J. Braz. Chem. Soc., Vol. 10, No. 6, 492-496, 1999.
Printed in Brazil.

0103 – 5053 $6.00 + 0.00

Article

Complex Oscillations in an Electrically Stimulated Membrane Model

E.J. Delgado[a]*, *and A.F. Münster*[b]

[a]*Department of Physical Chemistry, Facultad de Ciencias Químicas, Casilla 160-C, Universidad de Concepción - Concepción, Chile*

[b]*Institut für Physikalishe Chemie, Universität Würzburg, Marcusstrasse 9-11, 97070 Würzburg, Germany*

Este artigo investiga, teoricamente, a dinâmica de um modelo de membrana sob estimulação elétrica externa. Este sistema mostra vários tipos de respostas oscilatórias no potencial da membrana, quando uma corrente sinoidal AC é superposta à corrente DC aplicada através da membrana. À medida que a frequência da corrente AC varia, este comportamento varia de oscilações periódicas, P1, até oscilações do tipo explosivas, através de regiões de quase-periodicidade. As séries temporais que apresentam estes comportamentos são caracterizadas usando métodos de Teoria de Sistemas Dinâmicos, a saber: mapas de retorno, expoentes de Lyapunov, espectro de potências e dimensão de capacidade. Os resultados são discutidos em relação a membranas biológicas sob condições similares.

In this paper we theoretically investigate the dynamics of a membrane model under external electric stimulation. The system shows various types of oscillatory responses in the membrane potential when a sinusoidal AC electric current is superimposed on the DC current applied across the membrane. The behavior goes from periodic oscillations, P_1, to bursting type oscillations via quasiperiodicity, when the frequency of the AC current is varied. The time series displaying these behaviors are characterized using the methods of Dynamical System Theory, namely, return map, Lyapunov exponents, power spectrum and capacity dimension. The results are discussed in relation to biological membranes under similar conditions.

Keywords: *membrane oscillations, nonlinear phenomena, quasiperiodicity, bursting, sinusoidal stimulation*

Introduction

The effect of periodic perturbations on the dynamics of oscillatory chemical system has been extensively studied both theoretically and experimentally in the last decade[1-4], mainly on the famous Belousov-Zhabotinskii reaction, the cerium ion catalyzed oxidation of malonic acid by bromate. This interest has been motivated mainly by the desire to understand excitability and signal transmission in biological systems, for example, the synaptic transmission in the central nervous system; the excitation and contraction of cardiac muscle[5,6].

In the case of oscillations in artificial membranes the research has been also motivated by its implications in biological systems. A number of important biological phenomena are rhytmical and appear to result from the oscillatory interaction of a membrane with its environment, namely: sustained oscillations in neurons and pacemaker cells in the heart and secretory glands. Although the scale and the mechanisms of the processes in artificial membranes may not be close to those found in real biological systems, it is expected that they give fundamental information useful in elucidating the oscillation processes at biomembranes in living organisms.

Periodic perturbations of membrane systems have not been studied nearly as much as chemical systems, however there is a fair amount of published work on the subject[7-10]. The studies in this field have been focused on bifurcations, or transitions to complex oscillations and chaos that caused by the application of periodic or quasi-periodic stimulations to an excitable cell in a self-sustained state of periodic oscillatory behavior. In this paper, by using a broad pore membrane model, we report complex dynamics (bursting and quasiperiodicity) in the membrane potential when the system is driven by a periodic stimulating current. This is achieved perturbing the direct current applied across the membrane by superimposing a small amplitude sinusoidal AC electric current.

Model Equations

The model is an electrochemical device that consists of a highly porous ion-exchanger membrane which separates two electrolyte solutions of different and constant concentrations, permitting a steady diffusion process. Oscillations of the electrical voltage across the membrane and hydrostatic pressure occur when the membrane is polarized by an electrical current. The oscillations are brought about by periodic transitions of the salt content in the membrane caused by the antagonistic action of the hydrostatic and electro-osmotic pressure across the membrane. In this membrane oscillator system there are three kinds of driving forces: the membrane voltage, the difference of hydrostatic pressure and the gradient of concentration between the boundaries of the membrane. The equations governing the dynamics of the system are[11]:

