Modeling of Nonlinear Chemical Reaction Systems and Two-Parameter Stochastic Resonance

TAKASHI AMEMIYA¹, TAKAO OHMORI, MASARU NAKAIWA, TETSUYA YAMAMOTO² and TOMOHIKO YAMAGUCHI²

Department of Chemical Systems, National Institute of Materials and Chemical Research (NIMC), 1-1 Higashi, Tsukuba, Ibaraki 305-8565, Japan

¹*To whom correspondence should be addressed*

²*Permanent address: Department of Electrical Engineering, Tokyo Metropolitan College of Technology, Shinagawa, Tokyo 140-011, Japan.*

Accepted in final form 29 January 1999

Abstract. The idea of stochastic resonance (SR) is extended to *two-parameter* dynamical systems based on the Oregonator model of the Belousov-Zhabotinsky (BZ) reaction. The first case presents the photosensitivity of the reaction, and light flux and a flow rate are the two control parameters. The second case presents the effect of temperature on the oscillatory behaviors, and temperature and a flow rate are the control parameters. Stochastic resonance is demonstrated in the first case in which a signal and noise are applied to the different inputs, respectively. The scenario and novel aspects of SR in *two-parameter* systems are discussed, and the possibility of the analogous SR in biological systems is also pointed out.

Key words: Stochastic resonance, Signal detection, Noise, *Two-parameter* dynamical system, Non-linear chemical reaction, Belousov-Zhabotinsky (BZ) reaction.

1. Introduction

Biological systems are suffered from many kinds of environmental fluctuations, such as temperature, light, sounds, magnetic field; some of them are periodic or stochastic. Under such noisy conditions, biological systems may enhance a weak signal or information by a mechanism known as stochastic resonance (SR) [1], in which a weak signal can be enhanced by noise. Evidence of SR has been found in a lot of biological and living systems, including sensory neurons [2, 3], neuronal networks from brains [4], ion channels [5], and physiological systems [6, 7]. Theoretical studies of SR using FitzHugh-Nagumo (FHN) neuron models [8, 9] as well as non-dynamical systems [10] have confirmed the experimental findings of SR in biological systems.

Despite many examples of SR in biological systems and the other scientific fields [1, 11, 12], it should be noted that all the experimental studies have been carried out under the same conditions in which a signal and noise are applied to a system from identical physical sources [2–4, 8, 11, 13, 14]. Thus the modeling

studies of such systems deal with only *one parameter* that includes both a signal and noise. The source of noise may be different from that of a signal, and SR under such a condition should be more general than that reported so far.

In the present paper, we show SR in a model of *two-parameter* dynamical systems based on a real chemical reaction, i.e., the Belousov-Zhabotinsky (BZ) reaction [15]. We consider two cases, where a signal and noise can be applied to different physical inputs. The first case presents the photosensitivity of the system [16], where light flux and a flow rate are two control parameters. A periodic signal is applied to one of the parameters (e.g., the flow rate), noise is applied to the other parameter (e.g., the light flux), and SR under this condition is investigated. The second case presents the temperature dependence of the system [17, 18], where temperature and a flow rate are the two parameters. It provides another example of *two-parameter* systems, and the system behavior is examined in terms of the two bifurcation parameters.

2. Photosensitive Flow-Oregonator

2.1. MODELING

Here we present two modified Oregonator [19] models for the photosensitive BZ reaction to clarify the role of the two control parameters, the light flux and the flow rate. The first model (Model I) was proposed by Krug et al. [16], which has been used widely because of its simple mathematical expression. The second model (Model II) was proposed by Kádár et al. [20], which is an extension of the Model I based on the experimental results [20, 21]. The Model II was applied to a flow system later [22], and its dimensionless form is given by

$$\begin{aligned}\varepsilon \dot{x} &= x(1-x) + y(q-x) - \varepsilon \kappa_f x + p_2 \phi \\ \varepsilon' \dot{y} &= 2hz - y(q+x) - \varepsilon' \kappa_f (y-y_0) + p_1 \phi \\ \dot{z} &= x - z - \kappa_f z + \left(\frac{p_1}{2} + p_2\right) \phi\end{aligned}\tag{1}$$

where x , y , and z are the concentrations of the activator (HBrO_2), inhibitor (Br^-), and the catalyst; ε , ε' , q , y_0 , and h are constants; p_1 and p_2 are coefficients for the inhibitory and inductive effects of light [21, 22], respectively; and ϕ and κ_f are the light flux and the flow rate.

