

The influence of non-standard boundary conditions on the generation of spatial patterns

Milan Kučera, Filip Jaroš, Tomáš Vejchodský (Prague)

March 9, 2012

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$$\frac{\partial v}{\partial t} = d_2 \Delta v + g(u, v) \text{ in } (0, \infty) \times \Omega,$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \text{ on } \Gamma_N, \quad u = v = 0 \text{ on } \Gamma_D,$$

where $\Gamma_N \cap \Gamma_D = \emptyset$, $\Gamma_N \cup \Gamma_D = \partial\Omega$.

Assumptions:

There is a spatially homogeneous stationary solution $u \equiv \bar{u}$, $v \equiv \bar{v}$, i.e. $\bar{u}, \bar{v} \in \mathbb{R}^+$, $f(\bar{u}, \bar{v}) = g(\bar{u}, \bar{v}) = 0$.

Without loss of generality, we can shift this steady state to zero, and the new functions (denoted again by u and v) describe now the deviations from the original basic steady state \bar{u} , \bar{v} .

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After the shift of the steady state to zero, the new functions (denoted again by u and v) describe the deviations from the original basic steady state \bar{u} and \bar{v} , and the system reads as

$$\frac{\partial u}{\partial t} = d_1 \Delta u + b_{11}u + b_{12}v + n_1(u, v), \text{ in } (0, \infty) \times \Omega,$$

$$\frac{\partial v}{\partial t} = d_2 \Delta v + b_{21}u + b_{22}v + n_2(u, v), \text{ in } (0, \infty) \times \Omega,$$

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Signorini boundary condition (source) for v in $\Gamma_U \subset \partial\Omega$

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$$\frac{\partial u}{\partial n} = 0 \text{ on } \partial\Omega \setminus \Gamma_D, \quad \frac{\partial v}{\partial n} = 0 \text{ on } \partial\Omega \setminus \Gamma_U \cup \Gamma_D,$$

$$v \geq 0, \quad \frac{\partial v}{\partial n} \geq 0, \quad v \frac{\partial v}{\partial n} = 0 \text{ on } \Gamma_U.$$

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Unilateral condition (source) for v in $\Omega_U \subset \Omega$

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$$v \geq 0, \quad \frac{\partial v}{\partial t} - d_2 \Delta u - b_{21}u - b_{22}v - n_2(u, v) \geq 0 \text{ in } (0, \infty) \times \Omega_U,$$

$$v \left(\frac{\partial v}{\partial t} - d_2 \Delta u - b_{21}u - b_{22}v - n_2(u, v) \right) = 0 \text{ in } (0, \infty) \times \Omega_U,$$

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always the assumption $\Gamma_D \neq \emptyset$

Essential progress - Dirichlet conditions removed:

J. Eisner, M. Väh, Location of bifurcation points for a reaction-diffusion system with Neumann-Signorini conditions. Adv. Nonlin. Stud. 11 (2011), 809–836

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If $\Gamma_D = \emptyset$ and $\Gamma_U \neq \emptyset$ or $\Omega_U \neq \emptyset$ then there are bifurcations for arbitrarily small $\frac{d_2}{d_1}$.

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QUESTIONS:

IS THERE A REASONABLE BIOLOGICAL MOTIVATION FOR UNILATERAL CONDITIONS?

DO UNILATERAL SOURCES OR SINKS PLAY A ROLE IN SPATIAL PATTERNING IN BIOLOGY?

IS IT POSSIBLE TO EXPLAIN SOME CONCRETE PHENOMENA IN THIS WAY?

WHAT ABOUT A DARK STRIPE AROUND THE SPINE OR A WHITE BELLY WHICH IS OBSERVED AMONG SOME FELIDS?

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OBRAZEK JAGUARA

Biological hypothesis concerning unilateral sources

(1) The morphogens diffuse and undergo a chemical reaction in the extracellular space or they interact via special cells with receptors which produce morphogens (ligands) according to their concentrations (autocrine signalling). The concentration of one of the morphogens determines a prepattern.

(2) In some tissues (e.g. a neural crest) there are cells which produce morphogens only if their concentration is below certain thresholds (something like homeostasis known in some processes, e.g. in metabolism). If the concentration u or v is above a given threshold u_0 or v_0 then the related source is inactive, if the concentration u or v is about to decrease below u_0 or v_0 then the corresponding morphogen is produced and supplemented into the extracellular space.

(3) The threshold u_0 and v_0 mentioned is either equal or slightly less than the value of the basic stationary spatially homogeneous stationary state \bar{u} and \bar{v} , respectively.

