A BIFURCATION OF A SYNCHRONOUS OSCILLATIONS INTO A TORUS IN A SYSTEM OF TWO RECIPROCALLY INHIBITORY aVLSI NEURONS: EXPERIMENTAL OBSERVATION

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Abstract

We studied a system of two 'identical' oscillatory aVLSI neurons with reciprocal inhibitory connections. The system demonstrates different oscillatory behaviors depending on the strength of the inhibitory connections: antiphase, synchronous, phase-shifted, and quasiperiodic oscillations. We experimentally observed a bifurcation of synchronous oscillations into quasiperiodic oscillations with two independent frequencies. It was confirmed by the analysis of the phase between neuronal outputs, the cross-correlation function, the amplitude spectrum, and the correlation dimension. The observation of this bifurcation in a physical system suggests that this scenario might also occur in living half-center oscillators, such as those found in invertebrate central pattern generators.

Keawords: quasiperiodic oscillations, half-center oscillator, central pattern generator, silicon neuron

Summary

Neuronal systems with reciprocal inhibitory connections between two units (half-center oscillators) are common building blocks that play an important role in invertebrate and vertebrate central pattern generators (CPG) (Marder and Calabrese, 1996; Marder, 2000). This type of system is capable of providing oscillatory output with different form and phase relationships between the two units (Wang and Rinzel, 1992; Skinner et al., 1993) depending on the strength of inhibitory coupling.

The segmental swim CPGs of the lamprey comprise two reciprocally inhibitory units which are oscillatory neural networks located on opposite sides of the spinal cord. Under normal conditions, the two units oscillate in anti-phase. However, in the presence of strychnine, which blocks glycinergic inhibitory coupling, they oscillate synchronously (Cohen and Harris-Warrick, 1984). Previously, we developed and studied a two-neuron system implemented via aVLSI technology (Patel et al., 1999; Cymbalyuk et al., 2000). Experiments with aVLSI allowed simulation of two-neuron system behavior, demonstrating synchronous oscillations for the weak synaptic coupling, anti-phase oscillations for the strong synaptic coupling, and phase-shifted, synchronous oscillations, and quasiperiodic oscillations for the moderate strength of coupling (Cymbalyuk et al., 2000). We suggested that the synchronous oscillations in lamprey swim CPGs observed in strychnine could be accounted by weak mutually inhibitory interactions between the two units.

It is interesting to note that the quasiperiodic behavior observed in aVLSI model might also correspond to experimental observation in lamprey. Lesher *et al.* (1998) have shown that lamprey spinal central pattern generators might employ a chaos control mechanism based on a skeleton of unstable oscillations. According to this mechanism, the central pattern generators exhibit unstable oscillations rather than stable oscillations. It is synaptic connectivity or control signals that appear to provide stability to the desired regime. There are additional theoretical and experimental studies of neuronal networks showing potential role of quasiperiodic oscillations for the proper functioning and control the networks (Borisyuk et al., 1995; Lesher et al., 1998; Matsugu et al., 1998; Senn et al., 1998; Izhikevich, 1998; Butera et al., 1999; Del Negro et al., 2002; Bondarenko, 2002).

In our previous work (Cymbalyuk et al., 2000), we proved that in a mathematical model of our system of two identical mutually inhibitory aVLSI neurons that the synchronous limit cycle gives rise to a stable two-dimensional torus (quasiperiodic oscillations) through a sub-critical Neimark-Sacker torus bifurcation. Here, we prove experimentally that the aVLSI system undergoes the same transition from synchronous to quasiperiodic oscillations.

First, we study synchronization properties of two aVLSI neurons with inhibitory connections using Pearson's correlation coefficient, when the strength of the synaptic connections, I_{Bsyn} is varied. To estimate degree of order of observed neural outputs, the Shannon entropy S_{Sh} was calculated as a function of synaptic strength. We found an increase in Shannon entropy when decreasing synaptic current I_{Bsyn} from 10 μA to about 10 nA. S_{Sh} increases steeply for both neural outputs at the transition from anti-phase to phase-shifted oscillations. Shannon entropy remains almost unchanged for further decrease of I_{Bsyn} up to 3 pA, when oscillations become synchronous.

