babcock & Westervelt, 1987; Baldi & Atiya, 1994; Pakdaman, Malta, Grotta-Ragazzo, Arino, & Vibert, 1997).

Several kinds of information processing in nervous systems are considered to be carried out during transient states, not asymptotically stable states such as equilibrium and limit cycles, which range from sensory response to decision making (Fingelkurts & Fingelkurts, 2004; Friston, 1997, 2001; Kelso, 1995; Rabinovich, Huerta, & Laurent, 2008; Rabinovich, Varona, Selverston, & Abarbanel, 2006; Werner, 2007). It is because asymptotic states may not be realized within a short response time to stimuli. Thus transient dynamics can play a more important role in neural information processing than asymptotic states. For instance, chaotic itinerancy (Tsuda, 1991, 2001, 2009) and winnerless competition networks (Komarov, Osipov, & Suykens, 2010; Nekorkin, Kasatkin, & Dmitrichev, 2010; Rabinovich et al., 2001) for olfactory systems, which are related to heteroclinic cycles, have been widely studied. Further, long-lasting chaotic transients have been found in several neural networks: diluted random networks of integrate-and-fire neurons (Jahnke, Memmesheimer, & Timme, 2008; Zillmer, Brunel, & Hansel, 2009; Zillmer, Livi, Politi, & Torcini, 2006, 2007; Zumdieck, Timme, Geisel, & Wolf, 2004), discrete time recurrent networks of spiking neurons (Cessac, 2008; Cessac & Viéville, 2008; Destexhe, 2009; El Boustani & Destexhe, 2009; Kumar, Schrader, Aertsen, & Rotter, 2008) and a ring of Bonhoeffer–van der Pol models (Horikawa & Kitajima, 2012d).

Recently, metastable dynamical transient rotating waves have been found in a ring of unidirectionally coupled sigmoidal neurons without delays (Horikawa & Kitajima, 2009a). The system has a pair of stable spatially uniform steady states and is globally bistable. In addition, unstable traveling waves rotating in a ring can be generated owing to unidirectional coupling, and their instability decreases exponentially with the number of neurons. In the presence of these weakly unstable traveling wave solutions, rotating waves generated in transients show metastable dynamics: their duration (life time) increases exponentially with the number of neurons. Then the states of neurons can continue to oscillate within a practical time when the number of neurons is large, although the oscillations are unstable. As characteristics of these metastable dynamical transients, it has been shown that the duration of randomly generated rotating waves is distributed in a power law form and that spatiotemporal noise with intermediate intensity could increase the duration of rotating waves (noise-sustained propagation) (Horikawa & Kitajima, 2009c). These properties have been derived from a kinematical equation for the propagation of wave fronts in the rotating waves.

Their kinematics is qualitatively the same as that of a kink (front) and pairs of kink and antikink (pulses) in a symmetric bistable reaction–diffusion equation (the time-dependent Ginzburg–Landau equation, also called as the Allen–Cahn equation and the Schlögl model) (Bronsard & Kohn, 1990; Carr & Pego, 1989; Ei & Ohta, 1994; Fusco & Hale, 1989; Kawasaki & Ohta, 1982). There is interaction between a kink and antikink, the strength of which decreases exponentially with the distance between them. The motion of these transient spatial patterns is very slow when distance between a kink and antikink is large. Such extremely slow motion of interfaces is referred to as dynamical metastability or metastable dynamics. Metastable dynamical patterns have been found in several reaction–diffusion (-convection) systems as well as in two and three-dimensional spaces (Ward, 1996, 1998, 2001). Exponentially weak interaction also exists between pulses in neural field models described by nonlocal integro-differential equations (Bressloff, 2005), which are concerned with the propagation of electrical activity in brain slices. This interaction is due to an exponential decrease in a synaptic weight function with distance. Dispersion relation between speeds and interspike intervals in spikes propagating in a nerve fiber, and generally in excitable media described by reaction–diffusion equations, also has the form of an exponential function (Meron, 1992; Rinzel & Keller, 1973). This exponential dependence of a propagation speed on an interspike interval comes from the linear relaxation of membrane activity in a recovery process. In both neural cases, a single pulse (spike) is stable in itself and pulse locations and interspike intervals change. The changes in transients might thus not be of much interest, but they can have considerable effects on signal transmission in the refractory period in a nerve fiber (Horikawa, 1992).

The metastable dynamical rotating wave in a ring of unidirectionally coupled sigmoidal neurons is a spatially discretized version of metastable dynamical patterns in the spatially continuous systems. It has been shown that such metastable dynamical transient rotating waves exist commonly in bistable rings of unidirectionally coupled systems: bistable elements (Horikawa, 2012), cubic maps (Horikawa & Kitajima, 2012a), Lorenz systems (Horikawa & Kitajima, 2012b) and parametric oscillators (Horikawa & Kitajima, 2012c). Further, metastable dynamical rotating waves in the form of propagating oscillations have been found in a ring of synaptically coupled Bonhoeffer–van der Pol models, in which neurons alternate between firing and resting states in transients (Horikawa, 2011). Long-lasting transient rotating waves shown in a ring of ferromagnetic cores (Lindner & Bulsara, 2006) and a generalized repressilator model (one of genetic regulatory networks) (Strelkowa & Barahona, 2010, 2011) are also considered to be caused by the same metastable dynamics.

In this study, we consider the effects of asymmetric coupling and self-coupling on metastable dynamical transient rotating waves in a ring of sigmoidal neurons. Bidirectional coupling exists widely in nervous systems and has been employed in models of central pattern generators (Friesen & Stent, 1977, 1978; Ijspeert, 2008; Kling & Székely, 1968; Pearson, 1993), for instance. It plays an important role in applications of neural networks, e.g., associative memory and recurrent neural networks. Self-coupling or self-feedback can also have a large effect on the dynamics of neural networks. It has been shown that self-coupling can cause oscillations in a pair of excitatory and inhibitory sigmoidal neurons (Amari, 1972; Wilson & Cowan, 1972). Although spatiotemporal patterns (steady states and limit cycles) generated in a ring of piecewise linear neurons with asymmetric coupling and self-coupling have been studied (Setti et al., 1998; Thiran, 1997; Thiran et al., 1998), its transient dynamics hardly seems to have been dealt with. In a ring of sigmoidal neurons with symmetric bidirectional coupling and without self-coupling, pairs of steady