A bifurcation of a synchronous oscillations into a torus in a system of two mutually inhibitory aVLSI neurons: Experimental observation

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Abstract

We studied a system of two 'identical' oscillatory aVLSI neurons with mutually inhibitory connections. The system demonstrates different oscillatory behaviors depending on the strength of the inhibitory connections: antiphasic, synchronous, phase-shifted, and quasiperiodic oscillations. We experimentally observed a bifurcation of synchronous oscillations into quasiperiodic oscillations with two independent frequencies. This bifurcation 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 central pattern generators.

Key words: Quasiperiodic oscillations, Half-center oscillator, Central pattern generator, Silicon neuron

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1 Introduction

Neuronal systems with mutually inhibitory connections between two units are common building blocks that play an important role in invertebrate and vertebrate central pattern generators (CPGs) (10; 9). Models of such systems can produce oscillatory output with different form and phase relationships between the two units (15; 14), depending on the strength of inhibitory coupling. Similar phenomena have been observed in experiments. For example, the segmental swim CPGs of the lamprey comprise two reciprocally inhibitory units that 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 (4). Thorough understanding of the dynamics of such a system must encompass all behaviors of the system including those under experimentally modified conditions such as that with strychnine application.

Previously, we developed and studied a two-neuron system implemented via aVLSI technology (12; 5). Experiments with the aVLSI two-neuron system showed synchronous oscillations for weak synaptic coupling and anti-phasic oscillations for strong synaptic coupling. In addition, phase-shifted oscillations and quasiperiodic oscillations were observed for moderate strength of coupling (5). We suggested that the synchronous oscillations in lamprey swim CPGs observed in strychnine could be accounted for by weak mutually inhibitory interactions between the two units. While stationary oscillations are well acknowledged in neuroscience and commonly represented by limit cycles in models (in-phase or anti-phase oscillations), quasi-periodic oscillations are still treated as rather obscure dynamic regimes which belong strictly in the realm of modeling. Recent theoretical and experimental studies of neuronal networks demonstrated a potential role for quasiperiodic oscillations in the proper functioning and control of networks (2; 11; 13; 3; 8; 1; 6).

Here we study a mechanism by which quasi-periodic oscillations can be generated by a two unit neural network with the ubiquitous mutually inhibitory connections discussed above. In our previous work (5), 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.

2 Methods

Description of our silicon aVLSI neurons and methods of measurement is provided in detail in (5).

Pearson's correlation coefficient $r_{Pearson}$ is defined by the equation

$$r_{Pearson} = \frac{S_{ij}}{(S_{ii}S_{jj})^{1/2}}, \tag{1}$$

where $S_{ii} = \sum_{k=1}^{N}(u_{ki} - \overline{u}_i)^2$, $S_{jj} = \sum_{k=1}^{N}(u_{kj} - \overline{u}_j)^2$, and $S_{ij} = \sum_{k=1}^{N}(u_{ki} - \overline{u}_i)(u_{kj} - \overline{u}_j)$ for ith and jth neuronal outputs, $\overline{u}_i$ and $\overline{u}_j$ are their averaged values. Pearson's correlation coefficient is used for evaluation of the degree of synchronization between the two neuronal outputs.

The Shannon entropy is calculated from the equation

$$S_{Sh} = -\sum_{k=1}^{K} p_k \ln p_k, \tag{2}$$

where p_k are the probabilities of finding the trajectory in kth subinterval of the interval of the amplitude variation. Here, $K = 64$.

The frequency spectra are calculated using the digital fast Fourier transform from the time series of $N = 2048$ to $N = 16384$ points. The correlation dimension ν (7) is calculated using $N = 2048$ to $N = 16384$ points as well.