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A motivation of Hypotheses (2) and (3)

The stationary state \bar{u} , \bar{v} is asymptotically stable for initial time period of the development (e.g. as far as the domain is sufficiently small, etc.)

During this period, the concentrations of morphogens converge to \bar{u} , \bar{v} and are close to these values for considerable time.

Similarly to the principle of homeostasis, the organism accepts this steady state as natural and has a tendency to keep the concentration of morphogens close to \bar{u} , \bar{v} even if the stability of this spatially homogeneous equilibrium is lost (i.e. if the parameters reach the domain of Turing instability, e.g. the domain becomes sufficiently large) and the concentrations tend to a new spatially non-homogeneous state (spatial pattern).

Similar regulations based on negative feedback are known, e.g. Hh ligand (hedgehog) is absorbed by the multipass membrane protein Patched if the concentration of Hh ligand exceeds a given threshold.

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Biological hypothesis concerning unilateral sinks

There are regions (e.g. ventral side) where the efficiency of morphogens is reduced by the presence of proteinic agents. This can be modelled as a sink which is active only if the concentration exceeds a given threshold, which is close to the basic equilibrium as mentioned above.

The process might be similar to colour pattern formation in the case of mice (e.g. the mouse of genus *Peromyscus*). Agouti protein is expressed in ventral regions of the mice and delays the maturation of melanocytes, which are responsible for pigmentation. As a result, the ventral side of *Peromyscus* mice display white colouration.

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A concrete model - R. A. Barrio, C. Varea, J. L. Aragón, P. K. Maini 1999

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$$\frac{\partial u}{\partial t} = D\delta\Delta u + \alpha u + v - r_2 uv - \alpha r_3 uv^2$$

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Stationary spatially non-homogeneous solutions (spatial patterns) bifurcate from the trivial solutions only for D small (at least $D < 1$) and δ small in some sense (i.e. sufficiently large domain).

In the paper Liu, Liaw, Maini 2006, successful experiments were done for $D = 0.45$, $\delta = 6$ and in the second phase even $D = 0.15$, $\delta = 1.8$.

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Unilateral source in the interior of the domain

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A unilateral source of the inhibitor:

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A unilateral source of both - the activator and the inhibitor:

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A unilateral source of the inhibitor:

$$\frac{\partial u}{\partial t} = D\delta\Delta u + \alpha u + v - r_2 uv - \alpha r_3 uv^2$$

$$\frac{\partial v}{\partial t} = \delta\Delta v - \alpha u + \beta v + r_2 uv - \alpha r_3 uv^2 + a(y)(v + \varepsilon^-)$$

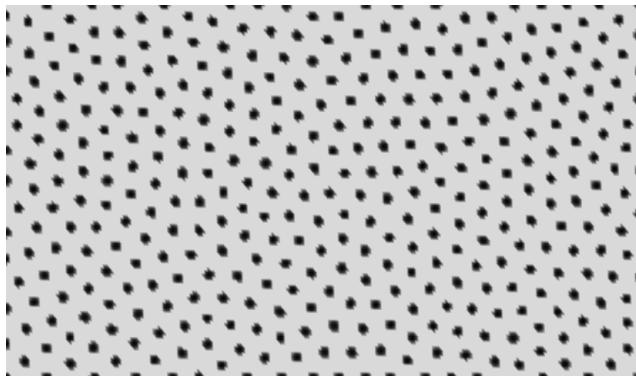
A unilateral source of both - the activator and the inhibitor:

$$\frac{\partial u}{\partial t} = D\delta\Delta u + \alpha u + v - r_2 uv - \alpha r_3 uv^2 + a(y)(u + \varepsilon_1)^-$$

$$\frac{\partial v}{\partial t} = \delta\Delta v - \alpha u + \beta v + r_2 uv - \alpha r_3 uv^2 + a(y)(v + \varepsilon_2)^-$$

$$\frac{\partial v}{\partial t} = \delta\Delta v - \alpha u + \beta v + r_2 uv - \alpha r_3 uv^2 + a(y)v^-$$

The classical case - no unilateral regulation



$$D = 0.45$$

$$\delta = 6$$

$$\alpha = 0.899$$

$$\beta = 0.91$$

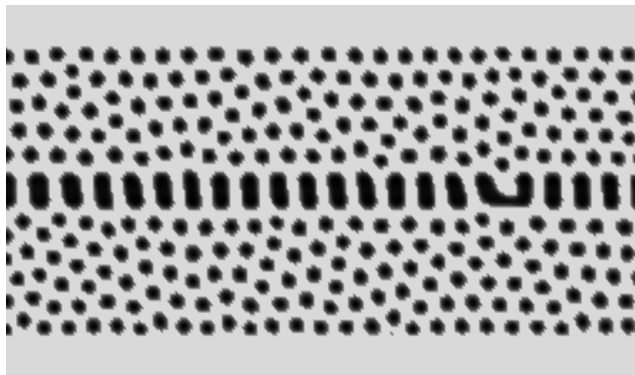
$$r_2 = 2$$

$$r_3 = 3.5$$

$$\Omega = 680 \times 400$$

Fig. 1: Initial condition noisy in $(-0.05, 0.05)$.