The main result of the paper is the observation of a bifurcation of synchronous oscillations into quasiperiodic oscillations with two independent frequencies in the behavior of the aVLSI half-center oscillator. The transition occurs in a relatively narrow interval of I_{Bsyn} from 2.7 to 3.15 nA. Several characteristics of neural outputs are calculated to locate the bifurcation: maps of V_1 versus V_2 (Fig. 1 e-h), phase between outputs of two neurons (Fig.1 i-l), three correlation functions for two outputs (cross-correlation function (Fig. 2 a-d) and autocorrelation functions for each neuron), amplitude spectra (Fig 2 e-h), and correlation dimensions D_2 (Fig. 2 i-l). At I_{Bsyn} = 2.6 nA we have synchronous oscillations (Fig. 1-2 a, e, i). In this case, the cross-correlation function is periodic function (Fig. 1 a), amplitude spectra (Fig. 2 e) show only one component at 69.2 Hz with a second harmonic at 138.0 Hz, and correlation dimension $D_2 = 1$. With an increase of I_{Bsyn} to 2.7 nA, quasiperiodic activity (torus) appears with two frequencies, 54.8 and 70.2, Hz and their harmonics. The limit cycle in the map (Fig. 1 e) is replaced by orbits that are characteristic of quasiperiodic oscillations and cover an area of the plane (V_1, V_2) (Fig. 1 f). The cross-correlation function becomes periodic with modulation (Fig. 2 b), and plot of correlation dimension D_2 shows the appearance of a two-dimensional process (Fig. 2 j). The fluctuations in phase of the neuronal outputs are close to periodic and are larger in amplitude (Fig 1 j). They are in the interval from –0.06 to 0.04. Further increase of I_{Bsyn} to 3.15 nA produces quasiperiodic activity with the frequencies 60.0 and 71.6 Hz and their harmonics (Fig. 2 g). The cross-correlation function becomes substantially modulated with a frequency of about 12 Hz that is close to the difference between the two frequencies in quasiperiodic neural outputs (Fig. 1 c). The correlation dimension D_2 is equal to 2 (Fig. 2 k). A third spectral component appears to be present but is too small to be detected with the cross-correlation function or with calculation of correlation dimension. Fluctuations of in the phase the neural output signals are close to periodic and become even larger (ranged from –0.17 to 0.09). When I_{Bsyn} increases to 79 nA, the two-neuron aVLSI system goes into antiphase oscillations with the main frequency at 21.6 Hz (Fig. 2 h). These oscillations are substantially non-sinusoidal (Fig. 1 d) as confirmed by the multiple harmonics in the amplitude spectrum (Fig. 2 h). The cross-correlation function is periodic (Fig. 2 d) and correlation dimension D_2 for this process is equal to 1 (Fig. 2 l). The phase of the neuronal outputs is stable around a value of 0.5 (Fig. 1 l).

Thus, our investigations show that a physical system of two 'identical' aVLSI neurons with reciprocal inhibitory connections demonstrates that the system produces different oscillatory behaviors depending on the strength of the inhibitory connections: anti-phase, synchronous, phase-shifted, and quasiperiodic oscillations. We experimentally observed a bifurcation of periodic neuronal outputs into quasiperiodic activity with two independent frequencies. This type of activity is confirmed by the analysis of phase between neuronal outputs, maps of V_1 versus V_2, cross-correlation functions, amplitude spectra, and correlation dimensions. The bifurcation of periodic activity into torus found in our aVLSI two-neuron system suggests that this scenario might also occur in living half-center systems, like those which could be found in invertebrate central pattern generator systems. In future work, the systems of aVLSI neurons could give some insight to the potential role for this transition mechanism for the function and control of nervous system.