In the Model I, the effect of light was involved only in dy/dt equation by the form of ϕ , i.e., $p_2 = 0$, and the values of p_1 in dy/dt and dz/dt equations are one and zero, respectively. Thus the light flux and the flow rate terms can not be separated in this model, because a linear relation holds between the two parameters (external control = $\varepsilon' \kappa_f y_0 + \phi$) under usual experimental conditions where all the out-flow terms are negligibly small: $\varepsilon \kappa_f \ll 1$, $\kappa_f \ll 1$, and $\varepsilon' \kappa_f \ll q$ [23]. In the Model II, however, the light flux and the flow rate control the system different

Figure 1. Bifurcation diagram of the modified Oregonator model, spanned by the light flux (ϕ) and the flow rate (κ_f): (-----) Model I ($p_2 = 0$ and the values of p_1 in dy/dt and dz/dt equations are one and zero, respectively) with $\varepsilon = 0.429$, $\varepsilon' = 0.00232$, $q = 9.52 \times 10^{-5}$, $h = 0.5$, and $y_0 = 47.6$; (—) Model II ($p_1 = 0.0125$, $p_2 = 0.766$) with $\varepsilon = 0.429$, $\varepsilon' = 0.00232$, $q = 9.52 \times 10^{-5}$, $h = 0.5$, and $y_0 = 47.6$. The lines divide the region into the steady state (SS) and the oscillatory state (OSC), where a Hopf bifurcation occurs.

ways. The linear-coupling of the two parameters in the Model I and the different role of the two parameters in the Model II will be demonstrated below.

2.2. LINEAR STABILITY ANALYSIS

The condition for a Hopf bifurcation [24], which is characteristic of the BZ reaction, was investigated in the *two-parameter* space. The values of constant parameters used are shown in the caption of Figure 1. The Model I gives a straight bifurcation line, representing a linear-coupling of the two parameters. The curved line from the Model II demonstrates the different role of the two parameters. Note that the Model II agrees with experimental results of the photosensitive BZ system quantitatively [20, 22].

2.3. PERIODIC AND STOCHASTIC MODULATION OF LIGHT FLUX AND FLOW RATE

Periodic and stochastic modulations in the light flux and in the flow rate are given as follows:

$$\begin{aligned}\phi &= \phi^0 \left(1 + \alpha_1 \sin\left(\frac{2\pi}{T_1}\right) + \beta_1 \xi(\delta) \right) \\ \kappa_f &= \kappa_f^0 \left(1 + \alpha_2 \sin\left(\frac{2\pi}{T_2}\right) + \beta_2 \xi(\delta) \right)\end{aligned}\quad (2)$$

where ϕ^0 and κ_f^0 are the constant components; α_1 and α_2 are the amplitudes of sinusoidal signals with periods T_1 and T_2 , respectively; β_1 and β_2 are the noise amplitudes of equally distributed random numbers, $\xi(\delta)$, between -1 and 1 ; and δ is the duration (5 s) of the pulse of a single noise event that occurred every 10 s. To quantify the SR effect, the distribution of an interspike interval was investigated [1]. The number of adjacent spikes (NAS), whose time interval was in the range from $(1 - 0.1)T_1$ to $(1 + 0.1)T_1$, or from $(1 - 0.1)T_2$ to $(1 + 0.1)T_2$, was plotted as a function of the noise amplitude.

2.4. SR UNDER THE CONDITION (I): PERIODIC SIGNAL IN FLOW RATE AND NOISE IN LIGHT FLUX

The responses of the Models I and II were first investigated under the condition (I). In both Models, the following responses were obtained; the total number of spikes increased monotonically with increasing the noise amplitudes, however, the NAS exhibited a maximum at an optimized noise amplitude [22]. Figure 2 shows the NAS as a function of the noise amplitude: (a) for the Model I, and (b) for the Model II, respectively. A maximum of the NAS, which is the fingerprint of SR, was obtained in each model.

2.5. SR UNDER THE CONDITION (II): PERIODIC SIGNAL IN LIGHT FLUX AND NOISE IN FLOW RATE

The system behaviors of the Model I and II were next studied under the condition (II). The responses of the two models were qualitatively similar to those under the condition (I). The results are also shown in Figure 2. In the case of the Model I (Figure 2(a)), there is no quantitative difference in the SR curves between the condition (I) and (II) within the standard deviations. This result is due to the linear coupling of the two parameters in this model as mentioned above.