3 Results

First, we studied the synchronization properties of two aVLSI neurons with mutually inhibitory connections using Pearson's correlation coefficient, when the strength of the synaptic connections, as determined by the aVLSI neuron parameter I_{Bsyn}, is varied. The data are shown in Fig. 1. For I_{Bsyn} from 3.2 pA to 2.7 nA, we observe synchronous oscillations with $r_{Pearson}$ close to 1 (closed squares in Fig. 1). In the interval of I_{Bsyn} from 1.4 to 8.7 nA, two branches of phase-shifted oscillations appear (open and closed triangles in Fig. 1). They co-exist with synchronous and quasiperiodic oscillations. The latter develop in the narrow interval from 2.7 to 3.15 nA (stars in Fig. 1). When I_{Bsyn} exceeds 10 nA, only anti-phasic oscillations exist in our two-neuron system (squares in Fig. 1).

To estimate the degree of order of the observed neural outputs, the Shannon entropy S_{Sh} was calculated as a function of synaptic strength (Fig. 2). We found an increase in Shannon entropy when I_{Bsyn} is decreased from 10 μA to about 10 nA. S_{Sh} increases steeply for both neural outputs at the transition from anti-phasic to phase-shifted oscillations. Shannon entropy remains almost unchanged for further decrease of I_{Bsyn} up to 3 pA, when oscillations become synchronous.

The principal 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 two-cell aVLSI oscillator. The transition occurs in a relatively narrow interval of I_{Bsyn} from 2.7 to 3.15 nA. Several characteristics of the neural outputs are calculated to locate the bifurcation: maps of V_1 versus V_2 (Fig. 3 a-d), phase between the outputs of the two neurons (Fig. 3 e-h), amplitude spectra (Fig. 3 i-l), and correlation dimensions ν.

Figure 3 (a, e, i) shows characteristics of synchronous oscillations at $I_{Bsyn} =$ 2.6 nA. In this case, the amplitude spectrum (Fig. 3 i) shows only one component at 69.2 Hz with a second harmonic at 138.0 Hz, and correlation dimension $\nu = 1$. With an increase of I_{Bsyn} to 2.7 nA, we observe quasiperiodic oscillations (torus) with frequencies 54.8 and 70.2 Hz and their harmonics. The map of quasiperiodic activity covers an area of the plane (V_1, V_2) (Fig. 3 b). Calculations of correlation dimension ν shows the appearance of a two-dimensional process and the fluctuations in phase of the neuronal outputs are close to periodic (Fig. 3 f). More developed quasiperiodicity is observed at $I_{Bsyn} = 3.15$ nA (Fig. 3 c, g, k). The correlation dimension ν becomes equal to 2. The spectrum of oscillations shows multiple peaks from harmonics of two main frequencies 60.0 and 71.6 Hz. The fluctuations in the phase of the neural output signals become larger (ranged from -0.17 to 0.09) but are still close to periodic. At relatively strong coupling, $I_{Bsyn} = 79$ nA, the oscillations become anti-phasic and square wave in form. This deviation from a sine-like waveform is clear from the amplitude spectrum which contains multiple equidistant peaks (Fig. 3 l). Correlation dimension ν for this process is equal to 1 and the phase of the neuronal outputs slightly fluctuates around a value of 0.5 (Fig. 3 h).

4 Conclusions

Our investigations show that a physical system of two 'identical' aVLSI neurons with mutually inhibitory connections can produce different oscillatory behaviors depending on the strength of the inhibitory connections: anti-phasic, 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, amplitude spectra, and correlation dimensions. The bifurcation of periodic activity into torus found in our aVLSI two-neuron system suggests that this scenario may also occur in living mutually inhibitory networks, like those found in central pattern generators. In future work, this system of aVLSI neurons may provide insight into the potential role of this transition mechanism in the function and control of the nervous system.

Acknowledgements

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Figure captions

Fig. 1. Pearson's correlation coefficients between the 1st and 2nd neuronal outputs versus the synaptic strength parameter, I_{Bsyn}. Here, closed squares, stars, triangles, and open squares show synchronous, quasiperiodic, phase-shifted, and anti-phasic oscillations, respectively. Open and closed triangles represent two branches of phase-shifted oscillations (see Fig. 6 from (5)).

Fig. 2. Shannon entropy for the two neuron outputs as functions of I_{Bsyn}. S^1_{Sh} and S^2_{Sh} stand for the 1st and 2nd neuron, respectively. Symbols are the same as in Fig. 1.

