Frequency Clustering in a Chain of Weakly Coupled Oscillators

Thomas Kirner [a] and Otto E. Rössler [b]

[a] Institute for Molecular Biotechnology, Department of Molecular Information Processing, Beutenbergstr. 11, Postfach 100 813, D–07708 Jena

[b] Universität Tübingen, Division of Theoretical Chemistry, Auf der Morgenstelle 8, D–72076 Tübingen

Z. Naturforsch. **52 a,** 578–580 (1997); received June 10, 1997

A numerical simulation of a chain of diffusively coupled nonlinear oscillators with a linear parameter gradient exhibits clusters of frequencies. The intention was to investigate the frequency–gradient in the stimulus conduction system of the heart. The phenomenon generalizes earlier findings on "frequency plateaus" described in the 1960's by Nicholas Diamant as a model of small–intestine transport. This "waxing and waining" phenomenon is a version of chaos. Thus, subtle chaos in the heart and waxing and waining type chaos in the intestine may be related.

1. Introduction

Weakly coupled oscillators with a gradient in their natural frequencies show "frequency plateaus" as is known both from experiment [1] and from a numerical confirmation on a digital computer [2]. The same phenomenon was also simulated on an analog computer [3] and analytically explained by Ermentrout and Kopell [4]. Frequency gradients are of importance for the small intestine since they enable directed food transport in a structurally stable manner. While a pure phase gradient would also be effective, it depends sensitively on initial conditions and is not asymptotically stable.

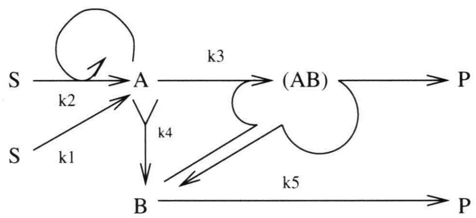
A frequency gradient is also a characteristic of the stimulus conduction system in the mammalian heart [16]. In the intestine the frequency plateaus were characterized as "waxing and waining", by Diamant [1], [2]. In the heart, chaotic behaviour is known to occur [5] - [9]. In the following, several regimes will be shown to arise in diffusively coupled oscillators with a cross–activating type of coupling.

2. An Abstract Reaction System

We use the following abstract chemical kinetics:

$$
\begin{array}{rcl}
\mathrm{S} & \rightarrow & \mathrm{A} \\
\mathrm{S+A} & \rightarrow & \mathrm{2A} \\
\mathrm{2A} & \rightarrow & \mathrm{B} \\
\mathrm{B} & \rightarrow & \mathrm{P} \\
\mathrm{A+B} & \rightleftharpoons & \mathrm{(AB)} \rightarrow \mathrm{P+B}
\end{array}
\qquad (1)
$$

or, equivavently, in the so–called biochemical notation:



The most sophisticated reaction (on the right) represents a Michaelis–Menten kinetics (substrate A, and B acting as the enzyme). The original substrate, S, is supposed to be a "pool" substance, that is, to remain (or be kept) approximately constant.

The rate equations of system (1) are, under the usual idealizing conditions (activativities equal to the concentrations, homogenous kinetics, isothermy, etc.), as follows:

$$
\begin{aligned}
\dot{a}_1 &= k_1 + k_2 a_1 - k_3 \frac{a_1 b_1}{(a_1 + K_m)} - k_4 a_1^2 \\
&\quad + D(a_2 - a_1) \\
\dot{b}_1 &= k_4 a_1^2 - k_5 b_1
\end{aligned}
$$

Reprint requests to Thomas Kirner.

$$
\begin{aligned}
\dot{a}_2 &= k_1 + k_2 a_2 - k_3 \frac{a_2 b_2}{(a_2 + K_m)} - k_4 a_2^2 \\
&\quad + D(a_1 + a_3 - 2a_2) \\
\dot{b}_2 &= k_4 a_2^2 - k_5 b_2 \qquad\qquad (2) \\
\vdots \quad & \vdots \qquad \vdots \\
\dot{a}_n &= k_1 + k_2 a_n - k_3 \frac{a_n b_n}{(a_n + K_m)} - k_4 a_n^2 \\
&\quad + D(a_{(n-1)} - a_n) \\
\dot{b}_n &= k_4 a_n^2 - k_5 b_n .
\end{aligned}
$$

3. Results

First, we consider the case of a single model compartment, obtained by putting either $D = 0$ or $D = \infty$. It allows for oscillatory solutions as the most complex dynamical behaviour since there are now only two variables. A stable limit cycle is born out of a Hopf Bifurcation. An unstable focus (a complex conjugate pair of eigenvalues with a positive real part) can easily be obtained in the Jacobian determinant of the locally linearized system at the steady state.