Electrical voltage

$$\frac{du}{d\tau} = (i-u)\left(\frac{u}{i} - f_c\right)\left[\frac{1}{1-f_c}\ln\frac{(i-u)(f_0-f_c)}{(u-\mathrm{i}f_c)(1-f_0)} - f_{y_0}\,k_d\,(\sigma u - p)\right]$$

Hydrostatic pressure

$$\frac{dp}{d\tau} = k_t\,k_d\,(\sigma\, u - p)$$

where u and i are the voltage and electrical current imposed accross the membrane, respectively; p is the hydrostatic pressure difference arising from the difference of the levels of the solutions, and τ is time. The parameters have the same meaning and values given in elsewhere[11], namely: ratio of concentrations, f_c = 0.1; sign of fixed charges, σ = -1; drift-parameter, k_d = 0.1; time-parameter, k_t = 1; and the electrical membrane resistance at vanishing volume flux f_0 = 0.2558. All variables and parameters in the above equations are in dimensionless form.

In most studies on oscillations in membrane systems, both experimental and theoretical, the electrical current applied through the membrane is constant. However, there exist experimental evidence in artificial and biological membranes[9,12,13] showing complex dynamics other than simple P1 oscillations, such as bursting, quasi-periodicity and chaos, when a periodic stimulating current is applied across the membrane. aiming at reproducing this complex behavior observed experimentally we have added a sinusoidal forcing term in the electric current, namely:

$$i = i_{DC} + A\sin(\omega\tau)$$

where A is the amplitude and ω is the frequency of the superimposed AC current, respectively. The analysis of this driven system requires necessarily the reconstruction of the attractor from the time series, because only two dynamical variables are directly accessible. In order to avoid this we have transformed the above driven system into an autonomous one adding the following two equations:

$$\frac{d\phi}{d\tau} = \nu$$

$$\frac{d\nu}{d\tau} = -\omega\phi$$

whose solution with proper initial conditions, namely $\phi(0) = 0$, is the forcing term in the current, *i.e.* $\phi = A\sin(\omega\tau)$. This new four equation autonomous system is equivalent to the original one and allows the computation of dimensions and Lyapunov exponents without the reconstruction of the attractor. The frequency ω was used as control bifurcation parameter.

Results and Discussion

The model equations exhibit various types of oscillatory responses in the membrane potential as the frequency ω of the periodic stimulation (AC current), superimposed on the DC current, is varied. The behavior goes from periodic to bursting via quasi-periodicity. Thus in the range $0.86 \le \omega \le 1.0$ the system displays periodic behavior (P1), Fig. 1. This periodic behavior is confirmed quantitatively by its maximum Lyapunov exponent equal to zero (indicating that the limit cycle conserves its information in time), its single main frequency (0.0156) in the power spectrum and its correlation dimension equal to one.

At frequencies below 0.85 the system shows quasi-periodicity. The transition from quasi-periodicity to limit cycle occurs in a somewhat unusual way. Normally one would expect a torus (secondary Hopf) bifurcation where two Floquet multipliers simultaneously intersect the unit circle in the plane of complex numbers. In fact, a torus bifurcation occurs at a frequency of $\omega = 1.03$, as determined using the program package CONT[14]. At $\omega = 0.8525$, however, the period-one limit cycle undergoes a saddle-node bifurcation where one non-trivial floquet multiplier intersects the unit circle at 1. It therefore looses stability by collision with an unstable limit cycle. This saddle-node bifurcation of limit cycles collides with a torus in analogy to the well-known sniper-bifurcation where a saddle-node of stationary states collides with a limit cycle[15]. As a consequence the modulation period of the quasiperiodic oscillations approaches infinity as the forcing frequency is increased towards the critical value of $\omega = 0.8525$, Fig. 2. The emerging torus is despicted in Fig. 3. The quasiperiodic state is confirmed by the power spectrum and the return map. In the first one it is possible to observe two main frequencies in non-integer ratio, in the second one it is a closed curve is obtained, Fig. 4. Both features, along with a capacity dimension close to 2.00 and a maximum Lyapunov exponent equal to zero, confirm quasiperiodicity. With a further decrease of the frequency, $\omega < 5 \times 10^{-3}$, the systems dynamics switch to burst type oscillations. Such an evolution manifests itself on the phase portrait and the Poincaré section as an increase of the global size of the torus at the expense of the size of its inner part which shrinks to a thin tube. On the power spectra, this scenario is associated with a decrease of the secondary frequency, which means that the thinner the center hole, the larger the duration of time spent by the trajectory inside the hole. As a consequence, the time series displays larger and larger windows of nearly stationary behavior, Fig. 5. In Fig. 6, the window length of the nearly stationary states as function of the driving frequency is shown.