On the other hand, the SR curves for the Model II are different between the condition (I) and (II). The peak of SR curve under the condition (I) appeared in a range of the noise amplitude that was 10-fold smaller than that under the condition (II). The height of the two peaks was also different. These differences are due to the different role of the two parameters as described in detail [21, 22].

2.6. SCENARIO OF TWO-PARAMETER SR

According to the threshold scenario of SR [1], a threshold is considered to be constant in time. In the case of the present *two-parameter* systems, however, a periodic signal in one parameter (e.g., the flow rate) modulates the threshold of the other parameter (e.g., the light flux) as shown in Figure 3. Stochastic resonance occurs when the noise applied to the light flux crosses the periodically modulated threshold. Exchanging the modulations in the two parameters also gives rise to SR

Figure 2. Number of adjacent spikes (NAS) whose time interval was within $\pm 10\%$ of the period of the sinusoidal signal. (a) Model I with $\kappa_f^0 = 1.1 \times 10^{-3}$, $\phi^0 = 1.21 \times 10^{-4}$: (●) a signal in the flow rate ($\alpha_2 = 0.045$, $T_2 = 300$ s, $\beta_2 = 0$) and noise in the light flux ($\alpha_1 = 0$); (○) a signal in the light flux ($\alpha_1 = 0.045$, $T_1 = 300$ s, $\beta_1 = 0$) and noise in the flow rate ($\alpha_2 = 0$). (b) Model II with $\kappa_f^0 = 1.7 \times 10^{-3}$, $\phi^0 = 1.66 \times 10^{-2}$: (●) a signal in the flow rate ($\alpha_2 = 0.05$, $T_2 = 300$ s, $\beta_2 = 0$) and noise in the light flux ($\alpha_1 = 0$); (○) a signal in the light flux ($\alpha_1 = 0.05$, $T_1 = 300$ s, $\beta_1 = 0$) and noise in the flow rate ($\alpha_2 = 0$). The other parameters are the same as those in Figure 1. The time series data of 60 000 s were analyzed. Error bars are the standard deviations of the NAS obtained with a set of six random numbers at each noise amplitude. The solid lines are to guide the reader's eye.

by the same scenario. The peak height and/or the range of the noise amplitude for the SR peak may be different depending on the role of the parameters in the dynamics of the systems.

2.7. DIRECTIONS OF HOPF BIFURCATION

We point out here two different directions of a Hopf bifurcation, subcritical and supercritical, in the model systems in connection with SR effects. Krug et al. [16]

Figure 3. Threshold scenario of SR for a *two-parameter* system. A periodic signal in one parameter (μ_1) changes a threshold of the other parameter (μ_2), which gives rise to SR when noise crosses the modulated threshold.

has shown by using an Hopf bifurcation formula [25] that the Model I exhibits a subcritical or supercritical Hopf bifurcation depending on the values of the constant parameters. A typical subcritical Hopf bifurcation is shown in Figure 4(a) for the Model II. On the other hand, a supercritical Hopf bifurcation is shown in Figure 4(b) for the Model II with different values of the constant parameters.

Subcritical Hopf bifurcations occur in the dynamics of nerve cells [26], and large-amplitude spiking behaviors have generally been found in biological systems such as excitable membranes [27] and neurons [28]. Experimental and modeling studies of SR in biological systems have been restricted to a system exhibiting spiking or subcritical behaviors [2, 4, 29]. In chemical reaction systems, however, both subcritical and supercritical behaviors can be realized in experiments [11, 30] as well as in models [16, 31]. In the present photosensitive BZ system, the inflow concentration of malonic acid (MA) can control the directions of the Hopf bifurcation experimentally, and also control them in the model by changing the values of ε and ε' . The quantitative comparison of SR effects between the two cases has not been demonstrated yet, and the photosensitive BZ system is useful to clarify this issue in both experiments and models.