Second, a diffusive coupling of two oscillators, with different parameter values in k_5, led to quasiperiodic–like behaviour in the parameter regime studied numericaly. In principle the appearence of chaotic behaviour has also to be reckoned with; compare [10] for an analogous but inhibitorily coupled system and [11] for the same system under a cross–activating type of coupling. A variation in the strength of the diffusive coupling or a variation in the parameter difference (gradient) both failed to produce a higher complexity in the numerical investigations performed. Only a near–zero Lyapunov characteristic exponent was found numerically beside the trivially zero one and two negative ones. That is, there was a quasiperiodic window, sandwiched between two periodic regimes of negative LCE's. Wether one has a periodic regime or a quasiperiodic window depends on the strength of coupling. In the simulation the quasiperiodic regime occured at $0.05 \le D \le 0.2$, while k_5 was 0.15 in one oscillator and 0.1 in the other; the rest of the parameters was $k_1 = 1.0$, $k_2 = 4.8$, $k_3 = 3.1$, $k_4 = 3.0$ and $K_m = 0.03$.

Third, eight oscillators ($n = 8$) were coupled in a parameter gradient. That is, the constant k_5 was varied linearly from 0.85 (highest frequency) down to 0.15 (at the low frequency end) in equal steps (in 0.01 decrements). The intrinsic frequencies of the oscillators thereby obtained under a condition of uncoupling ($D = 0$) were 0.3669; 0.3479; 0.3238; 0.2978; 0.2671; 0.2312; 0.1876 and 0.1351 per time unit. Under a variation of the diffusive coupling constant D, a transition from the uncoupled quasiperiodic behaviour (with eight exactly zero Lyapunov characteristic exponents) toward one with eight close to zero Lyapunov characteristic exponents occured, numerically. Then, a transition to chaotic behaviour (with several markedly positive LCEs) was found. In an intermediary range, a characteristic regime occured – "subtle chaos". It occurs in the vicinity of a higher–order torus (**n**–torus) and possesses only one small–positive Lyapunov characteristic exponent. Its Lyapunov dimension [12] was $D_L = n + \varepsilon$, whereby ε depends on the diffusion constant D. As D varied from 0.1 to 0.2, ε varied between 0 and 0.5. Figure 1 represents a so called Rob Shaw plot [13], obtained from the time series of the last (8th) oscillator. What is plotted are the differences between the maxima of three consecutive peaks, plotted against each other. This is similar to an next–amplitude plot if the attractor is highly dissipative (as is here the case). One sees a band–like clustering in the attractor.

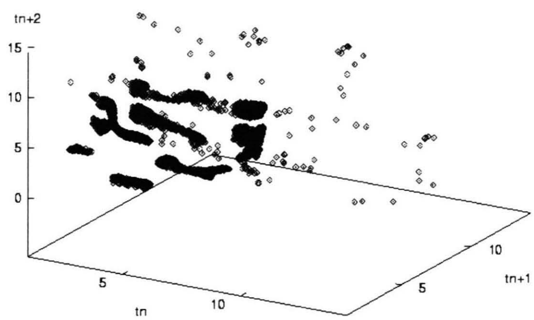


Fig. 1. Frequency–clustering in a chain of eight coupled cells. The cells are coupled with a parameter–gradient (corresponding to a frequency–gradient in the uncoupled case). The coupling is performed via the activating variable, with equal diffusive coupling constants $D = 0.2$. The other parameters are $k_1 = 1.0$, $k_2 = 4.8$, $k_3 = 3.1$, $K_m = 0.03$ and $k_4 = 3.0$; k_5 goes from 0.85 (oscillator with the highest intrinsic frequency) down to 0.15 (oscillator with the lowest intrinsic frequency).

