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Title:	*Wave-Pinning by Global Feedback in the Bistable Schlögl Model*
Journal Information:	*Extended Abstracts Spring 2018*
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Volume, pages:	*145-149*, DOI:[www.doi.org/10.1007/978-3-030-25261-8_22]

Wave-Pinning by Global Feedback in the Bistable Schlögl Model

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Abstract In this work, we introduce a wave-pinning mechanism in the bistable Schlögl model. Wave-pinning is induced by dynamically varying the unstable fixed point with a spatial global feedback. We present numerical simulations of the model in one and two dimensions for typical parameter values. The wave-pinning mechanism presented here can be used to reproduce the limited presence of phosphatidylinositol (3,4,5)-trisphosphate (PIP3) in the membrane of *Dictyostelium discoideum* cells, which plays a crucial role in the polarization and motility of the cell.

1 Introduction

Pattern formation is an ubiquitous phenomena in nature. Examples range from stripe pattern on a zebra's coat [3], to dissolution or growth of crystals in solutions [4]. Typically, these systems are modeled by means of nonlinear reaction–diffusion equations. A minimal model for pattern formation was formulated by Friedrich Schlögl to describe nonequilibrium phase transitions [5]. Although the model is commonly known as the Schlögl model, the same model was previously formulated by Zel'dovich and Frank–Kamenetskii to describe flame propagation [6]. In the past 50 years, the Schlögl model has been adapted to describe many other systems in physics and biology, including gas discharge between two glass plates or cardiac dynamics.

The bistable Schlögl model describing the evolution of a concentration field $u(x, t)$ is given by the reaction–diffusion equation

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A. Korobeinikov et al. (eds.), *Extended Abstracts Spring 2018*,
Trends in Mathematics 11, https://doi.org/10.1007/978-3-030-25261-8_22

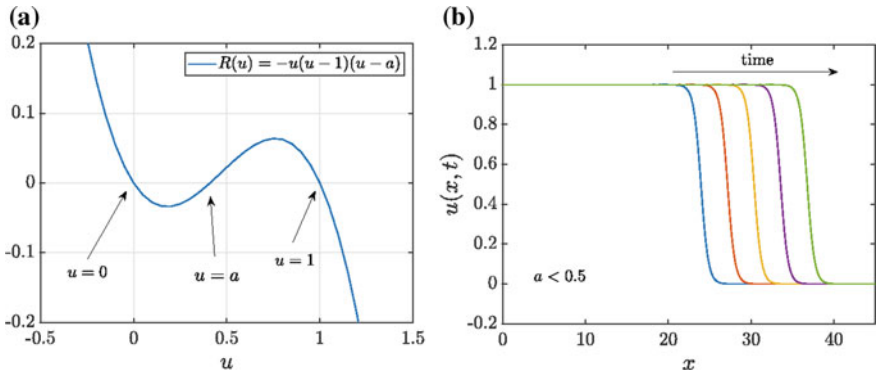

Fig. 1 **a** Reaction term for the Schlögl model as a function of u. The fixed points are indicated with arrows (in this case $a = 0.4$). **b** Concentration profiles for different times

$$\frac{\partial u}{\partial t} = D_u \nabla^2 u - k\, u(u-1)(u-a), \tag{1}$$

where D and k are the diffusion and reaction coefficients, respectively. In our case, $u(x,t)$ stands for the concentration of PIP3 in the cell membrane. The reaction term $R(u) = -k\, u(u-1)(u-a)$ can be interpreted as the derivative of a potential field, i.e., $R(u) = -\partial_u V(u)$. In the one-dimensional case, the model has the analytical (traveling wave) solution

$$u(x,t) = \frac{1}{2}\left[1 - \tanh\left(\frac{1}{2}\sqrt{\frac{k}{2D_u}}(x - ct)\right)\right], \quad c = \sqrt{\frac{2D_u}{k}}(1-2a). \tag{2}$$

From (2), one can see that the wave velocity c is positive, zero, or negative depending on the value of the unstable fixed point a. In Fig. 1, we show the reaction term of the Schlögl model and indicate the fixed points (panel (a)), and plot the traveling wave solution at different times for typical parameter values (panel (b)).