Figure 4. Two different directions of a Hopf bifurcation of the Model II: (a) subcritical bifurcation with $\varepsilon = 0.429$, $\varepsilon' = 0.00232$, $q = 9.52 \times 10^{-5}$, $h = 0.5$, $p_1 = 0.0125$, $p_2 = 0.766$, $\kappa_f = 1.0 \times 10^{-3}$, and $y_0 = 47.6$; (b) supercritical bifurcation with $\varepsilon = 0.644$, $\varepsilon' = 0.00348$, $q = 9.52 \times 10^{-5}$, $h = 0.5$, $p_1 = 0.0125$, $p_2 = 0.766$, $\kappa_f = 1.0 \times 10^{-3}$, and $y_0 = 47.6$. Note that the difference in the values of ε and ε' between subcritical and supercritical cases results from difference in the concentration of malonic acid (MA); the concentration is 1.5 times higher for supercritical case than that for subcritical case.

3. Effect of Temperature on Flow-Oregonator

3.1. MODELING

Here another *two-parameter* system controlled by temperature and a flow rate is presented. The Oregonator model is also employed, and the differential rate equations are given by

$$\begin{aligned} dX/dt &= k_{o1}AY - k_{o2}XY + k_{o3}AX - 2k_{o4}X^2 - k_fX \\ dY/dt &= -k_{o1}AY - k_{o2}XY + hk_{o5}MZ - k_f(Y - Y_0) \\ dZ/dt &= 2k_{o3}AX - k_{o5}MZ - k_fZ \end{aligned} \quad (3)$$

where X , Y , Z , and Y_0 are the dimension form of x , y , z , and y_0 in Equation (1), $A = \text{BrO}_3^-$, $H = \text{H}^+$, $M = \text{MA}$ (malonic acid), h is the stoichiometric factor, and k_{oi} 's ($i = 1 \sim 5$) are the rate constants. The effect of temperature on the dynamics of the BZ reaction was found to be reflected into the model [17, 18]. Namely, the dependence of the reaction rate constants of k_{o1} and k_{o5} on temperature was taken into account by using the Arrhenius equation:

$$\begin{aligned} k_{o1} &= H^2 A_1 \text{Exp} \left(\frac{-E_{a1}}{RT} \right) \\ k_{o5} &= A_5 \text{Exp} \left(\frac{-E_{a5}}{RT} \right) \end{aligned} \quad (4)$$

where A_1 and A_5 are temperature-independent frequency factors, E_{a1} and E_{a5} are the activation energies, R is the gas constant, and T is temperature in kelvins. The values of the activation energies, $E_{a1} = 50 \text{ kJ mol}^{-1}$, $E_{a5} = 70 \text{ kJ mol}^{-1}$, were employed from the literature [17], and the frequency factors, $A_1 = 1.66 \times 10^9 \text{ (M}^{-3} \text{ s}^{-1}\text{)}$, $A_5 = 2.4 \times 10^{12} \text{ (M}^{-1} \text{ s}^{-1}\text{)}$ were determined in this study to be consistent with the experimental results [17, 18].

3.2. LINEAR STABILITY ANALYSIS

Stability of the steady state of the model (3) with the temperature-dependent rate constants (4) was investigated in the space of temperature and the flow rate by the Routh-Hurwitz criteria [32]. The result is shown in Figure 5; the dotted and the white regions show locally stable and unstable steady states, respectively. We confirmed by numerical integration of the model that oscillations occur within the locally unstable steady state region in the two-parameter space.

Figure 5. Phase diagram of the model of Equation (3) with the temperature-dependent rate constants (Equation (4)), spanned by temperature (T) and the flow rate (k_f) with the following values of the parameters: $k_{o2} = 3 \times 10^6$ ($\text{M}^{-1} \text{s}^{-1}$), $k_{o3} = 42$ ($\text{M}^{-1} \text{s}^{-1}$), $k_{o4} = 3 \times 10^3$ ($\text{M}^{-1} \text{s}^{-1}$), $q = 9.52 \times 10^{-5}$, $h = 0.5$, $A = 0.1$ M, $H = 1$ M, and $M = 0.2$ M. Dotted and white regions indicate locally stable and unstable steady states, respectively. Numerical integration of Equation (3) with the rate constants of Equation (4) exhibits oscillations in the unstable steady state region.

3.3. OSCILLATORY BEHAVIOR

The characteristics of the oscillations in this model is that the period decreases and the amplitude becomes small by increasing the temperature. Typical time series data for the model are shown in Figure 6. The directions of the bifurcation seem to change from subcritical (Figure 6(a)) to supercritical (Figure 6(b)) at a critical value of the temperature. The qualitatively similar dependence of the oscillatory behaviors, i.e., decrease in both periods and amplitudes with increase in the temperature, has been observed in several systems such as chemical reactions in gas phase [33], or in solution phase [17, 18], and ionic transport in membranes [34].

