Spatio-Temporal Organization in Nonequilibrium Systems

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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:

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

(diffusion coefficient D_u; parameters a=0.4, ϵ=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_{pst}=0.01, b_{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.

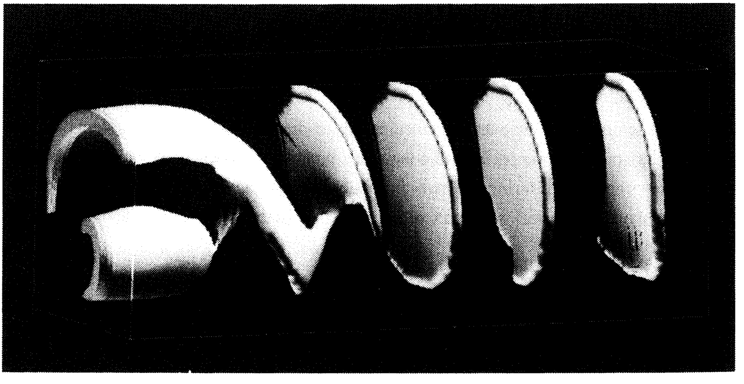

Figure 1 Three-dimensional representation of the variable v after 7800 iterations. Points having v<0.27 are plotted transparently.

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.

References

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