In the next section, we introduce a global feedback relation in model (1) to control the size of the wavefronts, in Sect. 3 we present and discuss numerical simulations of the model with global feedback (in 1D and 2D) and, finally, we draw our conclusions in Sect. 4.

2 Wave-Pinning by Global Feedback

A control of the size of the wave is important to model pattern formation in *Dictyostelium discoideum* cells, where the area covered by the pattern is limited and it never covers the entire cell membrane [1]. Thus, we introduce a global feedback control mechanism in the Schlögl model that stops the wavefront when a critical size is reached. The governing equation will now read

$$\frac{\partial u}{\partial t} = D_u \nabla^2 u - ku(u-1)(u-a(u)), \tag{3}$$

with the feedback-control mechanism given by

$$a = a_0 + \Delta a \Big(\int_A u \, dA - p \, A \Big), \tag{4}$$

where A is the area of the domain, Δa the strength of the global feedback input, and p the critical fraction of area covered by the wavefront. Note the way in which the global feedback is introduced in the model differs from that used in previous studies [2, 4], where the global feedback induces a vertical shift in the reaction term R and, therefore, the value of the stable fixed points (in our case $u = 0$, $u = 1$) also change.

3 Results and Discussion

In this section, we present numerical simulations of the model (3)–(4) in one and two dimensions with no flux boundary conditions using an explicit finite difference scheme. The parameter values used are $D_u = 0.1$, $k = 1$, $a_0 = 0.5$, $L = 45$. Although these values have physical meaning and corresponding units we omit their description for brevity.

3.1 Simulations in 1*D*

In Fig. 2, we present the results of the simulations in 1D (setting $\nabla = \partial_x$, $A = L$ and $dA = dx$ in (3)–(4)), using the initial condition: $u(x, 0) = 1$ for $x \in [0, L/2]$ and $u(x, 0) = 0$ for $x \in (L/2, L]$. In panel (a), we show the evolution of the PIP3 concentration wave for the case $p = 0.65$ and $\Delta a = 0.02$. We observe how the wave travels forward until $\int u \, dx = 0.65 \, L$ and then stops. The global feedback is pushing the fixed point toward $a = 0.5$, which is precisely the value of the unstable fixed point in the Schlögl model leading to a velocity of the traveling wave equal to 0 (see Eq. (2)). To better visualize this phenomena, known as wave-pinning, we show in panel (b) the position and velocity of the point in the domain where $u = 0.5$ that we define as $x = s(t)$, i.e., $u(s(t), t) = 0.5$. We observe that the speed of the wave, represented by $\dot{s}(t)$, increases during a short transient period and then decreases toward zero.

In panels (c) and (d), we show the reaction term and the potential, respectively, at three different times during wave propagation. Initially, the fixed point $u = 1$ is more stable than $u = 0$. As time increases, $(\int u \, dx - p \, L) \to 0$ and $a \to 0.5$ making the potential symmetric with respect $u = 0.5$ and the fixed points $u = 0$ and $u = 1$ become equally stable.