3.4. TWO-PARAMETER SR

The large-amplitude oscillatory behavior and the curved boundary between the oscillatory and stable steady state regions indicate that *two-parameter SR* may also be realized in this system. The scenario of the SR as shown in Figure 3 can be applied to this system as well. Stochastic resonance in chemical or biochemical systems induced by temperature has not been reported so far, and is now under study in our laboratory.

4. Conclusion and Remark

We have shown *two-parameter* dynamical systems based on the Oregonator model of the BZ reaction, in which SR may occur when a signal and noise are applied to

Figure 6. Time series data calculated from the model of Equation (3) with Equation (4). (a), (b): the flow rate was increased in time with different values of temperature ((a) $T = 298$ K and (b) $T = 326$ K); (c): temperature was increased in time with a constant value of the flow rate ($k_f = 1.0 \times 10^{-3} \text{ s}^{-1}$). The other values of the parameters are the same as those in Figure 5.

Figure 6. Continued.

the different physical inputs. The different role of the two parameters in the models was confirmed by a linear stability analysis, and in particular, was demonstrated in the SR results in the photosensitive case.

Temperature is known to affect chemical and biochemical oscillators significantly, and therefore SR induced by temperature will occur in these oscillators. However, temperature dependence of real biological systems is somehow different from that of chemical or biochemical oscillators [17]. Circadian rhythms, for instance, show temperature compensation. A suitable model is necessary to study the effect of temperature on real biological systems.

One of the advantages to use the Oregonator model is that each control parameter corresponds to the real physical input in the experimental systems, thus one can readily apply the control techniques used in the models to the experiments. The Oregonator model exhibits similar dynamics as the FHN neuron model, indicating that *two-parameter SR* or, in general, *multi-parameter SR* can be realized in biological systems, which has not been demonstrated yet.

Acknowledgement

We would like to thank Drs K. Kato and K. Seki of NIMC for valuable comments and discussion.

References

1. Gammaitoni, L., Hänggi, P., Jung, P. and Marchesoni, F.: Stochastic resonance, *Rev. Mod. Phys.* **70** (1998), 223–287.

