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Effects of self-coupling and asymmetric output on metastable dynamical transient firing patterns in arrays of neurons with bidirectional inhibitory coupling

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HIGHLIGHTS

- Metastable dynamical transient patterns in arrays of inhibitorily coupled neurons are studied.
- Bifurcations of steady solutions in an array of coupled asymmetric sigmoidal neurons are shown.
- Inhibitory self-coupling is essential for the emergence of metastable dynamical transients.
- Metastable transient firing patterns are observed in arrays of coupled Class 1 spiking neurons.

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ABSTRACT

Metastable dynamical transient patterns in arrays of bidirectionally coupled neurons with self-coupling and asymmetric output were studied. First, an array of asymmetric sigmoidal neurons with symmetric inhibitory bidirectional coupling and self-coupling was considered and the bifurcations of its steady solutions were shown. Metastable dynamical transient spatially nonuniform states existed in the presence of a pair of spatially symmetric stable solutions as well as unstable spatially nonuniform solutions in a restricted range of the output gain of a neuron. The duration of the transients increased exponentially with the number of neurons up to the maximum number at which the spatially nonuniform steady solutions were stabilized. The range of the output gain for which they existed reduced as asymmetry in a sigmoidal output function of a neuron increased, while the existence range expanded as the strength of inhibitory self-coupling increased. Next, arrays of spiking neuron models with slow synaptic inhibitory bidirectional coupling and self-coupling were considered with computer simulation. In an array of Class 1 Hindmarsh–Rose type models, in which each neuron showed a graded firing rate, metastable dynamical transient firing patterns were observed in the presence of inhibitory self-coupling. This agreed with the condition for the existence of metastable dynamical transients in an array of sigmoidal neurons. In an array of Class 2 Bonhoeffer–van der Pol models, in which each neuron had a clear threshold between firing and resting, long-lasting transient firing patterns with bursting and irregular motion were observed.

1. Introduction

Metastable dynamical transient patterns have recently been observed in model arrays of coupled neurons (Horikawa, 2011, 2013, 2014a; Horikawa & Kitajima, 2009a, 2009b). The duration of metastable dynamical transient states increases exponentially with the number of neurons. When the number of neurons comprising them is large, such systems take a long time to reach their asymptotically stable states in a short time. Transient spatiotemporal patterns remain for an extremely long time and are regarded as stable, but then change into "true" stable states rather suddenly. Such metastable dynamical transients have been found in various spatially continuous systems (Ward, 1996, 1998, 2001) and a discrete reaction–diffusion system (Chow, Mallet-Paret, & Van Vleck, 1997; Estep, 1994; Grant & Van Vleck, 1995), and these studies have attracted much attention. In nervous systems, several kinds of information processing ranging from sensory response to decision making are considered to be carried out during transient states, not asymptotically stable states. For the significance of transient dynamics in nervous systems, please refer to Fingelkurts and Fingelkurts (2004), Friston (1997, 2001), Kelso (1995), Rabinovich, Huerta, and Laurent (2008), Rabinovich, Varona, Selverston, and Abarbanel (2006) and Werner (2007), and references therein. However, the mechanism and properties of metastable dynamical

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transients in neural networks have more than just physiological importance; they are an interesting case of transient dynamics.

Metastable dynamical transients in arrays of neurons were first found in the form of rotating waves in a ring of unidirectionally coupled sigmoidal neurons (Horikawa & Kitajima, 2009a). Neurons alternate between positive and negative states (i.e., $x_n > 0$ and $x_n < 0$, respectively, where x_n is the state of the nth neuron) as wave fronts pass so that they oscillate. The system causes a stable traveling wave and shows a stable oscillation if the number of inhibitory couplings is odd (Amari, 1978), which corresponds to a ring oscillator in the field of electronic circuits. When the number of inhibitory couplings is even, e.g., there are no inhibitory couplings and every coupling is excitatory, the traveling wave and oscillation are unstable. Rotating waves are generated in transients until the system reaches one of the stable steady solutions such that the states of all neurons are positively or negatively saturated. However, the transient rotating waves last for exponentially longer time as the number of neurons increases. Further, it has been shown that such exponentially long-lasting transient rotating waves disappear in the presence of variations and asymmetry in the sigmoidal output function of the neuron (Horikawa & Kitajima, 2009b).

Further, effects of asymmetric bidirectional coupling and self-coupling have also been examined. It has been shown that such coupling causes the pinning of rotating waves, i.e., the propagation speeds of wave fronts decrease to zero so that the rotating waves change into stable spatially nonuniform steady solutions (Horikawa, 2014a). When rotating waves are not pinned, these kinds of couplings alter the growth rate of the exponential increase in the duration of transient rotating waves. The exponential growth rate varies inversely with the propagation speeds of wave fronts. The duration of transient rotating waves even in rings of small numbers of neurons becomes extremely long when rotating waves are nearly pinned.

