

# **Spatio-Temporal Organization in Nonequilibrium Systems**

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## Table of Contents

<b>BZ-waves propagation along a line of diffusion-jump</b> <i>Agladze, K.I. and De Kepper, P.</i>	1-7
<b>Models of cytoplasmic motion</b> <i>Alt, W.</i>	8-10
<b>Pattern formation and topological defects in nonlinear optics</b> <i>Arecchi, F.T.</i>	11-12
<b>Wave phenomena in an excitable surface reaction</b> <i>Bär, M., Eiswirth, M., Rotermund, H.H. and Ertl, G.</i>	13-15
<b>Dynamic instabilities in a coupled electrochemical and biochemical reaction system</b> <i>Baier, G. and Urban, P.</i>	16-18
<b>Bifurcations and symmetries of spiral waves</b> <i>Barkley, D.</i>	19-20
<b>Experiments on interacting electrochemical oscillators</b> <i>Bell, J.C., Wang, Y., Jaeger, N.I. and Hudson, J.L.</i>	21-24
<b>Convection in gasses at elevated pressures</b> <i>Bodenschatz, E., Morris, S.W., de Bruyn, J.R., Cannell, D.S. and Ahlers, G.</i>	25
<b>Evolutionary consequences of spatial pattern formation</b> <i>Boerlijst, M.C. and Hogeweg P.</i>	26-28
<b>Spatial structures in reaction-diffusion systems</b> <i>Borckmans, P., De Wit, A. and Dewel, G.</i>	29-31
<b>Localized solutions of envelope and phase equations</b> <i>Brand, H.R. and Deissler, R.J.</i>	32-33
<b>Spiral drift in a light-sensitive active medium with spatial gradient of excitability</b> <i>Braune, M. and Engel, H.</i>	34-36
<b>Mathematical modeling of oscillations and waves of oxidation and reduction in the cerium and ferroin-catalyzed BZ-reaction</b> <i>Buchholtz, F.</i>	37-39
<b>Pattern formation in populations of chemotactic bacteria</b> <i>Budrene, E.O.</i>	40
<b>Transitions to tertiary and quarternary states of fluid flows</b> <i>Busse, H.-G. and Clever, R.M.</i>	41-43

<b>Stochastic effects in nonlinear chemical systems</b> <i>Careta, A. and Sagués, F.</i>	44-45
<b>Pattern formation in oscillators submitted to a parametric forcing close to the frequency cut-off</b> <i>Coulet, P., Frisch, T. and Sonnino, G.</i>	46-58
<b>Spiral waves of excitation in isolated cardiac muscle</b> <i>Davidenko, J.M., Pertsov, A.M., Salomonsz, R. Baxter, W.T. and Jalife, J.</i>	59-62
<b>Spiral waves in a small disk and on a small sphere</b> <i>Davydov, V.A. and Zykov, V.S.</i>	63-64
<b>Cellular automaton modeling of pattern formation by filamentous fungi</b> <i>Deutsch, A., Dress, A. and Rensing, L.</i>	65-67
<b>Oscillations and waves of cytosolic calcium: properties of a model based on calcium-induced calcium release</b> <i>Dupont, G. and Goldbeter, A.</i>	68-70
<b>Symmetry breaking instability in a model of chemical reaction and molecular diffusion</b> <i>Dutt, A.K.</i>	71-74
<b>Chemical pattern formation: An overview</b> <i>Epstein, I.R.</i>	75-77
<b>Pattern formation in the oscillatory regime of the CO-oxidation on Pt(110)</b> <i>Falcke, M. and Engel, H.</i>	78-81
<b>Period doublings, period three, chaos, and quasiperiodicity in the peroxidase - oxidase reaction: Experimental and theoretical studies</b> <i>Geest, T., Larter, R., Steinmetz, C. and Olsen, L.F.</i>	82-84
<b>A cellular automaton model of excitable media</b> <i>Gerhardt, M.</i>	85-88
<b>Developmental complexity and evolutionary order</b> <i>Goodwin, B.</i>	89
<b>Theorist's view of a beautiful experiment: how many states of Rayleigh-Bénard turbulence?</b> <i>Grossmann, S. and Lohse, D.</i>	90-92

