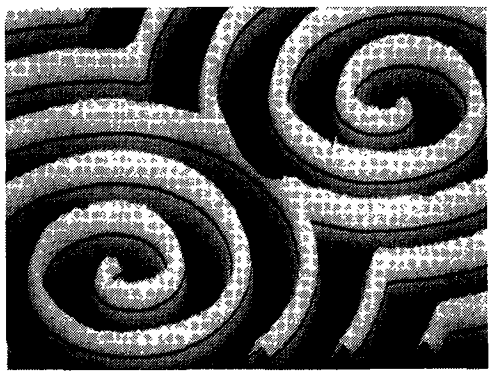
SPIRAL WAVE DYNAMICS

Stefan C. Müller
Max-Planck-Institut für molekulare Physiologie
Rheinlanddamm 201, 44139 Dortmund, FRG
E-mail: mullersc@mpi-dortmund.mpg.de

Excitable systems play an important role in the field of spatio-temporal selforganization. In biology, they serve as media for signal transmission, for instance in pulse propagation along nerve fibers or across the chambers of the heart. Selforganization, in general, occurs by symmetry-breaking transitions from homogeneous to structured states. In excitable media the coupling of nonlinear reactions with diffusion can result in the formation of traveling waves which, in two-dimensional extended media, have circular or spiral-shaped geometries. Two model systems are especially suited for in depth investigations of the wave dynamics: a chemical system, namely the excitable Belousov-Zhabotinsky reaction, and a biological system, which is the cellular slime mold Dictyostelium discoideum during early stages of cell aggregation.



Spiral symmetry in the Belousov-Zhabotinsky reaction

We have studied the formation and dynamic evolution of spiral waves in both systems in quantitative detail by applying computerized video imaging techniques. Emphasis was given to elucidate the structure and the properties of the spiral core. Spirals in well excitable preparations of the Belousov-Zhabotinsky reaction, as observed by light absorption, have approximately Archimedian shape. Their tip rotates on a circle along the boundary of the core (diameter $\approx$ 0.7 mm) inside which the amplitude of excitation decreases towards the rotation center, which is a singular point (diameter < 10 μm) with quasi-stationary chemistry. When decrasing the excitability of the solution, the steady and rigid tip rotation undergoes a transition to a compound motion, close to that of an epicycloid, and the spiral shape becomes non-Archimedian. Other transitions to more complex quasiperiodic and possibly chaotic motion are also observed [1,2].

The dynamic behaviour of propagating chemical waves was also investigated under the influence of an externally applied electric field. Depending on polarity and strength, this field leads to acceleration, slowing down, reversal or splitting of wave fronts due to its action on the drift of ions participating in the reaction [3]. Spiral waves are subjected to a drift in space accompanied by spiral deformation and changes in the wavelength, analogous to the Doppler shift. Due to a drift component perpendicular to the field direction spirals of opposite chirality can be forced to collide with each other. This results in mutual annihilation or complex interaction of their cores [4].

An efficient tool for external control of spiral wave parameters is found in a light-sensitive, ruthenium-catalyzed preparation of the Belousov-Zhabotinsky reaction. If the ruthenium complex is photochemically excited, it catalyzes the production of the inhibitor species of the reaction, bromide. Thus, externally applied illumination suppresses the excitabiltiy of the medium. A thin beam of laser light was used to produce an unexcitable disk that can serve as an artificial core of a spiral. The radius of the disk determines the spiral wavelength and spirals with continuously changing pitch are easily produced. They contain all the information necessary to derive the disperion relation of the medium. Such disks are also used to anchor meandering spirals to rigid rotation and to produce multi-armed spirals that rotate at equal distances around the disk boundary. After switching off the laser beam, these multiple tips move synchronously into the disk area where they collide with each other and form interesting interaction patterns [5,6].

If illumination is applied globally to the photosensitive reaction layer, one can control the dynamics of spirals in the entire system by periodic modulation of the light intensity. The modulation of excitabilty forces meandering spiral tips to phase-locked motion, a spectrum of open and closed hypocycloidal trajectories, and complex multifrequency patterns. These experimental results are reproduced by numerical simulations with a two-variable Oregonator model which was extended by a term describing the light-induced bromide production. They also show the existence of entrainment bands in the plane of modulation period and amplitude [7].

The slime mold *Dictyostelium discoideum* is well suited for the study of cellular communication and a widely investigated biological example of a self-organizing nonlinear system. About ten thousand individual amoebae of this myxomycete undergo aggregation to form a single organism (a pseudoplasmodium). Subsequently, they differentiate to form a fruiting body bearing spores. The depletion of their food source serves as signal to trigger the onset of the corresponding developmental cycle. The aggregation is coordinated and organized by traveling waves of cyclic adenosinemonophosphate (cAMP). During this phase the majority of the population rests in an excitable state, while other cell groups serve as periodic pacemakers by producing cAMP according to an oscillatory mechanism. By means of diffusion their neighborhood becomes excited and relays the biochemical signal. A propagating wave results which shows, in general, the geometry of concentric circles (target patterns) or rotating spirals. These structures are usually investigated by darkfield photography [8].

An important particularity of the Dictyostelium system is the existence of an additonal non-diffusive transport mechanism: chemotaxis forces the cells to a movement in the direction of the strongest increase of cAMP-concentration. We analyzed the chemotactic motion in quantitative detail by applying a mutual-correlation method for the determination of velocity fields. The direction of the velocities of amoebae and chemical wave propagation are antiparallel, their magnitudes having a ratio of approximately 1:10. The centers of spiral patterns have characteristic properties of attracting domains towards which finally all cells flow as a response to the signal sent out by the travelling wave of increased messenger concentration.

At a later stage in the development of *Dictyostelium discoideum* a slug forms as a migratory stage. Its anterior part consists of prestalk cells that ultimately build the stalk of a fruiting body, while the prespore cells in the remainder differentiate to spores. The individual cells in these slugs follow also well-defined patterns of motion. We found that at this stage the chemotactic cell response is controlled by a three-dimensional scroll-shaped wave of messenger concentration in the highly excitable prestalk zone of the slug that decays in the less-excitabe prespore region into planar wave fronts. In the interface of both regions a complex twisted scroll wave is formed that reduces the wave frequency in the prespore zone [9]. These results yield an explanation of collective self-organized cell motion in a multicellular organism.

1. S.C. Müller, Th. Plesser, B. Hess, Science 230, 661 (1985)
2. Zs. Nagy-Ungvarai, J. Ungvarai, S.C. Müller, Chaos, 3, 15 (1993)
3. H. Sevcikova, M. Marek, S.C. Müller, Science 257, 951 (1992)
4. J. Schütze, O. Steinbock, S.C. Müller, Nature 356, 45 (1992)
5. O. Steinbock, S.C. Müller, Phys. Rev. E 47, 1506 (1993)
6. O. Steinbock, S.C. Müller, Int. J. of Bifurcation and Chaos 3, 437 (1993)
7. O. Steinbock, V. Zykov, S.C. Müller, Nature 366, 322 (1993)
8. F. Siegert, C.J. Weijer, J. Cell Sci. 93, 325 (1989)
9. O. Steinbock, F. Siegert, S.C. Müller, C.J. Weijer, Proc. Nat. Acad. Sci. USA 90, 7332, (1993)