Fig. 3. Maps of neuron potentials V_1 versus V_2 (a-d), the phase between the outputs of the two neurons (e-h), and amplitude spectra (i-l) for the aVLSI oscillator system. I_{Bsyn}: 2.6 nA (a, e, i); 2.7 nA (b, f, j); 3.15 nA (c, g, k); 79 nA (d, h, l).

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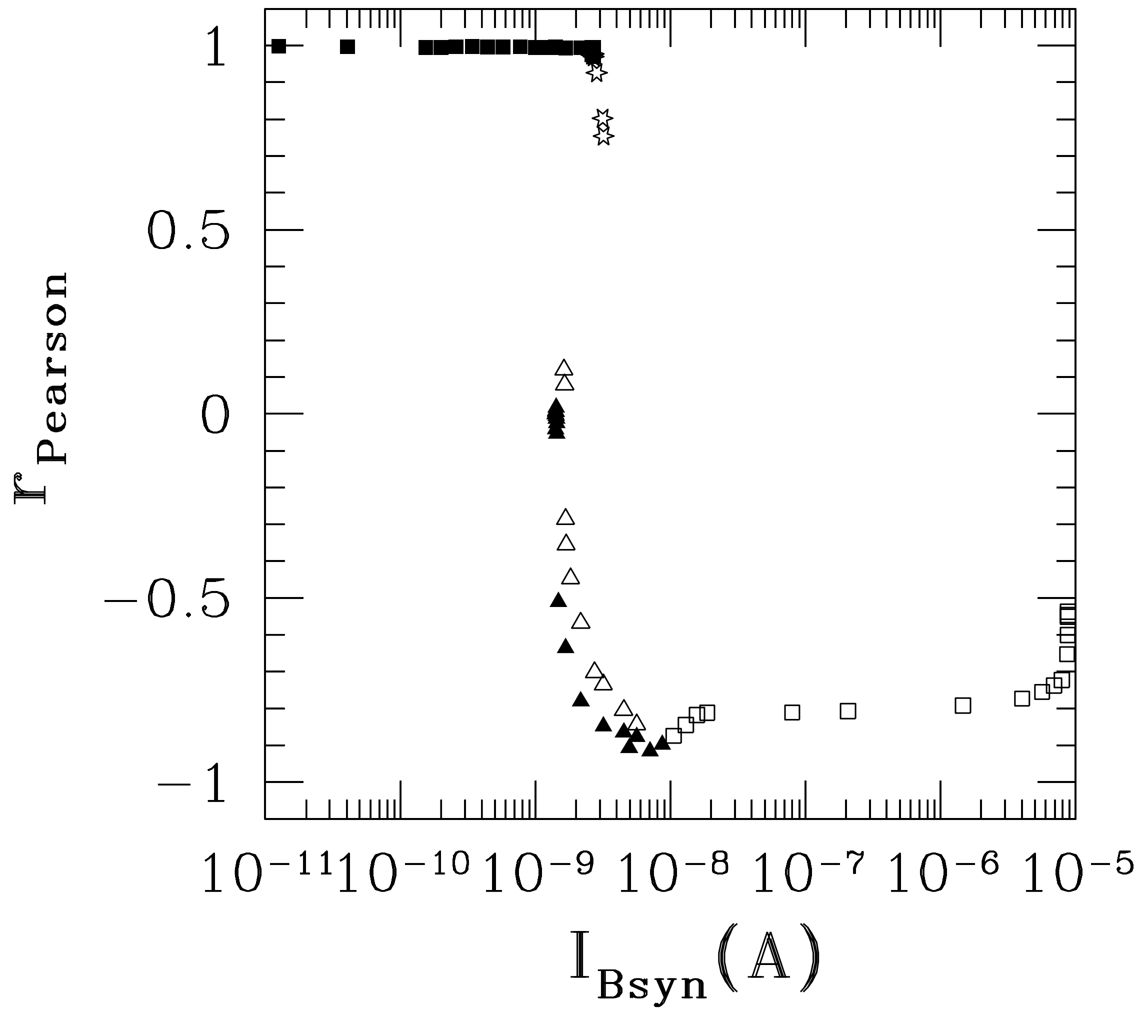

