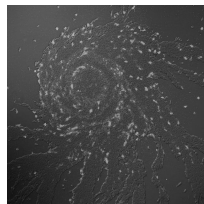
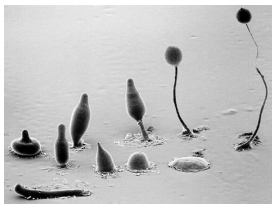


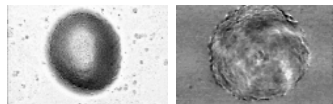
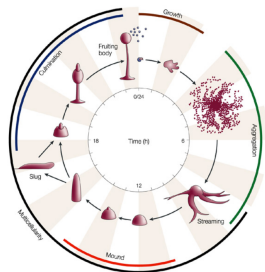
# A simple 2D-model of cell sorting induced by propagation of chemical signals along spiral waves

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From: <http://dictybase.org/> ©M.J. Grimson & R.L. Blanton (left),  
R. M. Bickford & D. A. Knecht (right)

# Sorting in the mound stage of *Dictyostelium discoideum*



**From:** R.L. Chisholm, R.A. Firtel  
*Insights into morphogenesis from a simple developmental system*, Nat. Rev. Mol. Cell Biol. 5, 531-541 (2004)

**From:** F. Siegert, C.J. Weijer  
*Spiral and concentric waves organize multicellular Dictyostelium mounds* Curr. Biol. 5, 937-943 (1995)

## A simple model for the sorting at the mound stage

- Two-dimensional model
- Propagation of cAMP along a train of spiral waves with constant angular speed  $-\omega_0$
- Two type of cells, both with positive chemotactic sensitivity but different reaction strengths
- Continuous cell distribution in the whole plane with densities  $m$  and  $n$ ,  $m + n = N_0$
- $\Omega_0$ : constant angular speed of cell rotation
- No influence of cell motion / differentiation on propagation of the chemical signal
- Very thin action range of the chemical

Chemical waves with moderately increasing wavelength  $\implies$   
Trapped cell states with most of the more sensitive cells in a  
bounded region

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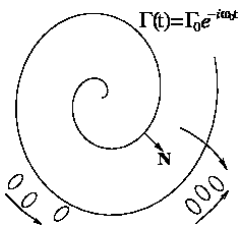
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## Model derivation from the assumptions



$$\frac{\partial m}{\partial t} + \text{div}(j_m) = 0, \quad \frac{\partial n}{\partial t} + \text{div}(j_n) = 0 \quad \text{with} \quad \text{div}(j_m + j_n) = 0$$

$$\text{Fluxes:} \quad j_m = -D\nabla m + m\mathbf{b} + J_{chem} \quad j_n = -D\nabla n + n\mathbf{b} - J_{chem}$$

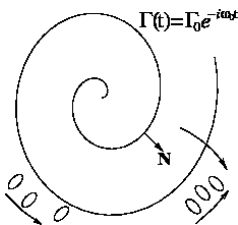
$$\mathbf{b}(x_1, x_2) = (-\Omega_0 x_2, \Omega_0 x_1)$$

Choice of a coordinate system rotating with the spiral wave

$\Rightarrow$  wave at rest & cell rotation at speed  $\Omega := \Omega_0 + \omega_0$

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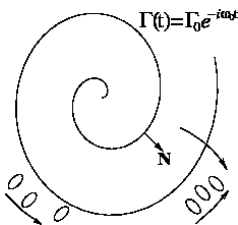
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$$J_{chem} = \chi(m^+, n^+) \delta_\Gamma \mathbf{N} = \chi(m^+, N_0 - m^+) \delta_\Gamma \mathbf{N} \quad \text{with}$$

- $\mathbf{N} = \mathbf{N}(x)$ : outer normal unit vector to the spiral at point  $x \in \Gamma$ ;
- $\delta_\Gamma$ : measure concentrated on the spiral  $\Gamma$ ;
- $\chi(0, n) = \chi(m, 0) = 0$ ;
- $(\cdot)^+$ ,  $(\cdot)^-$ : limit values from outer, inner side respectively.

**Ansatz:**  $\chi(m, n) = Amn$ ,  $A : \Gamma \rightarrow \mathbb{R}$ ,

$$\implies \frac{\partial m}{\partial t} - D\Delta m + \operatorname{div}(m\mathbf{b}) + \operatorname{div}(Am^+(N - m^+)\delta_\Gamma \mathbf{N}) = 0$$

with (simplification)  $A = \text{Const.} < 0$ ,  $|A| \ll 1$ .

In our first investigation  $J_{chem} = Am^+ \delta_\Gamma \mathbf{N}$

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# The evolutive problem

$$\Gamma : \quad \rho = \rho(\theta)$$

$$\begin{cases} \frac{\partial m}{\partial t} = D\Delta m - \operatorname{div}(\mathbf{b}(x)m) & t > 0, x = (x_1, x_2) \in \mathbb{R}^2 \setminus \Gamma \\ m^+ - m^- = Am^+ & t > 0, x \in \Gamma \\ \frac{\partial m^+}{\partial N} - \frac{\partial m^-}{\partial N} = Bm^+ & t > 0, x \in \Gamma \end{cases}$$

$$\mathbf{b}(x) = (-\Omega x_2, \Omega x_1), \quad \Omega : \text{angular speed}$$

$$\frac{d}{dt} \left( \int_{\mathbb{R}^2 \setminus \Gamma} m(x, t) dx \right) = 0 \Rightarrow B = \frac{A}{D} \mathbf{b}(x) \cdot \mathbf{N}$$