<b>Dependence of the spatial and temporal dynamics on the acidity in the ferroin-catalyzed Belousov-Zhabotinsky reaction</b> <i>Guria, G.T., Zhabotinsky, A.M., Plessner, Th., Kiyatkin, A.B. and Epstein, I.R.</i>	93-95
<b>Pattern formation in the early <i>Drosophila</i> embryo</b> <i>Hoch, M. and Jäckle, H.</i>	96-99
<b>Instabilities in propagating reaction-diffusion fronts</b> <i>Horváth, D., Petrov, V., Scott, S.K. and Showalter, K.</i>	100-101
<b>The role of "excess work" in nonequilibrium thermodynamic systems</b> <i>Hunt, K.L.C., Hunt, P.M., Peng, B., Chu, X. and Ross, J.</i>	102-104
<b>Ginzburg-Landau parameters for reaction-diffusion systems</b> <i>Hynne, F., Sørensen, P.G., Ipsen, M., Kristiansen, K.R. and Florian, M.</i>	105-107
<b>Transition from order to spatiotemporal turbulence in catalytic NO reduction</b> <i>Imbihl, R.</i>	108-110
<b>Nonlinear forecasting as a tool to diagnose heart disease</b> <i>Jørgensen, B.L., Junker, A., Mickley, H., Møller, M., Christiansen, E. and Olsen L.F.</i>	111-112
<b>Transient bimodality in turbulence 1-turbulence 2 transition in electrohydrodynamic convection in nematic liquid crystals</b> <i>Kai, S., Andoh, M. and Yamaguchi, S.</i>	113-116
<b>Reactive dynamics in a multi-species lattice-gas automaton</b> <i>Kapral, R., Lawniczak, A. and Masiar, P.</i>	117-118
<b>Scroll waves in myocardium</b> <i>Keener, J.P. and Panfilov, A.V.</i>	119-121
<b>Excitation wave propagation through narrow pathways</b> <i>Kogan, B.Y., Karplus, W.J. and Billett, B.S.</i>	122-127
<b>Coupled excitable cells</b> <i>Kosek, K. and Marek, M.</i>	128-131
<b>Hyperchaos in a surface reaction</b> <i>Kruel, Th.-M., Eiswirth, M., Schneider, F.W. and Ertl, G.</i>	132-134
<b>Intracellular calcium waves: propagation, annihilation and excitability</b> <i>Lechleiter, J.D. and Clapham, D.</i>	135-137

<b>Scaling relations in thermal turbulence: global measurements and boundary layers estimate</b> <i>Libchaber, A.</i>	138-140
<b>Patterns of temperature waves on electrically heated catalytic ribbons</b> <i>Luss, D.</i>	141-143
<b>Reaction-diffusion patterns in heterogeneous media</b> <i>Malchow, H. and Sattler, C.</i>	144-145
<b>Microtubules: Structure, dynamics, oscillations, and spatial patterns</b> <i>Mandelkow, E., Marx, A., Trinczek, B. and Mankelkow, E.-M.</i>	146-150
<b>Pattern formation in neural activator-inhibitor networks</b> <i>Markus, M. and Schepers, H.E.</i>	151-153
<b>Spatial long-range coherence in squid giant axons</b> <i>Matsumoto, G.</i>	154-155
<b>Molecular evolution in traveling waves</b> <i>McCaskill, J.S.</i>	156-157
<b>Complex biological pattern formation by linking several pattern forming reactions</b> <i>Meinhardt, H.</i>	158-161
<b>A big chemical-wave: accelerating propagation and surface deformation induced by a spontaneous convection</b> <i>Miike, H., Yamamoto, H. and Kai, S.</i>	162-165
<b>Diffusive coupling of spatio-temporal patterns in nonequilibrium systems</b> <i>Mimura, M.</i>	166-170
<b>Spiral waves in the Oregonator model: A study of time-space correlations</b> <i>Müller, K.H. and Plessner, Th.</i>	171-175
<b>Growth patterns in two-phase systems</b> <i>Müller-Krumbhaar, H.</i>	176
<b>Formation of temporal patterns in the swimming behaviour of Halobacteria: Possible dynamical mechanisms</b> <i>Naber, H.</i>	177-179
<b>Dynamics of spiral waves in the Belousov-Zhabotinsky reaction</b> <i>Nagy-Ungvári, Zs.</i>	180-181

