Wave mechanisms of pattern formation in microbial populations

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The occurrence of spatially ordered structures plays an important role in biology (examples: morphogenesis,.ecosystems, dynamics of populations, etc). Turing (1952) proposed a reaction-diffusion process that is the basis for most theoretical studies of stationary biological pattern formation. We have found evidence of an alternative to the Turing model that is based on waves as displayed in excitable media.

In experimental studies of E. coli populations (bacterial strains *E.coli* J62L and *E.coli* wild type C, on the tryptone -agar medium , and with peptone replaced by casamine acids) we observed that interacting taxis waves modulate stationary pattern formation. Taxis waves consuming two different substrates (serine and aspartic acid) were involved. Taxis waves consuming serine stop when they collide. However taxis waved supported by aspartic acid can be initiated at collision lines. Colliding and annihilating in turn, the waves give rise to stationary pattern formation and wave theory provides an alternative to the classical Turing hypothesis..

We have also simulated the described wave mechanism of pattern formation by *E.coli* on a mathematical model.

$$\frac{\partial b_i}{\partial t} = \nabla(\mu(s_i)\nabla b_i - b_i\chi(s_i)\nabla s_i) + F_1(b_i, s_i) + R_i(b, s),$$

$$\frac{\partial s_i}{\partial t} = D\nabla^2 s_i + F_2(b_i, s_i), \quad i=1,2$$

where b - bacterial concentration; S - concentration of the substrate that provokes chemotaxis; μ(S) - bacterial diffusion coefficient; D - coefficient of diffusion S; χ(S) - coefficient of chemotaxic motility; F_1,F_2 - functions describing production and degradation of bacteria and substrate, respectively, R_i(b,s) describes the transformation of bacteria consuming one substrate to bacteria consuming another one.

The propagation patterns calculated with this model were quite similar to that observed in the experiments.

Table 1. Amino acid composition of the medium after passage of taxis waves in bacteria *E.coli* J62L.

Amino Acids	Concentration, mM			
	Control	1	2	2′
alanine	1.4	1.4	1.5	1.5
arginine	2.0	2.1	2.1	2.1
* aspartate	0.3	0.2	0.04	0.03
glutamate	0.7	0.7	0.6	0.6
histidine	0.5	0.5	0.5	0.5
isoleucine	0.4	0.5	0.4	0.4
leucine	1.5	1.5	1.4	1.3
lysine	0.8	0.8	0.8	0.8
methionine	0.2	0.2	0.2	0.2
phenylalanine	0.9	0.9	0.9	0.9
proline	0.00	0.00	0.00	0.00
* serine	0.5	0.08	0.03	0.04
threonine	0.3	0.3	0.2	0.2
tyrosine	0.9	1.0	1.0	1.0
valine	1.0	1.0	1.0	1.0

The medium compositions in control and after passing waves 1, 2, 2′ are shown in columns "Control", "1", "2" and "2′" respectively.

* - aminoacids consumed by bacterial bands.

Measurements were performed on Amino Acid Analyser T339 (Microtechna Praha); accuracy of measurements 20%.

Figure legends

Fig.1. A mechanism for a non-Turing structure formation resulting from collision and annihilation of taxis waves in of two colonies E.coli J62L.

a) Propagation of the first and the second taxis waves (The snapshot was made 4h 20 min after inoculation, the reference point t=0.)

b) Formation of the collision line of the second taxis waves and origination of waves 2' at the collision line (t=85min)

c) Collision of waves 2 and 2' (t=140 min).

The experiments were carried out in Petri dishes of 9 cm in diameter filled with a layer of agar nutrient medium of 1mm thick at 37 C. The medium contained 1% peptone, 0.5% NaCl, 0.35% agar "Difco". The inoculation was performed with a capillary filled with bacterial suspension in the nutrient medium, the inculation sites are seen as dark spots.

Fig.2. A cross-shaped structure resulting from the wave interaction of four bacterial colonies.

a) Taxis waves 1 and 2, propagating from sites of inoculation.

b) Collision of the first (1) taxis waves.

c,d) Lines of collision of the first taxis waves

e) Taxis waves 2' produced at the collision lines

f-h) Formation of structure.

i) A cross-shaped structure.

The experimental conditions are the same as in Fig.1.