The responses of these model equations to the sinusoidal stimulation have close similarities with experimental results reported previously for both artificial and biological

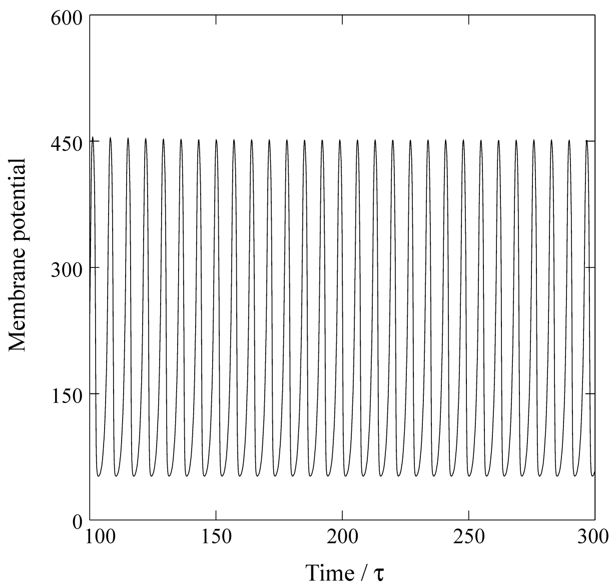

Figure 1. Time serie of membrane potential for DC current intensity $i_{CD} = 500$, AC current amplitude A = 25 and frequency $\omega = 0.90$.

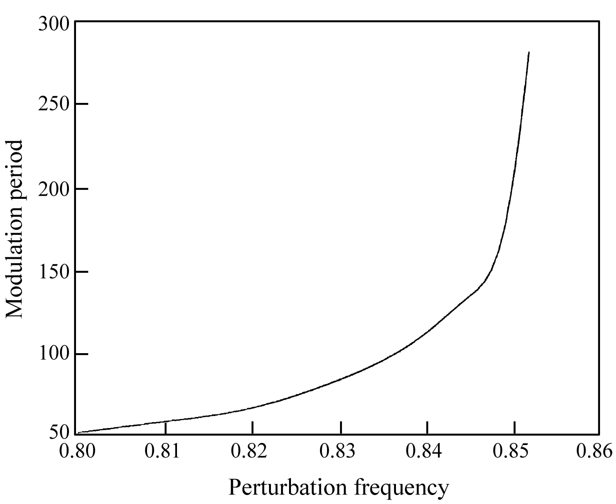

Figure 2. Increase of modulation period close to limit point for the same parameters values given in Fig. 1.

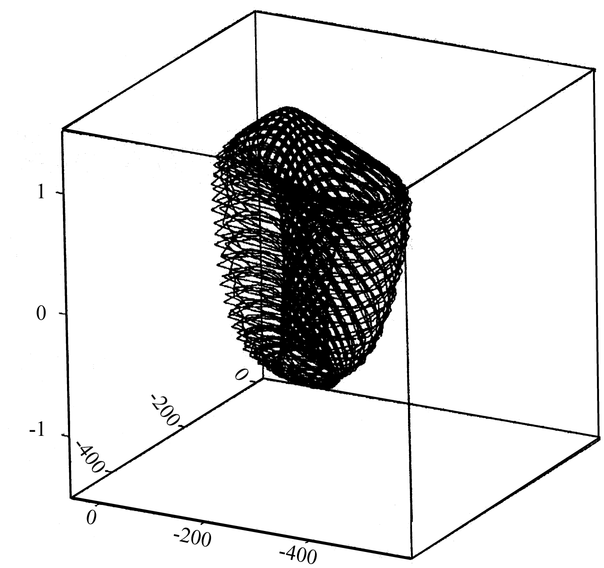

Figure 3. The attractor showing a torus structure typical for quasiperiodicity. Parameters values given in Fig. 1 except $\omega = 0.25$.