<b>Unstable wave propagation in the Belousov-Zhabotinsky reaction</b> <i>Nagy-Ungvarai, Zs., Ungvarai, J., Hess, B., Pertsov, A.M. and Müller, S.C.</i>	182-183
<b>Reaction diffusion patterns in the catalytic CO oxidation on Pt(110) - Front propagation and spiral waves -</b> <i>Nettesheim, S., v. Oertzen, A., Rotermund, H.H. and Ertl, G.</i>	184-186
<b>Measuring an accelerating propagation of a big wave by sequential image processing</b> <i>Nomura, A., Miike, H. and Hashimoto, H.</i>	187-189
<b>Experiments at the boundary of two worlds: Reaction, diffusion, electric conduction and multicomponent convection in gel and fluid reactors</b> <i>Mszticzius, Z., Farkas, H., Schubert, A., Swift, J., McCormic, W.D. and Swinney, H.L.</i>	190-193
<b>Turing instability in the CIMA reaction</b> <i>Ouyang, Q. and Swinney, H.L.</i>	194-196
<b>Self-organized criticality in a semiconducting charge density wave compound</b> <i>Parisi, J., Peinke, J., Dumas, J. and Kittel, A.</i>	197-199
<b>Asymptotics of spiral waves</b> <i>Pelcé, P. and Sun, J.</i>	200-204
<b>Turing-Hopf localized structures</b> <i>Perraud, J.-J., Dulos, E., De Kepper, P., De Wit, A., Dewel, G. and Borckmans, P.</i>	205-210
<b>Electrohydrodynamic convection in nematics: The homeotropic case</b> <i>Pesch, W., Herrich, A. and Kramer, L.</i>	211-213
<b>Interaction of chemical waves with convective flows induced by density gradients: A comparison between experiments and computer simulations</b> <i>Plesser, Th., Wilke, H. and Winters, K.H.</i>	214-216
<b>Scaling exponents, wrinkled graphs, and the high Reynolds number geometry of turbulence</b> <i>Procaccia, I.</i>	217-220
<b>Spatio-temporal patterns in gas discharge systems</b> <i>Purwins, H.-G. and Willebrand, H.</i>	221
<b>Self-trapping of travelling-wave pulses</b> <i>Riecke, H.</i>	222-223

<b>Spiral turbulence in Taylor-Couette-flow</b> <i>Roesner, K.G.</i>	224-225
<b>Chemical implementation of computers</b> <i>Ross, J.</i>	226-229
<b>Induction of temporal patterns in the locomotor behavior of Halobacterium - an indication of nonlinear dynamics</b> <i>Schimz, A. and Hildebrand, E.</i>	230-232
<b>Pattern formation in molecular evolution - A physicist's look at biology</b> <i>Schuster, P.</i>	233-234
<b>Observation of defect dynamics in small system</b> <i>Sepulchre, J.A. and Babloyantz, A.</i>	235-237
<b>Spatio-temporal patterns of on-going and evoked activity in cat visual cortex</b> <i>Shoham, D., Ullman, S. and Grinvald, A.</i>	238-240
<b>Three-dimensional autowaves control cell motion in Dictyostelium slugs</b> <i>Siegert, F., Steinbock, O., Weijer, C.J. and Müller, S.C.</i>	241-243
<b>Wave propagation and cell movement control morphogenesis of the cellular slime mould Dictyostelium discoideum</b> <i>Siegert, F. and Weijer, C.J.</i>	244-246
<b>Spatio-temporal patterns in ionic diffusion chemical system</b> <i>Snita, D., Dvorák, L. and Marek, M.</i>	247-249
<b>Pairs of pacemakers</b> <i>Spoerel, Ü., Peuker, A. and Busse, H.-G.</i>	250-253
<b>Rotating vortex initiation in excitable media: pulse chemistry control</b> <i>Stamer, C.F., Krinsky, V.I., Romashko, D.N., Aliev, R.R. and Stepanov, M.R.</i>	254-256
<b>Light-controlled spiral waves</b> <i>Steinbock, O. and Müller, S.C.</i>	257-259
<b>Second control loop in the Belousov-Zhabotinsky reaction investigated at different acidities</b> <i>Varga, M. and Försterling, H.-D.</i>	260-262
<b>Waves in a liquid, locally heated along a wire</b> <i>Vince, J.M., Dubois, M. and Bergé, P.</i>	263-265

<b>Spontaneous nucleation in a reactive lattice gas automaton</b> <i>Weimar, J.R.</i>	266-269
<b>Numerical experiments on filament motion</b> <i>Winfree, A.T.</i>	270-273
<b>Hydrodynamic fluctuations in nematics</b> <i>Winkler, B.L., Hörner, F., Richter, H. and Rehberg, I.</i>	274-276
<b>Artificial retina - photo image processing in the Belousov-Zhabotinsky reaction in gels</b> <i>Yamaguchi, T., Ohmori, T. and Matumura-Inoue, T.</i>	277-280
<b>Dynamic mode of entrainment in coupled chemical oscillators</b> <i>Yoshikawa, K.</i>	281-283
<b>Mechanism of stratification in a thin-layered excitable reaction-diffusion system with an oxygen gradient</b> <i>Zhabotinsky, A.M., Kiyatkin, A.B. and Epstein, I.R.</i>	284-286
<b>Effects of disorder in convective systems</b> <i>Zimmermann, W.</i>	287-288
<b>Kinematics of spiral wave with indistinct front</b> <i>Zykov, V.S.</i>	289-290



## Three-Dimensional Autowaves Control Cell Motion in Dictyostelium Slugs

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During the developmental cycle of Dictyostelium a slug forms as a migratory stage, in which the behavior of about  $10^5$  individual cells is coordinated to that of a single organism. The direction of chemotactic cell motion is controlled by propagating waves of excitation. Cell motion occurs in a direction opposite to the direction of signal propagation [1]. The anterior part of the slug (20% of all amoebae) consists of prestalk cells, which ultimately build the stalk of the fruiting body. The remainder is formed by prespore cells which differentiate to spores in the fruiting body.