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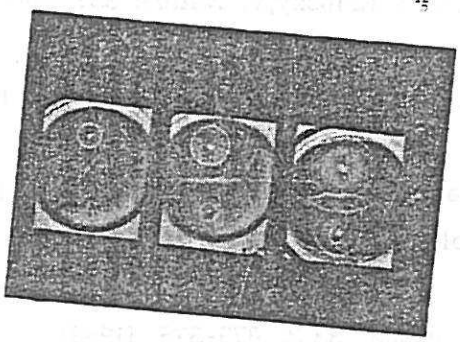


Fig 1

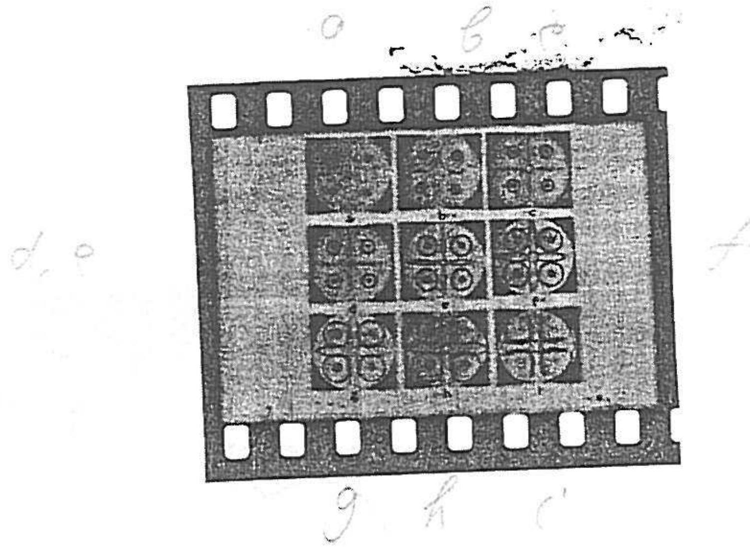
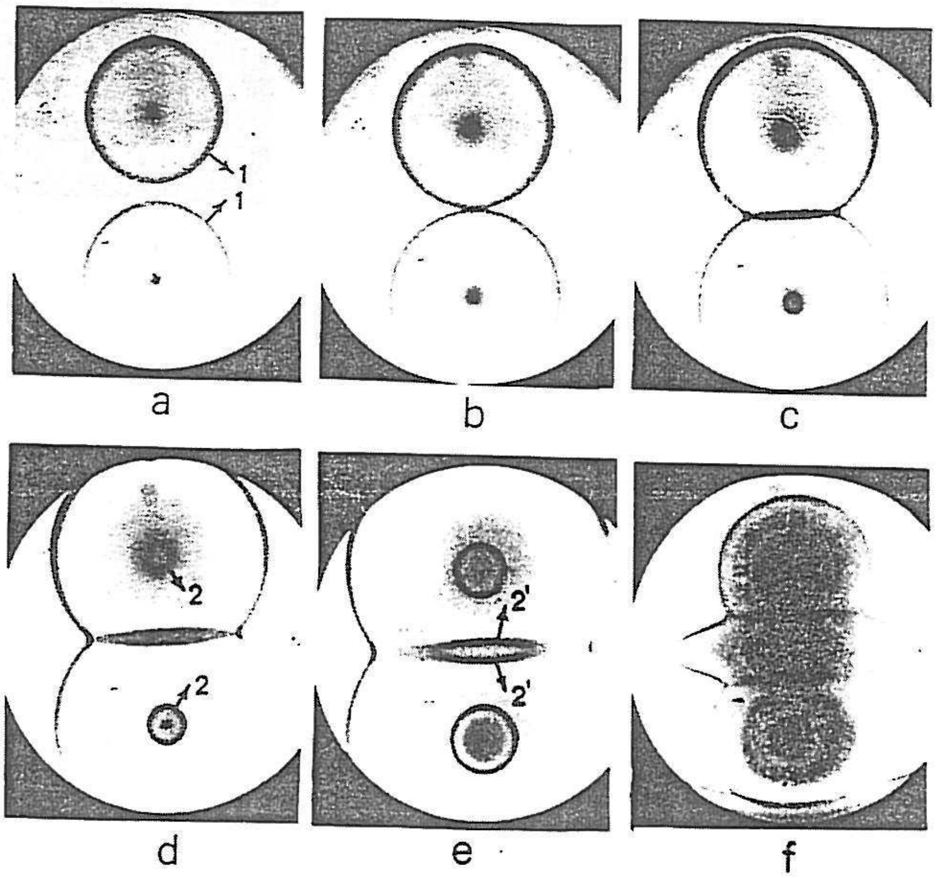