Unilateral regulation of v



$$D = 0.45$$

$$\delta = 6$$

$$\alpha = 0.899$$

$$\beta = 0.91$$

$$r_2 = 2$$

$$r_3 = 3.5$$

$$\Omega = 680 \times 400$$

Fig. 2: Regulation of v :

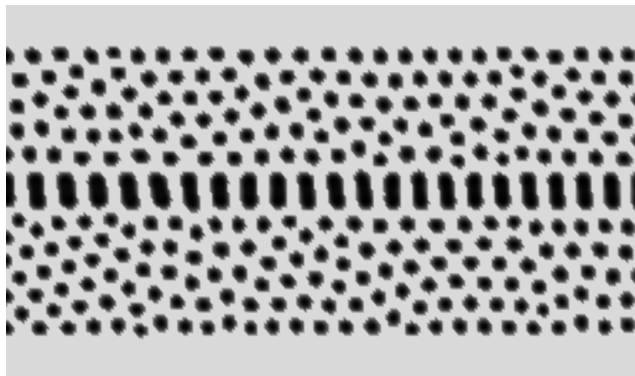
$a_{v-} = 0.066$ (a very slight source on the neural crest)

$a_{v+}^b = 0.12$ (a slight sink on the belly)

$\theta_{v-} = \theta_{v+}^b = 0$ (thresholds at zero)

$w_1 = 28, w_2 = 30$ (width of the source and sink)

Unilateral regulation of v



$$\begin{aligned}D &= 0.45 \\ \delta &= 6 \\ \alpha &= 0.899 \\ \beta &= 0.91 \\ r_2 &= 2 \\ r_3 &= 3.5 \\ \Omega &= 680 \times 400\end{aligned}$$

Fig. 3: Regulation for v :

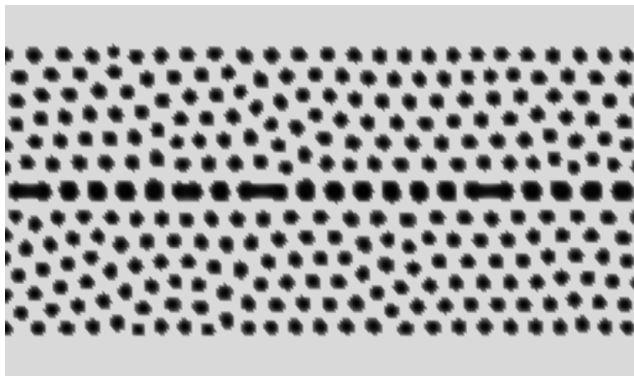
$a_{v-} = 0.065$ (very slight source on the neural crest)

$a_{v+}^b = 0.12$ (slight sink on the belly)

$\theta_{v-} = 0.02, \theta_{v+} = 0$ (nonzero threshold)

$w_1 = 28, w_2 = 30$ (width of sources)

Unilateral regulation of v



$$D = 0.45$$

$$\delta = 6$$

$$\alpha = 0.899$$

$$\beta = 0.91$$

$$r_2 = 2$$

$$r_3 = 3.5$$

$$\Omega = 680 \times 400$$

Fig. 4: Regulation for v :

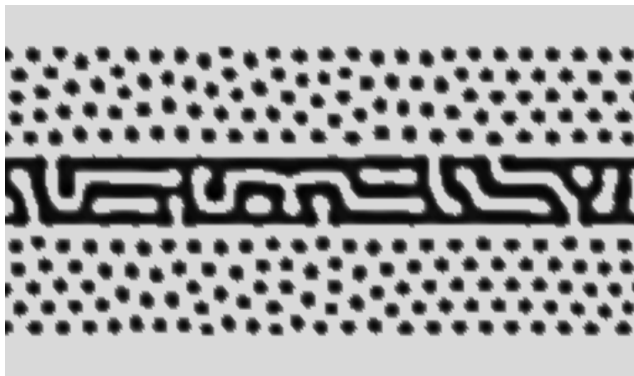
$a_{v-} = 0.065$ (very slight source on the neural crest)