According to recent analysis of cell motion, amoebae in the prespore zone move straight forward in the direction of slug migration, while cells in the prestalk zone move perpendicular to the direction of slug migration, that is they rotate around the slug axis [2]. We proposed that the underlying mode of signal propagation was caused by a change in excitability along the long axis of the slug. This hypothesis is based on the finding that during aggregation the cells that will become prestalk show high frequency oscillations in optical density when isolated, while cells that will become prespore show slow oscillations [2].

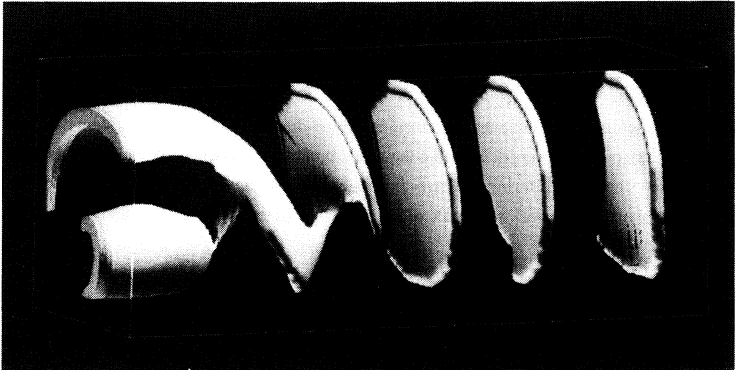
We were interested in the question whether a three-dimensional excitable system exhibits such behaviour we have performed computer simulations, based on previous simulations of wave propagation during the two-dimensional aggregation phase. For this purpose we calculated numerical solutions of an excitable reaction-diffusion system [3] in a cylinder:

$$\frac{\partial u}{\partial t} = D_u \Delta u + \frac{1}{\epsilon} u(1-u) \left( u - \frac{v+b}{a} \right), \quad \frac{\partial v}{\partial t} = u - v \quad ;$$

(diffusion coefficient  $D_u$ ; parameters  $a=0.4$ ,  $\epsilon=1/150$ ,  $b$  controlling the excitability; time per iteration  $dt=0.0103$ ). The propagator  $u$  and the controller species  $v$  are functions of

time and the three spatial coordinates. The variable  $u$  obeys nonlinear reaction kinetics and qualitatively models the extracellular cAMP concentration, while  $v$  represents the fraction of the cAMP-receptor in its active state. The difference in excitability between the prestalk and prespore region is modelled by a step function of parameter  $b$  along the symmetry axis of the cylinder ( $b_{\text{pst}}=0.01$ ,  $b_{\text{psp}}=0.023$ ).

The initial condition is a scroll wave along the long axis of the slug having uniform excitability ( $b=0.01$ ). It rotates stably in the homogeneous system. When introducing the described change in excitability (after  $t=880$  iterations), the scroll wave undergoes a complex transformation into a new pattern (Figure 1). While the wave rotation in the region of high excitability (prestalk region) remains stable during the entire calculation, the scroll wave in the region of low excitability (prespore region) increases its wave length and rotation period, and subsequently the whole structure becomes twisted in middle segments of the cylinder. The process of twisting and the higher frequency in the prestalk region causes a dramatic change of the pattern in the less excitable prespore zone: Planar wave fronts appear that are oriented perpendicular to the long axis of the cylinder. Detailed analyses show that the shape of these wave fronts is slightly convex, thus focussing cell motion and stabilizing the slug geometry. This spatial arrangement is stable over more than 30 periods of scroll wave rotation. The interface between the region of scroll wave rotation and planar wave propagation displays more complex dynamics and alternating phases of weak and strong twisting.



**Figure 1** Three-dimensional representation of the variable  $v$  after 7800 iterations. Points having  $v < 0.27$  are plotted transparently.

The corresponding filament of wave rotation is oriented along the long axis of the slug in the prespore zone, but it becomes helical at the interface and bends away from the axis before ending at the cylinder boundary. Movies of the filament evolution reveal irregular changes in location and shape, but most of the time it stays attached to the boundary.

Our calculations demonstrate that the observed pattern of chemotactic cell motion in *Dictyostelium* slugs can be explained readily by scroll waves of a chemotactic signal in the prestalk zone that decay into planar wave fronts in the prespore zone. This change in the pattern of wave propagation is caused by a step in excitability along the long axis of the slug. The simulations have furthermore shown that the filament of the scroll wave in the prestalk zone is a stable structure, a region of steady and low concentration of the excitation variable, conditions that most likely direct stalk formation by controlling expression of stalk specific genes.

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