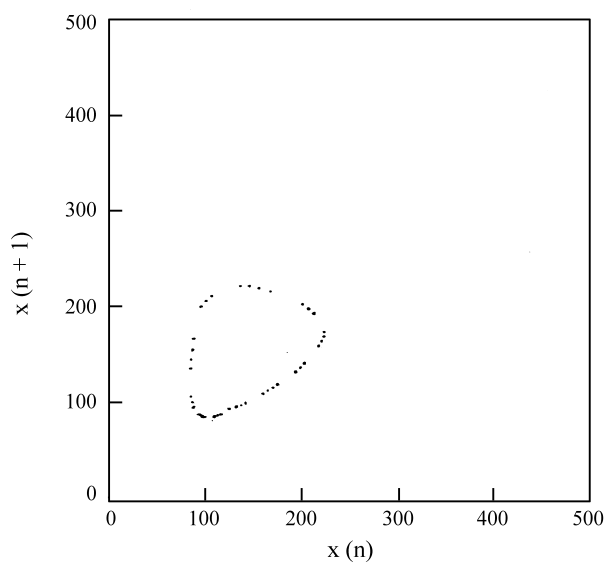

Figure 4. The return map of the attractor in Fig. 3 shows a closed curve as would be expected for a quasiperiodic attractor.

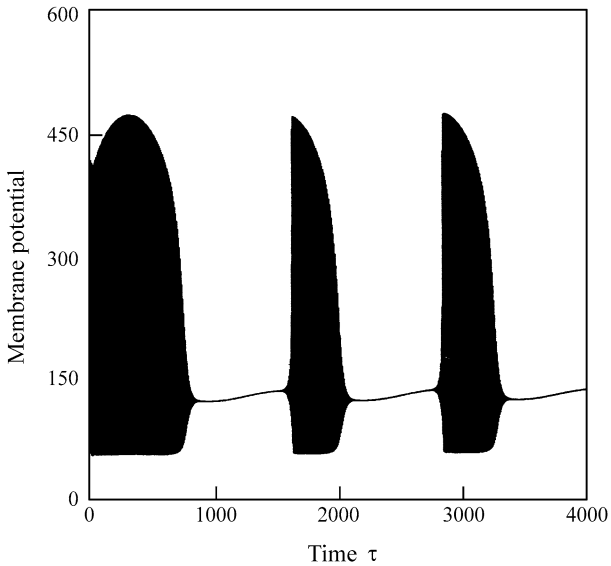

Figure 5. Bursting type oscillations for the same parameters values given in Fig. 1 except $\omega = 5 \times 10^{-3}$.

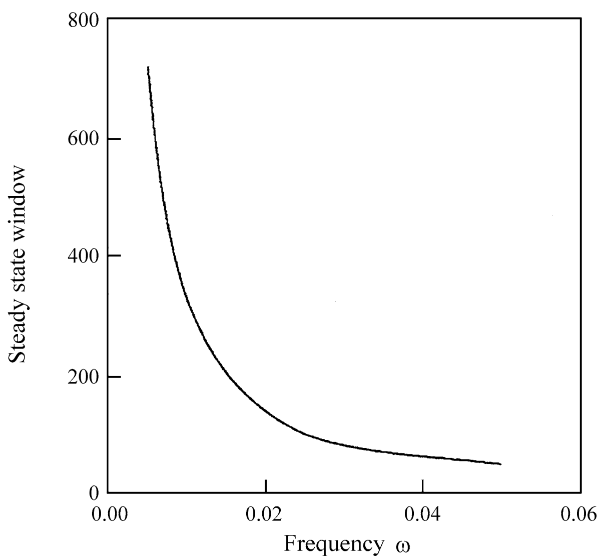

Figure 6. Window length of the nearly stationary states as function of the driving frequency.