Such metastable dynamical transient rotating waves have also been observed in a ring of Bonhoeffer–van der Pol (BVP) neuron models coupled unidirectionally with slow inhibitory synapses (Horikawa, 2011). In the asymptotically stable states of a ring with an even number of these spiking neurons, neurons in firing and resting states are located alternately in the ring, i.e., odd-numbered and even-numbered neurons are firing and resting, respectively, or vice versa. In transients, there are two kinds of inconsistencies in the states of neurons, in which two adjacent neurons are in the same states, i.e., firing–firing or resting–resting. These inconsistencies propagate in the direction of coupling and the states of the neurons change at their passage. Such propagating oscillations last for a long time, and their durations increase exponentially with the number of neurons.

In contrast with the positive and negative steady states of sigmoidal neurons, the firing and resting states of spiking neurons differ from each other qualitatively. This difference in the two states of spiking neurons can be modeled using the asymmetric output function of a sigmoidal neuron. The effects of such asymmetry in neurons' sigmoidal output function on the pinning conditions for rotating waves have been studied (Horikawa, 2014b). As mentioned above, the exponential increase in the duration of transient rotating waves is lost in the presence of such asymmetry in a sigmoidal output function if coupling is excitatory (Horikawa & Kitajima, 2009b). However, it can be shown that metastable dynamical rotating waves remain even in the presence of this asymmetry if coupling is inhibitory.

Further, metastable dynamical transient static (non-propagating) patterns have been observed in a ring of bidirectionally coupled sigmoidal neurons (Horikawa, 2013). These metastable dynamical patterns are spatially discrete versions of a kink and antikink patterns in the symmetric 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). Two bumps consisting of the positive and negative states of the neurons are generated in transients until the system reaches a spatially uniform steady state. That is, the bump, either positive or negative, that is comprised of fewer neurons than the other, reduces in size and eventually disappears. The movement of the boundaries of the two bumps is extremely slow when the numbers of neurons in the bumps are large; i.e., their speeds decrease exponentially with the number of neurons in the bumps. The duration of the transient bump patterns increases exponentially with the number of neurons. In the same way as the case of rotating waves in a ring of unidirectionally coupled neurons, asymmetry in the neurons' sigmoidal output function causes the increase in the duration of transient static bump patterns to change from exponential to linear if the bidirectional coupling is excitatory. However, it can be shown that the asymmetry has little effect on the exponential increase in their duration if the bidirectional coupling is inhibitory. Since a spiking neuron can be modeled with an asymmetric sigmoidal neuron as mentioned above, it is expected that metastable dynamical transient non-propagating firing patterns emerge in arrays of spiking neurons with inhibitory bidirectional coupling.

In this paper, we study the effects of self-coupling on non-propagating metastable dynamical transient patterns in an array of inhibitorily and bidirectionally coupled neurons with asymmetric output. Arrays of neurons and other kinds of elements with various kinds of coupling have been extensively studied in various fields. Static patterns, periodic, quasiperiodic and chaotic oscillations, propagating waves, splay states, synchronization and other spatiotemporal phenomena as well as their stability and bifurcations in arrays of coupled systems have been examined, and recently metastable dynamics and the effects of delays have attracted much attention. Since the relevant studies comprise a wide range of topics, we avoid citing literature here; please see references in our papers for arrays of coupled oscillators (Horikawa, 2011, 2014b), coupled neuron models (Horikawa, 2014a), synaptically coupled spiking neurons (Horikawa, 2011), BVP oscillators with various kinds of coupling (Horikawa & Kitajima, 2012), and sigmoidal neurons with delays (Horikawa, 2014a, 2014b) As for general interest in arrays and lattice of coupled elements, please refer to recent papers (Barrio, Rodríguez, Serrano, & Shilnikov, 2015; Belykh, Reimbayev, & Zhao, 2015; Levanova, Osipov, & Pikovsky, 2014; Perlikowski, Yanchuk, Popovych, & Tass, 2010; Yanchuk, Perlikowski, Wolfrum, Stefański, & Kapitaniak, 2015).

Bidirectional and self-coupling between neurons as well as between populations of neurons is common in artificial neural networks as well as the central nervous system. In artificial neural networks, these kinds of coupling have been widely used in associative memory, recurrent neural networks and cellular neural networks. In the central nervous system, the examples textbooks show include bidirectional coupling in lateral inhibition in the visual pathway, projections between the entorhinal cortex and CA1 cells in the hippocampus, interactions between Purkinje cells and basket cells in the cerebellum cortex and interactions between populations of pyramidal cells (Churchland & Sejnowski, 1992; Shepherd, 1988). Central pattern generators, which generate periodic oscillations for rhythmic motion (Friesen & Stent, 1977, 1978; Kling & Székely, 1968, for early work), consist of closed loops of neurons including bidirectional coupling. Self-couplings, which are referred to as autapses (Van der Loos & Glaser, 1972) in the field of neurophysiology, have also been considered to play important roles in information processing in the nervous system; see Section 3.4.