V. E. Bondarenko et al., Fig. 1.

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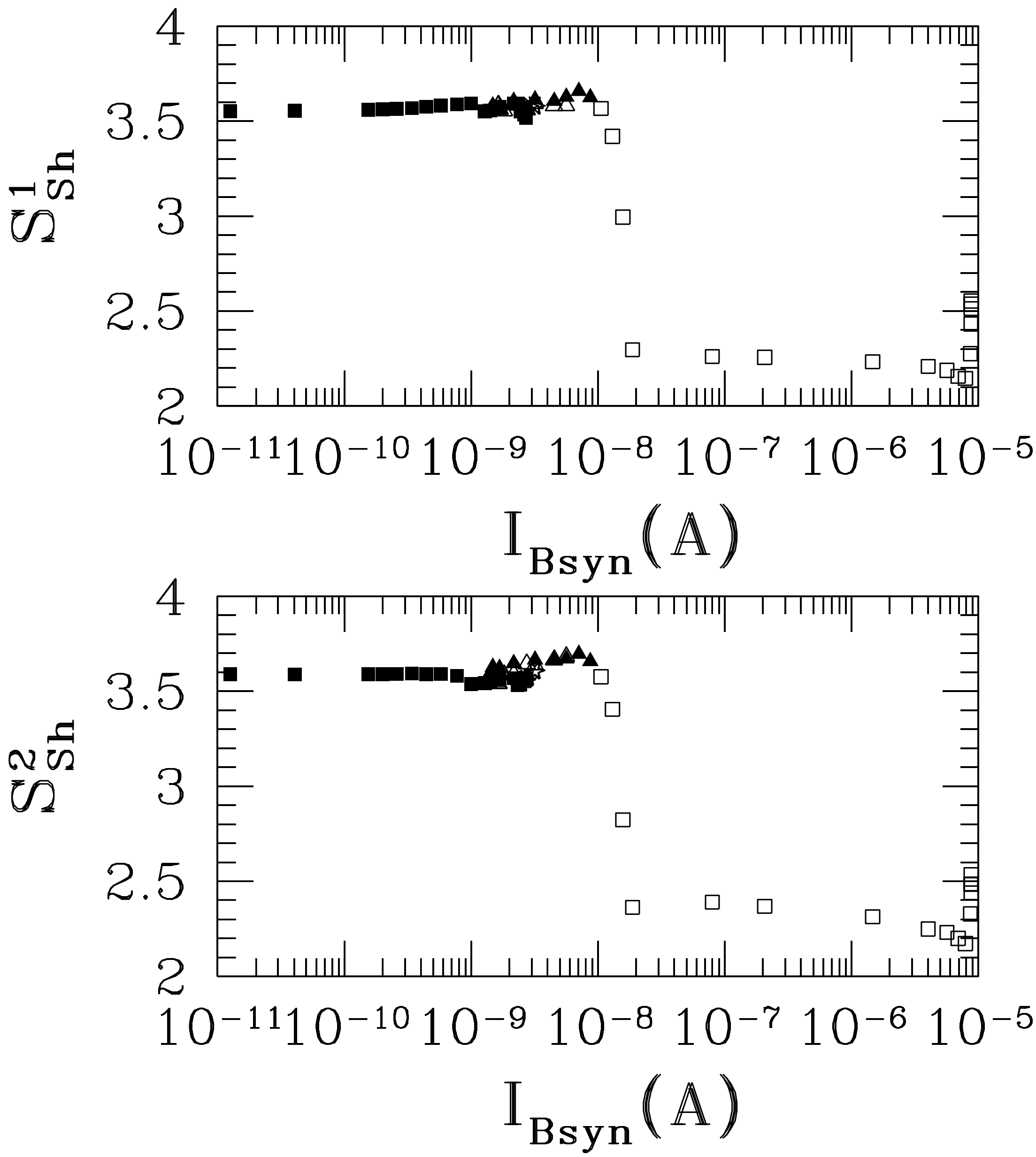