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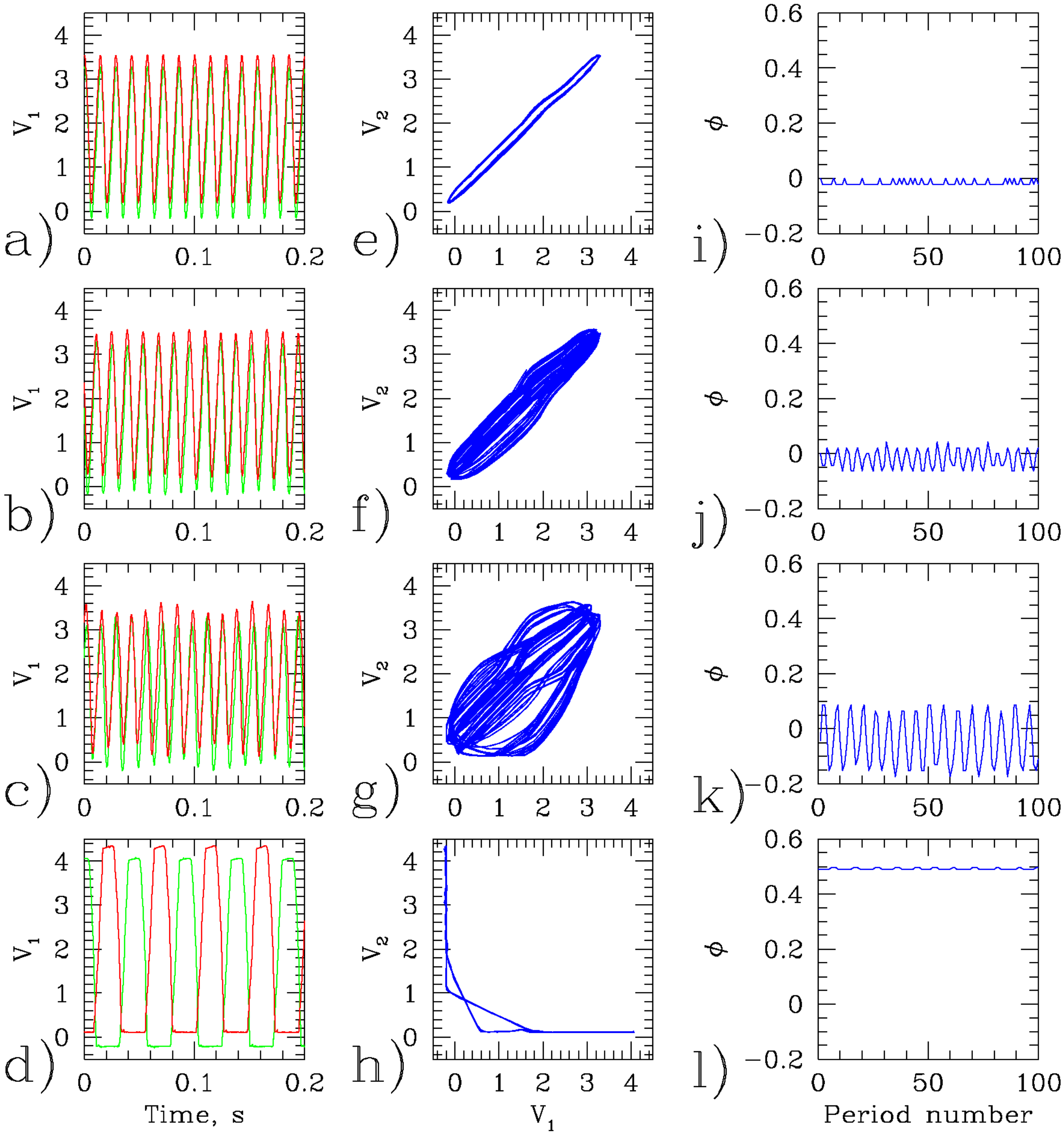

Fig. 1. Output time series of activities (a-d, red and green lines represent potentials of the first (V_1) and second (V_2) neurons, correspondingly), maps of neuron potentials V_1 versus V_2 (e-h), and the phase between the outputs of the two neurons (i-l) for aVLSI half-center oscillator system. Synaptic currents I_{Bsyn} are: 2.6 nA (a, e, i); 2.7 nA (b, f, j); 3.15 nA (c, g, k); 79 nA (d, h, l).