membranes under similar conditions. The rhythm of autonomous biological oscillators can be markedly affected by periodic perturbation. Thus, this forcing can lead to quasiperiodicity, intermittency, chaos and bursting type oscillations. Many nerve cells in both vertebrate and invertebrate nervous systems display the behavior known as bursting. This consists of the generation of membrane action potentials in regular sequences of "bursts" which are separated by periods of inactivity during which the cell membrane may be hyperpolarized. Among the more commonly studied nerve cells which display this behavior are abdominal ganglion cells of molluscs[16,17], cardiac pacemaker, stomatogastic ganglion cells of crustacea[18,19], and electrical activity in pancreatic β-cells[20]. Bursting is important for two reasons[21]. First, it is a relatively simple neural pattern and yet one which is involved in the control of many physiological and behavioral activities such as blood circulation, respiration, mastication and locomotion. Second, nerve cells involved in epileptic seizure activity have been observed to burst during interictal (*i.e.* between seizures) states.

Finally, it is important to stress that a knowledge of the mechanisms underlying this complex behavior may lead to an increased understanding of the basic physico-chemical phenomena that occur during biological membrane oscillations.

Acknowledgment

Finantial support from Dirección de Investigación de la Universidad de Concepción, Grant P.I.No. 97.22.13-1.2, is gratefully acknowledged.

References

1. Rehmus, P.; Ross, J. *Oscillations and Traveling Waves in Chemical Systems*; Wiley-Interscience; New York, p. 287, 1984.
2. Schneider, F.W. *Ann. Rev. Phys. Chem.* **1985**, *36*, 347.
3. Markman, G.; Bar-Eli, K. *J. Phys. Chem.* **1994**, *98*, 12248.
4. Förster, A.; Hauck, T.; Schneider, F.W. *J. Phys. Chem.* **1994**, *98*, 184.
5. Dolnik, M.; Marek, M. *J. Phys. Chem.* **1991**, *95*, 7267.
6. Dolnik, M., Marek, M.; Epstein, I.R. *J. Phys. Chem.* **1992**, *96*, 3218.
7. Saida, Y.; Matsuno, T.; Toko, K.; Yamafuji, K. *Jpn. J. Appl. Phys.* **1993**, *32*, 1859.
8. Aihara, K.; Matsumoto, G.; Ichikawa, M. *Phys. Lett.* **1985**, *A111*, 251.
9. Aihara, K.; Numajiri, T.; Matsumoto, G.; Kotani, M. *Phys. Lett.* **1986**, *A116*, 313.
10. Aihara, K.; Matsumoto, G. In *Chaos in Biological Systems*; H. Degn, A.V. Holden, L.F. Olsen, Eds.; Plenum; New York, p. 121, 1987.
11. Drouin,H.R.L. *Ber. Bunsenges. Phys. Chem.* **1995**, *99*, 164.
12. Hayashi, H.; Ishizuka, S.; Ohta, M.; Hirakawa, K. *Phys. Lett.* **1982**, *A88*, 435.
13. Chialvo, D.R.; Gilmour Jr., R.F.; Jalife, J. *Nature* **1990**, *343*, 653.
14. Marek, M.; Schreiber, I. *Chaotic Behaviour of Deterministic Dissipative Systems*; Academia; Prague, Apendix B, 1991.
15. Noszticzius, Z.; Wittmann, M.; Stirling, P. *J. Chem. Phys.* **1987**, *86*, 1922.

16. Gorman, A.L.F.; Thomas, M.V. *J. Physiol.(London)* **1978**, *275*, 357.
17. Junge, D.; Stephens, C.L. *J. Physiol.(London)* **1973**, *235*, 155.
18. Selverston, A.I.; Russell, D.F.; Miller, J.P.; King, D.C. *Prog. Neurobiol.* **1976**, *7*, 215.
19. Watanabe, A.; Obara, S.; Akiyama, T. *J. Gen. Physiol.* **1967**, *50*, 839.
20. Atwater, I.; Dawson, C.M.; Scott, A.; Eddlestone, G.; Rojas, E. In *Biochemistry and Biophysics of the Pancreatic Beta Cell*; Georg Thieme; New York, p. 100, 1980.
21. Plant, R.E. *J. Math. Biology* **1981**, *11*, 15.

Received: March 16, 1999