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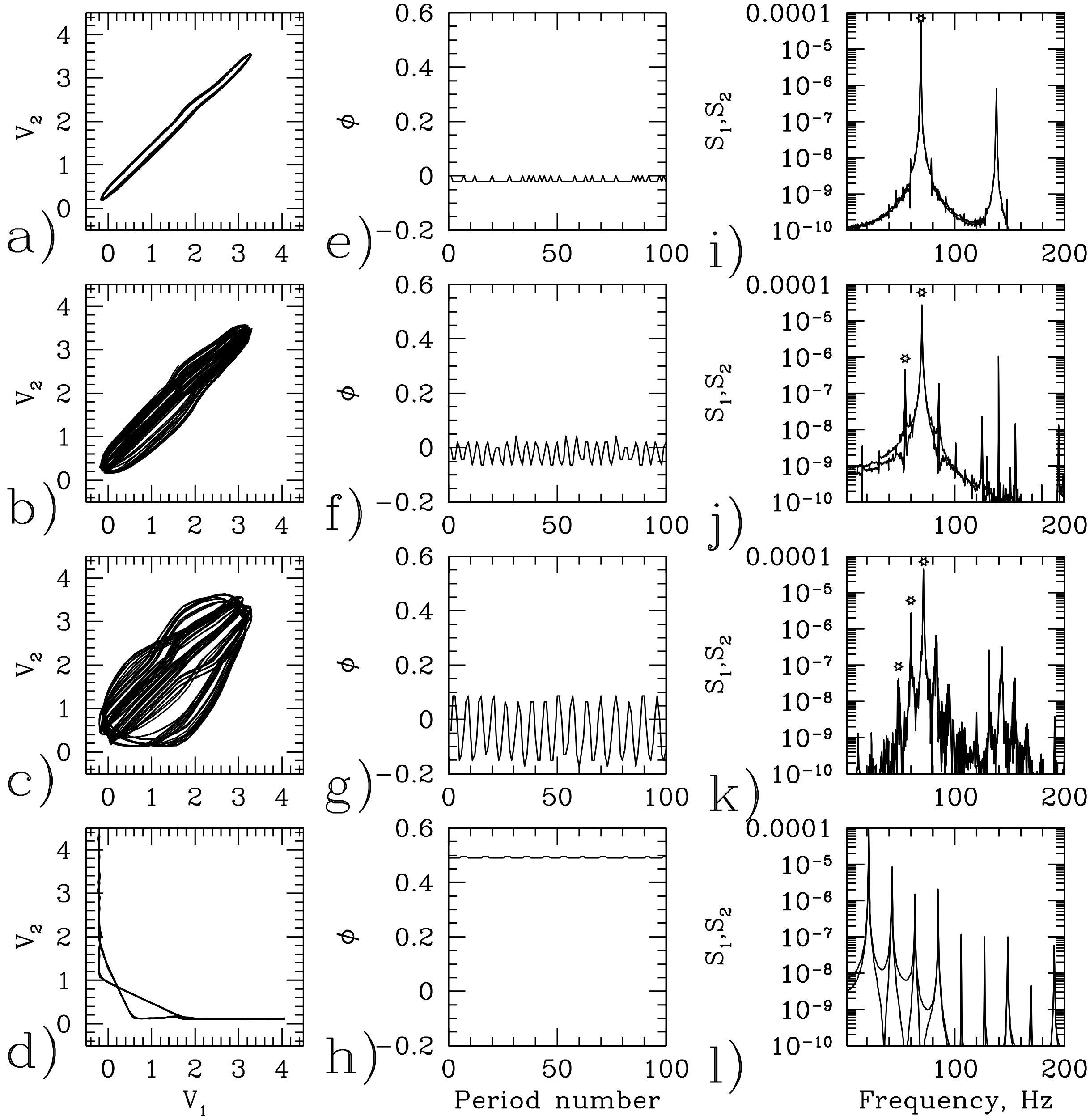

V. E. Bondarenko et al., Fig. 3.