Fig 2



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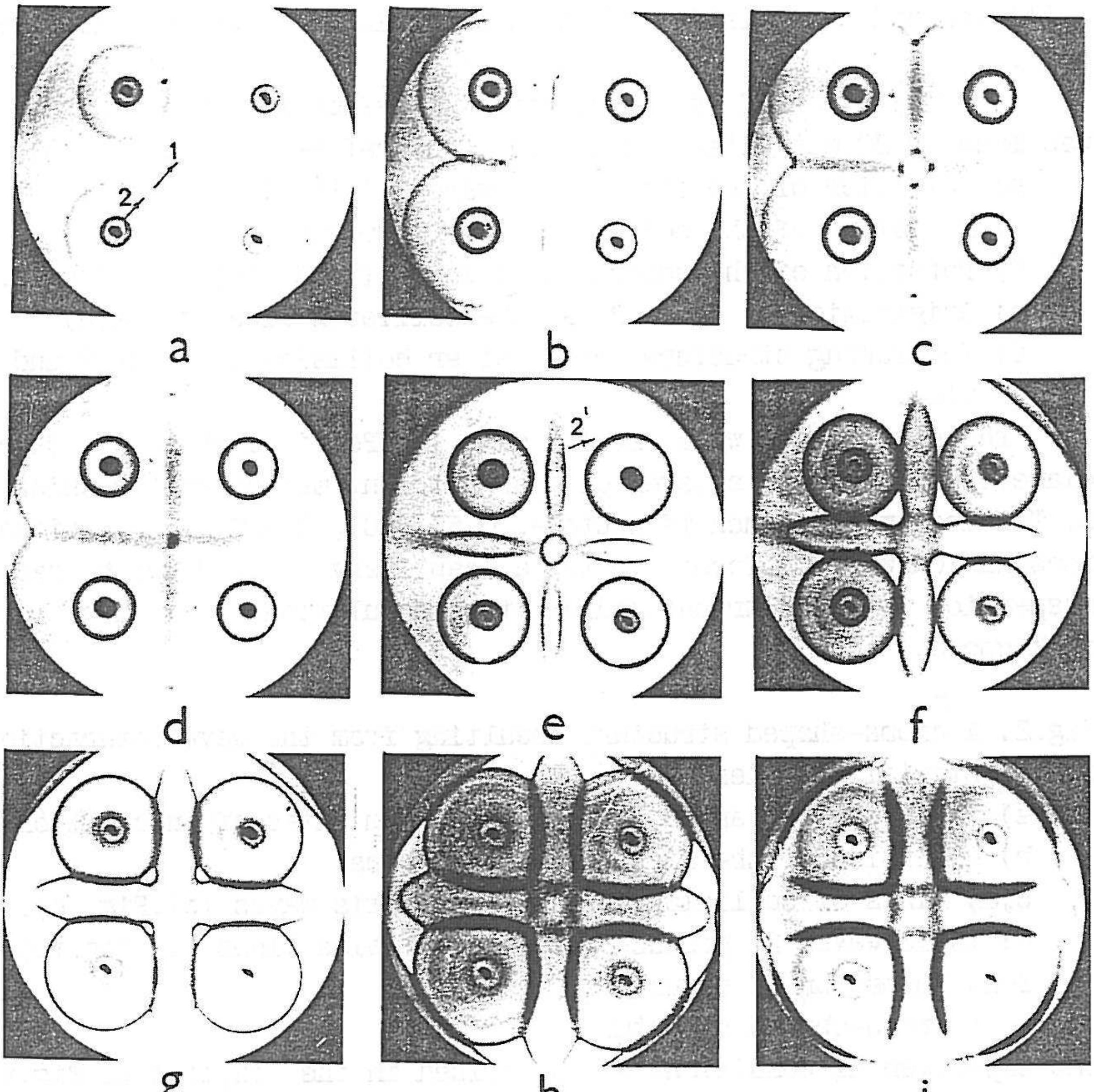

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Figure captions

Fig.1. A mechanism for a non-Turing structure formation resulting from collision and annihilation of taxis waves in of two colonies E.coli J62L.

a) Propagation of the first taxis waves(marked by 1). (The snapshot was made 4h 20 min after inoculation, the reference point t=0.)

b) Collision of the first taxis waves (t=15 min).

c) Formation of the collision line (t=30 min).

d) Formation of the second taxis waves (t=55 min) marked by 2.

e) Origination of waves 2' at the collision line (t=85min)

f) Non-Turing structure formed after collision of waves 2 and 2' (t=140 min).

The experiments were carried out in Petri dishes of 9 cm in diameter filled with a layer of agar nutrient medium of 1mm thick at 37 C. The medium contained 1% peptone, 0.5% NaCl, 0.35% agar "Difco".The inoculation was performed with a capillary filled with bacterial suspension in the nutrient medium, the inoculation sites are seen as dark spots.

Fig.2. A cross-shaped structure resulting from the wave interaction of four bacterial colonies.

a) Taxis waves 1 and 2, propagating from sites of inoculation.

b) Collision of the first (1) taxis waves.

c,d) Lines of collision of the first taxis waves (cf.Fig.1c).

e) Taxis waves 2' produced at the collision lines (cf.Fig.1e).

f-h) Formation of structure.

i) A cross-shaped structure.

The experimental conditions are described in the caption to Fig.1.