2. Douglass, J.K., Wilkens, L., Pantazelou, E. and Moss, F.: Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance, *Nature* **365** (1993), 337–340.
3. Levin, J.E. and Miller, J.P.: Broadband neural encoding in the cricket cercal sensory system enhanced by stochastic resonance, *Nature* **380** (1996), 165–168.
4. Gluckman, B.J., Netoff, T.I., Neel, E.J., Ditto, W.L., Spano, M.L. and Schiff, S.J.: Stochastic resonance in a neuronal network from mammalian brain, *Phys. Rev. Lett.* **77** (1996), 4098–4101.
5. Bezrukov, S.M. and Vodyanoy, I.: Noise-induced enhancement of signal transduction across voltage-dependent ion channels, *Nature* **378** (1995), 362–364.
6. Cordo, P., Inglis, J.T., Verschueren, S., Collins, J.J., Merfeld, D.M., Rosenblum, S., Buckley, S. and Moss, F.: Noise in human muscle spindles, *Nature* **383** (1996), 769–770.
7. Collins, J.J., Imhoff, T.T. and Grigg, P.: Noise-enhanced tactile sensation, *Nature* **383** (1996), 770–770.
8. Wiesenfeld, K., Pierson, D., Pantazelou, E., Dames, C. and Moss, F.: Stochastic resonance on a circle, *Phys. Rev. Lett.* **72** (1994), 2125–2129.
9. Longtin, A.: Synchronization of the stochastic Fitzhugh-Nagumo equations to periodic forcing, *Nuovo Cimento* **17** (1995), 835–846.
10. Bezrukov, S.M. and Vodyanoy, I.: Stochastic resonance in non-dynamical systems without response thresholds, *Nature* **385** (1997), 319–321.
11. Hohmann, W., Müller, J. and Schneider, F.W.: Stochastic resonance in chemistry. 3. The minimal-bromate reaction, *J. Phys. Chem.* **100** (1996), 5388–5392.
12. Barzykin, A.V., Seki, K. and Shibata, F.: Periodically driven linear system with multicative colored noise, *Phys. Rev. E* **57** (1988), 6555–6563.
13. Löcher, M., Johnson, G.A. and Hunt, E.R.: Spatiotemporal stochastic resonance in a system of coupled diode resonators, *Phys. Rev. Lett.* **77** (1996), 4698–4701.
14. Hibbs, A.D., Singsaas, A.L., Jacobs, E.W., Bulsara, A.R., Bekkedahl, J.J. and Moss, F.: Stochastic resonance in a superconducting loop with a Josephson junction, *J. Appl. Phys.* **77** (1995), 2582–2590.
15. Burger, M. and Field, R.J.: *Oscillations and traveling waves in chemical systems*, Wiley, New York, 1985.
16. Krug, H.-J., Pohlmann, L. and Kuhnert, L.: Analysis of the modified complete oregonator accounting for oxygen sensitivity and photosensitivity of Belousov-Zhabotinsky systems, *J. Phys. Chem.* **94** (1990), 4862–4866.
17. Ruoff, P.: Antagonistic balance in the oregonator: about the possibility of temperature-compensation in the Belousov-Zhabotinsky reaction, *Physica D* **84** (1995), 204–211.
18. Nagy, G., Körös, E., Oftedal, N., Tjelflaat, K. and Ruoff, P.: Effect of temperature in cerium-ion-catalyzed bromate-driven oscillators, *Chem. Phys. Lett.* **250** (1996), 255–260.
19. Field, R.J. and Noyes, R.M.: Oscillations in chemical systems. IV. Limit cycle behavior in a model of a real chemical reaction, *J. Chem. Phys.* **60** (1974), 1877–1884.
20. Kádár, S., Amemiya, T. and Showalter, K.: Reaction mechanism for light sensitivity of the $\text{Ru}(\text{bpy})_3^{2+}$ -catalyzed Belousov-Zhabotinsky reaction, *J. Phys. Chem. A* **101** (1997), 8200–8206.
21. Hanazaki, I., Mori, Y., Sekiguchi, T. and Rábai, G.: Photo-response of chemical oscillations, *Physica D* **84** (1995), 228–237.
22. Amemiya, T., Ohmori, T., Nakaiwa, M. and Yamaguchi, T.: Two-parameter stochastic resonance in a model of the photosensitive Belousov-Zhabotinsky reaction in a flow system, *J. Phys. Chem. A* **102** (1998), 4537–4542.
23. Amemiya, T., Ohmori, T., Nakaiwa, M. and Yamaguchi, T.: Toward two-parameter stochastic resonance: numerical study of the photosensitive Belousov-Zhabotinsky reaction in a flow system, *ACH-Models Chem.* **135** (1998), 231–240.

24. Gray, P. and Scott, S.K.: *Chemical oscillations and instabilities, non-linear chemical kinetics*, Clarendon Press, Oxford, 1994.
25. Hsü, I.-D. and Kazarinoff, N.D.: An applicable Hopf bifurcation formula and instability of small periodic solutions of the Field-Noyes model, *J. Math. Anal. Appl.* **55** (1976), 61–89.
26. Koch, C. and Segev, I. (eds.): *Methods in neuronal modeling: From synapses to networks*, MIT Press, Cambridge, MA, 1989.
27. Hille, B. (eds.): *Ionic channels of excitable membranes*, Sinauer Associates, Massachusetts, 1992.
28. Koch, C.: Computation and the single neuron, *Nature* **385** (1997), 207–210.
29. Braun, H.A., Wissing, H., Schäfer, K. and Hirsch, M.C.: Oscillation and noise determine signal transduction in shark multimodal sensory cells, *Nature* **367** (1994), 270–273.
30. Sørensen, P.G., Lorenzen, T. and Hynne, F.: Quenching of chemical oscillations with light, *J. Phys. Chem.* **100** (1996), 19192–19196.
31. Hynne, F., Sørensen, P.G. and Nielsen, K.: Quenching of chemical oscillations: General theory, *J. Chem. Phys.* **92** (1990), 1747–1757.
32. Murray, J.D.: *Mathematical Biology*, Springer-Verlag, Berlin, 1989.
33. Johnson, B.R., Griffiths, J.F. and Scott, S.K.: Characterization of oscillations in the $\text{H}_2 + \text{O}_2$ reaction in a continuous-flow reactor, *J. Chem. Soc. Faraday Trans.* **87** (1991), 523–533.
34. Urabe, K. and Sakaguchi, H.: Characteristics of current induced potential oscillations of a triolein impregnated membrane placed between identical salt solutions, *Biophys. Chem.* **59** (1996), 33–39.