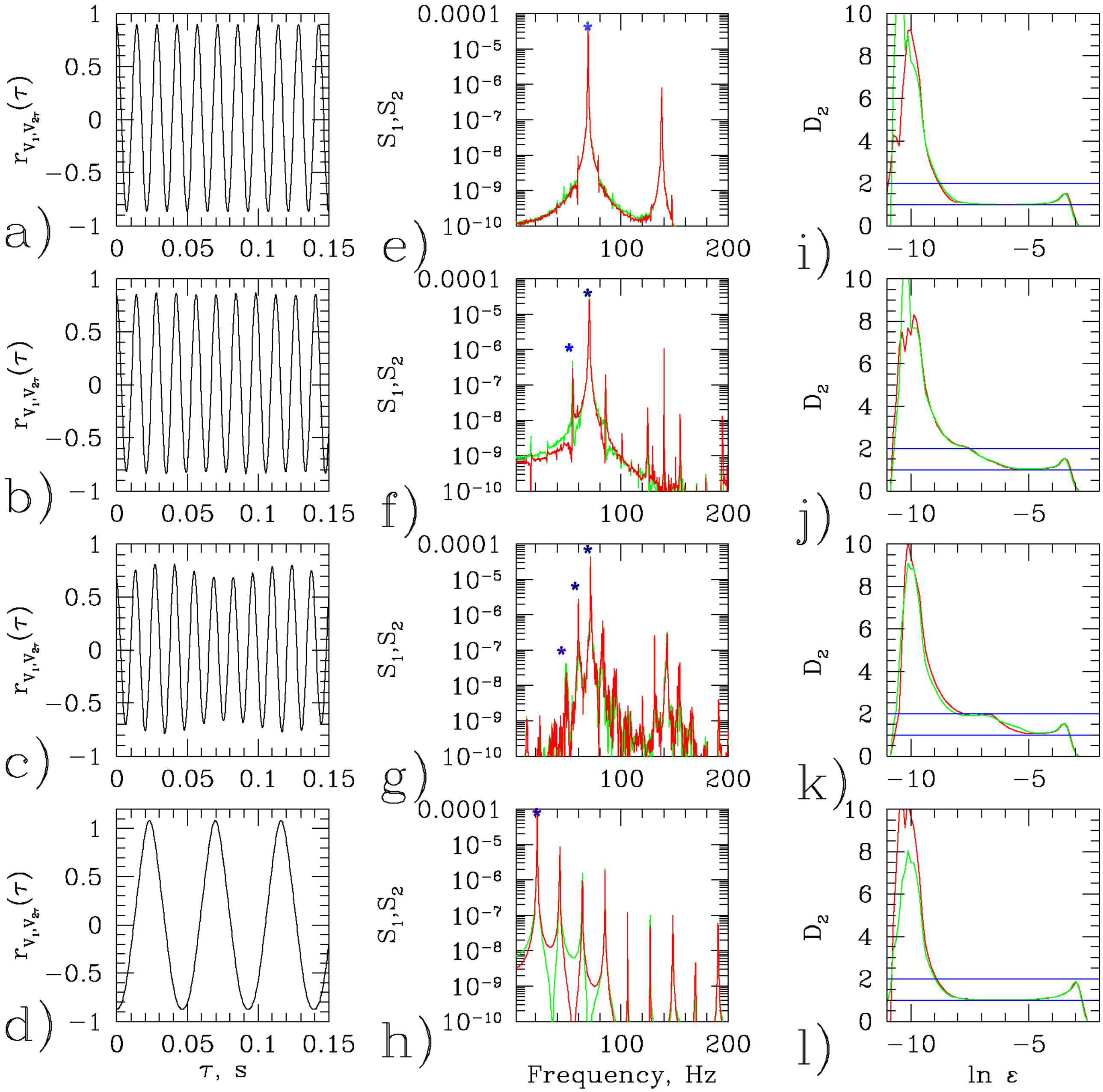

Fig. 2. Cross-correlation functions $r_{V1,V2_{\tau}}$ (τ) (a-d), amplitude spectra (e-h), and correlation dimensions D_2 (i-l) for the aVLSI half-center oscillator system (lines are colored in according with Fig. 1). Synaptic currents I_{Bsyn} correspond to those on the Fig. 1. For correlation dimensions only slopes for embedded dimension 21 are shown.