$a_{v+}^b = 0.12$ (slight sink on the belly)

$\theta_{v-} = 0.02, \theta_{v+} = 0$ (nonzero threshold)

$w_1 = 12, w_2 = 30$ (width of sources)

Unilateral regulation of v



$$\begin{aligned}D &= 0.45 \\ \delta &= 6 \\ \alpha &= 0.899 \\ \beta &= 0.91 \\ r_2 &= 2 \\ r_3 &= 3.5 \\ \Omega &= 680 \times 400\end{aligned}$$

Fig. 5: Regulation for v :

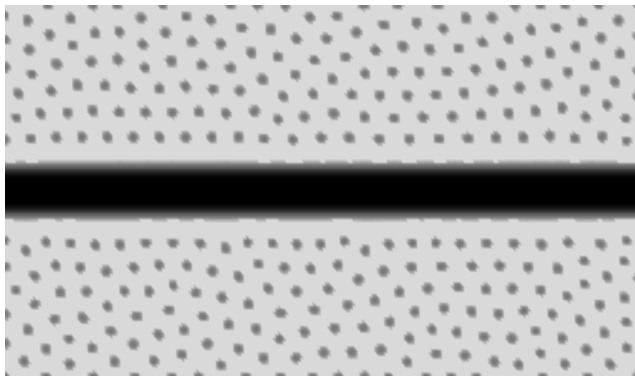
$a_{v-} = 0.066$ (very slight source on the neural crest)

$a_{v+}^b = 0.12$ (slight sink on the belly)

$\theta_{v-} = -0.07, \theta_{v+} = 0$ (nonzero threshold)

$w_1 = 68, w_2 = 30$ (width of sources)

Unilateral regulation of both u and v



$$D = 0.45$$

$$\delta = 6$$

$$\alpha = 0.899$$

$$\beta = 0.91$$

$$r_2 = 2$$

$$r_3 = 3.5$$

$$\Omega = 680 \times 400$$

Fig. 6: Regulation of both u and v :

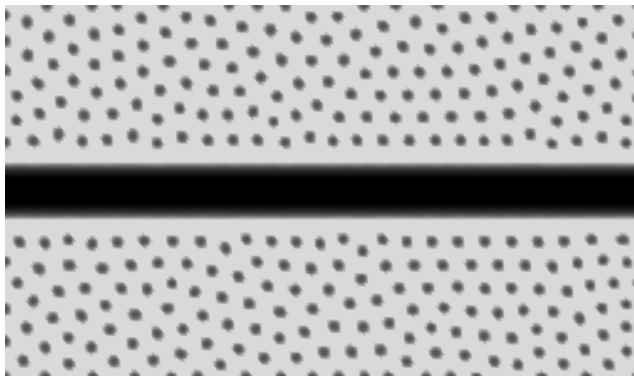
$$a_{u-} = a_{v-} = 5 \quad (\text{strong source on the neural crest})$$

$$a_{u+} = a_{v+} = 0.5 \quad (\text{slight sink on the neural crest})$$

$$\theta_{u-} = \theta_{v-} = \theta_{u+} = \theta_{v+} = 0.5 \quad (\text{thresholds})$$

$$w_1 = 40 \quad (\text{width of the source and sink})$$

Unilateral regulation of both u and v



$$D = 0.45$$

$$\delta = 6$$

$$\alpha = 0.899$$

$$\beta = 0.91$$

$$r_2 = 2$$

$$r_3 = 3.5$$

$$\Omega = 680 \times 400$$

Fig. 7: Regulation of both u and v :

$$a_{u-} = a_{v-} = 3.8 \quad (\text{weaker source on the neural crest})$$

$$a_{u+} = a_{v+} = 0.5 \quad (\text{slight sink on the neural crest})$$

$$\theta_{u-} = \theta_{v-} = \theta_{u+} = \theta_{v+} = 0.5 \quad (\text{thresholds})$$

$$w_1 = 40 \quad (\text{width of the source and sink})$$

Higher ratio of diffusions $D = 0.8$



$$D = 0.8$$

$$\delta = 6$$

$$\alpha = 0.899$$

$$\beta = 0.91$$

$$r_2 = 2$$

$$r_3 = 3.5$$

$$\Omega = 238 \times 140$$

Fig. 8: Higher ratio of diffusions $D = 0.8$, regulation for v :

$a_{v-} = 0.08$ (small source on the neural crest)

$\theta_{v-} = 0$ (zero threshold)

$w_1 = 40$ (width of the source)