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## Stationary problem and its approximation

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$$m > 0, \quad \int_{\mathbb{R}^2} m(x) dx < \infty$$

$$\Omega \frac{\partial p}{\partial \theta} = \frac{\partial^2 p}{\partial \rho^2} + \frac{1}{\rho} \frac{\partial p}{\partial \rho} + \frac{1}{\rho^2} \frac{\partial^2 p}{\partial \theta^2} \quad \rho \rightarrow \infty \quad \Omega \frac{\partial p}{\partial \theta} = \frac{\partial^2 p}{\partial \rho^2} \quad (p(\rho, \theta) := m(\rho e^{i\theta}))$$

$$\begin{cases} \Omega p_\theta = p_{\rho\rho} & (\rho, \theta) \in S \\ p(\rho(\theta), \theta + 2\pi) - p(\rho(\theta), \theta) = Ap(\rho(\theta), \theta + 2\pi) & \theta \geq 0 \\ \text{Second boundary condition in polar coordinates} \end{cases}$$

$$S = \{(\theta, \rho) \mid \theta > 0, \max(\rho(\theta - 2\pi), 0) < \rho < \rho(\theta)\} \text{ (polar domain)}$$

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## Distributional formulation

$A < 0, |A| \ll 1$  &  $\rho(\theta) = \theta \Rightarrow \exists$  positive solution  $p(\rho, \theta) \stackrel{\theta \rightarrow \infty}{\sim} e^{\frac{A\theta}{2\pi}}$

Since now on  $\rho(\theta) = \theta$

Distributional formulation of s.s. problem

$$-\Delta m + \operatorname{div}(\mathbf{b}(x)m) + \operatorname{div}(Am^+(x)\delta_{\Gamma}(x)\mathbf{N}(x)) = 0$$

Superposition principle  $\Rightarrow$

$$m(x) = C + A \int_{\Gamma} m^+(y) \nabla_y G(x, y) \cdot \mathbf{N}(y) d\sigma(y), \quad C \in \mathbb{R}^+, x \notin \Gamma$$

with

$$-\Delta_x G + \operatorname{div}_x(\mathbf{b}(x)G) = \delta_y(x) \quad x \in \mathbb{R}^2 \setminus \{y\}$$

## Distributional formulation

$A < 0, |A| \ll 1$  &  $\rho(\theta) = \theta \Rightarrow \exists$  positive solution  $p(\rho, \theta) \stackrel{\theta \rightarrow \infty}{\sim} e^{\frac{A\theta}{2\pi}}$

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Distributional formulation of s.s. problem

$$-\Delta m + \operatorname{div}(\mathbf{b}(x)m) + \operatorname{div}(Am^+(x)\delta_\Gamma(x)\mathbf{N}(x)) = 0$$

Superposition principle  $\Rightarrow$

$$m(x) = C + A \int_\Gamma m^+(y) \nabla_y G(x, y) \cdot \mathbf{N}(y) d\sigma(y), \quad C \in \mathbb{R}^+, x \notin \Gamma$$

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## Reduction to an integral equation

$$G(x, y) = H(x, y) - \frac{1}{2\pi} \log \|x - y\| + \frac{1}{2\pi} \log \|y\|$$

with  $(q \in [1, 2))$

$$x \mapsto H(x, y) \in W_{loc}^{2,q}(\mathbb{R}^2), \quad \text{and } y \mapsto \|H(\cdot, y)\|_{W_{loc}^{2,q}} \in C^0(\mathbb{R}^2)$$

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## Sometimes polar coordinates are better

$$G(\rho, \theta; R, \xi) := G(\rho e^{i\theta}, R e^{i\xi}) = -\frac{\chi_{[0, \infty)}(\rho - R)}{2\pi} \log\left(\frac{\rho}{R}\right) + W(\rho, \theta; R, \xi)$$

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## Fundamental properties of the kernel $f_{\Gamma}$

$$X_{\mu} := \left\{ \lambda \in C^0([0, \infty)) \mid \|\lambda\|_{\mu} := \sup_{\theta \geq 0} |\lambda(\theta) e^{\mu\theta}| < \infty \right\} \quad (\mu > 0)$$

N. C. for existence of a solution in  $X_{\mu}$ :  $C + \frac{A}{2\pi} \int_0^{\infty} m^+(\xi) d\xi = 0$

**Lemma:**

- $f_{\Gamma}$  is regular outside  $\{\theta = \xi\}$ , and  $f_{\Gamma}(0, \xi) \equiv 0$ ,
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## Statement of the main theorem

Let  $C = 1$

**Theorem:** There exists  $A_\Omega > 0$  s.t. for every  $A \in (-A_\Omega, 0)$  the integral equation has a positive solution  $m^+ \in X_{\mu(A)}$  with  $\mu(A) \in \left(0, \frac{|A|}{2\pi}\right)$

*Sketch of the Proof:*

If  $m^+$  in  $X_\mu$  with  $\mu < \frac{|A|}{\pi(2-A)} \leq M_\Omega \Rightarrow \frac{|A|}{2\pi} \int_0^\infty m^+(\xi) d\xi = 1$ , and polar integral equation equivalent to

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Construction of sequence  $\{\lambda_n\}_{n \in \mathbb{N}_0}$  of approximate solutions:

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