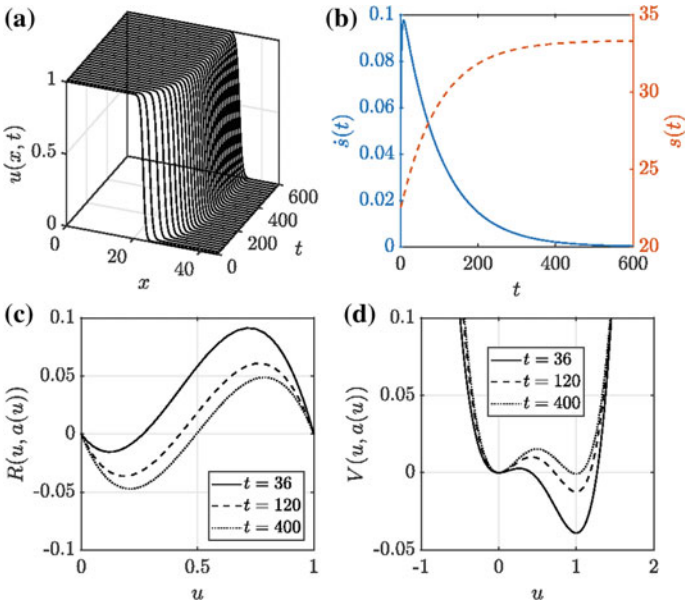

Fig. 2 **a** Space and time evolution of the concentration of PIP3 predicted by the model with global feedback. **b** Speed (left y-axes) and position (right y-axes) of the wavefront as a function of time. **c** Reaction term and **d** Potential at different times

3.2 Simulations in 2D

In Fig. 3, we compare 2D numerical simulations of the Schlögl model with and without global feedback at several times. In this case, the imposed initial condition is $u(x, y, 0) = 1$ for $r \leq L/2$ and $u(x, y, 0) = 0$ for $r > L/2$, where $r = \sqrt{x^2 + y^2}$. The simulations for the Schlögl model without global feedback (panels (a)–(d)) show how a PIP3 concentration wave travels unperturbed through the medium and at $t = 720$ has already covered most of the domain (the entirety of the domain is covered around $t \approx 1000$). In the case of the model with global feedback (panels (e)–(h)), the wave evolves initially fast (in agreement with the observations for the 1D case), then slows down, and eventually stops when the area covered equals the critical area $0.5\,L^2$ (note for these simulations we have used $p = 0.5$ and and $\Delta a = 5 \cdot 10^{-4}$). We propose this mechanism as a mass conservation constraint to model the limited availability of PIP3 on the cell membrane.

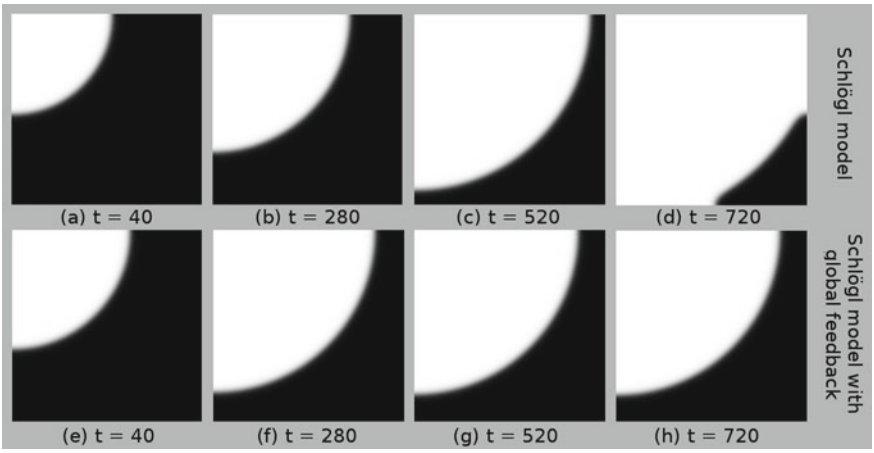

Fig. 3 Propagation of a wave in the Schlögl model (**a**–**d**) and in the Schlögl model with global feedback with $p = 0.5$ (**e**–**h**)

4 Conclusions

In this work, we have introduced a wave-pinning mechanism in the bistable Schlögl model. The mechanism consists of the control of the total size of the wavefront by means of a global feedback that varies dynamically the value of the unstable fixed point of the model. The wave-pinning mechanism presented provides a route to model the limited availability of PIP3 to form patterns that result in the polarization and motility of *Dictyostelium discoideum* cells.

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