Finally, a numerical simulation involving 100 oscillators (k_5 varied in a linear gradient from 0.3 to 0.25) is shown in Figure 2. Hereby the oscillators were diffusively coupled with zero flux boundary conditions. Plateaus are visibly formed by oscillators with

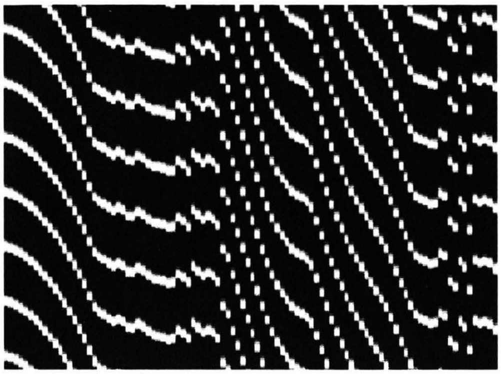


Fig. 2. Frequency–plateaus in a chain of a hundred coupled cells. Space is along the horizontal axis, time's axis goes down vertically. White color encodes a high level of A_i. The coupled cells are subject to a parameter gradient (frequency gradient). The coupling is accomplished by diffusion between the activating variables (with diffusive coupling constant $D = 0.025$ through out). The other parameters are $k_1 = 1.0, k_2 = 4.8, k_3 = 3.1, K_m = 0.03$ and $k_4 = 3.0$; and k_5 goes down from 0.3 to 0.25. The oscillator with the highest intrinsic frequency is on the left. The vertical time difference is $\Delta t = 32$ time units, corresponding to 32000 time steps in a Runge–Kutta–forth order algorithm.

similar frequencies. The visible plateaus are not constant over time.

4. Discussion

A numerical simulation of a chain of coupled oscillators has been presented. The aim was to investigate the phenomena which arise when oscillators that are subject to a parameter–gradient are coupled. The motivation was the frequency gradient known to exist in the stimulus conduction system in the mammalian heart and in the small intestine. Both systems have a function of transport. The frequency gradient stabilizes the transport in one direction and prevents a "reflux". We found – perhaps not surprisingly – that in such a system chaotic behaviour can occur without external influences. This result could explain the endogenous frequency scatter in the heart which occurs also in deafferenced hearts [14]. Our finding at the same time confirms the intuitive impression, to be gained from Diamant's suminal papers, that what he dubbed "waxing and waining" actually represents a form of chaos. At the same time, an unexpectedly close connection arises between heart and gut. Is the "healthy irregularity of the heart" (Arnold Mandell [15]) related to the healthy irregularities of other bodily systems like the intestine and the brain?

Acknowledgements

We thank Kunihiko Kaneko, Ichiro Tsuda, Joachim Peinke, Achim Kittel, Gottfried–Mayer Kress, Hans H. Diebner, Georg Hartmann, Gerold Baier, Sven Sahle, Ursula Kummer, Axel Hoff, Valentin Alber, Petra Foerster, Maria Athelogou and John McCaskill for discussions. The paper was presented at 6th Annual Meeting of ENGADYN, Tüchersfeld 1996.

[1] N. E. Diamant and A.Bortoff, Amer. J. Physiol. **216**, 310 (1969).
[2] N. E. Diamant, P. K. Rose, and E. J. Davison, Amer. J. Physiol. **219**, 1684 (1970).
[3] S. K. Sarna, E. E. Daniel, and Y. J. Kingma, Amer. J. Physiol. **221**, 166 (1971).
[4] G. B. Ermentrout and N. Kopell, SIAM J. Math. Anal. **15**, 215 (1984).
[5] A. L. Goldberger, D. R. Rigney, and B. J. West, Aci. Am. **262**, 42 (1990).
[6] C. Peng, S. V.Buldyrev, J. M. Hausdorff, S. H. Havlin. J. E. Mietus, M. Simons, H. E. Stanley, and A. Goldberger, Int. Phys. Beh. Sci. **29**, 283 (1994).
[7] G. Schmidt and G. E. Morfill, PACE **17**, 2336 (1994).
[8] J. P. Zbilut, G.Mayer–Kress, P. A. Sobotka, M. O' Toole, and J. X. Thomas Jr., Biol. Cybern. **61**, 371 (1989).
[9] O. E. Rössler, R. Rössler, and H. D. Landahl, Arrhythmia in a periodically forced excitable system, Sixth international Biophysics Congress, Abstracts, Kyoto September 3–9, 1978, p. 296.
[10] O. E. Rössler, Z. Naturforsch. **31a**, 1168 (1976).
[11] T. Kirner, Diploma thesis, University of Tübingen 1996.
[12] J. Argyris, G. Faust, and M. Haase, Die Erforschung des Chaos, Vieweg Verlag, Braunschweig–Wiesbaden 1994.
[13] R. Shaw, Z. Naturforsch. **36a**, 80 (1981).
[14] J. P. Zbilut, G.Mayer–Kress, and K. Geist, Math. Biosci. **90**, 49 (1984).
[15] Personal communication 1984.
[16] Cf., e. g. H. Reichel and A. Bleichert, Leitfaden der Physiologie des Menschen, p. 289, Enke, Stuttgart 1987.