Coupled Reaction-Diffusion Systems and 1-D Pattern Formation

Part III: Pattern Formation on a Growing Domain

Group Members

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Outline

1. Introduction
   - Reaction and Diffusion
   - Why are growing domains fun?
2. Implementation
   - How to program 1-D domain growth?
   - Choosing parameters
3. Results
   - Examples for different growth functions
   - Robustness of final spatial pattern
   - Find period doubling
   - Different reaction models
   - Effect of noise
   - Funkier stuff

Outline

General form of the Turing Model

$$\frac{\partial \mathbf{u}}{\partial t} = \mathbf{D}\nabla^2\mathbf{u} + \gamma\mathbf{f}(\mathbf{u}) \tag{1}$$

- $\mathbf{u} = \begin{bmatrix} u \\ v \end{bmatrix}$, concentration of two chemicals or morphogens: u (activator), v (inhibitor)
- $\mathbf{D} = \begin{bmatrix} 1 & 0 \\ 0 & d \end{bmatrix}$, diffusivity of u and v
- $\mathbf{f}$, reaction functions.
- γ, relative strength of reaction vs. diffusion.

Two example models of reactions

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$$f(u,v) = a - u + u^2 v \tag{2}$$

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These two models have different activation-inhibition relationships between u and v, which affect pattern formation on stationary and growing domains.

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- **Growth** is a fundamental process of biological systems. Organisms or populations of organisms usually *develop or grow* into a certain size rather emerge all of a sudden into their full-blown forms.

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- Size isn't everything about biological development. Growth sometimes accompanies functional differentiation of cells or tissues.
- Excessive and insufficient growth may have physiological or pathological consequences.
- Connecting to Turing's Model, the counterpart of morphogens could be ***growth*** *factors* (literally).

Back to morphogenesis: previous findings in simulations

See a review: Maini et al (2012). 

- A tangible example: angelfish stripe-doubling

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- Period doubling sequence can be destroyed by noise.
- different reaction models show different period doubling mechanism: peak splitting (Schnakenberg) vs. peak insertion (Gierer-Meinhardt).

Goal of the present project

Explore the effects of domain growth on spatial pattern generation in terms of:

- different growth functions
- different reaction functions

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Compare results with preexisting findings.

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Finite Element Method on stationary domain

Discrete weak formulation (Galerkin Approximation) of Turing's Model on a stationary 1-D domain of size L, with Neumann Boundary Conditions (NBCs).

$$\int_0^L u_t\phi_i dx + \int_0^L u_x\phi_i' dx = \gamma \int_0^L f\phi_i dx \tag{6}$$

$$\int_0^L v_t\phi_i dx + d\int_0^L v_x\phi_i' dx = \gamma \int_0^L g\phi_i dx \tag{7}$$

Test functions $\phi_i \quad (i = 1, 2, \ldots N)$ form a basis for discretized $u = u_h$ and $v = v_h$:

$$u = \sum_{j=1}^{N} c_j^{(u)}\phi_j \qquad u_x = \sum_{j=1}^{N} c_j^{(u)}\phi_j' \tag{8}$$

$$v = \sum_{j=1}^{N} c_j^{(v)}\phi_j \qquad v_x = \sum_{j=1}^{N} c_j^{(v)}\phi_j' \tag{9}$$

Finite Element Method on stationary domain

Then we have

$$\frac{d}{dt}\sum_{j=1}^{N} c_j^{(u)} \int_0^L \phi_j\phi_i dx + \quad \sum_{j=1}^{N} c_j^{(u)} \int_0^L \phi_j'\phi_i' dx = \gamma \int_0^L f\phi_i dx \tag{10}$$

$$\frac{d}{dt}\sum_{j=1}^{N} c_j^{(v)} \int_0^L \phi_j\phi_i dx + d\sum_{j=1}^{N} c_j^{(v)} \int_0^L \phi_j'\phi_i' dx = \gamma \int_0^L g\phi_i dx \tag{11}$$

Let $\mathbf{\Psi}_{ij} = \int_0^L \phi_i'\phi_j' dx$, $\mathbf{M}_{ij} = \int_0^L \phi_i\phi_j dx$, $\mathbf{b^{(f)}}_i = \int_0^L f\phi_i dx$, $\mathbf{b^{(g)}}_i = \int_0^L g\phi_i dx$, and $\mathbf{c}_j = c_j$, then the problem becomes:

$$\mathbf{M}\frac{d}{dt}\mathbf{c^{(u)}} + \quad \mathbf{\Psi}\mathbf{c^{(u)}} = \gamma\mathbf{b^{(f)}} \tag{12}$$

$$\mathbf{M}\frac{d}{dt}\mathbf{c^{(v)}} + d\mathbf{\Psi}\mathbf{c^{(v)}} = \gamma\mathbf{b^{(g)}} \tag{13}$$

Domain growth

In the present project, we explored **uniform** growth of the whole domain: $0 \leqslant x \leqslant L(t)$, where $L(t)$ may follow three different growth functions:

- linear growth: $L(t) = L_0 + rt$

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$L_0 = L(0)$ is the initial domain size.

Domain growth

To simplify the computation of domain growth, we adopted Crampin et al's (1999) method: at each time step, we map the domain to $[0, 1]$

$$(x, t) \to (\bar{x}, \bar{t}) = (\frac{x}{L(t)}, t) \tag{14}$$

$$(x, t) = (L(t)\bar{x}, \bar{t}) \tag{15}$$

The formulation in (1) becomes a non-autonomous system:

$$\frac{\partial \bar{\mathbf{u}}}{\partial t} = \frac{\mathbf{D}}{L^2(t)} \nabla^2 \bar{\mathbf{u}} + \gamma \mathbf{f}(\bar{\mathbf{u}}) \tag{16}$$

By solving (16), we have $\bar{\mathbf{u}} = \bar{\mathbf{u}}(L(t)\bar{x})$. We can dilate the solution by $L(t)$ for each time to obtain $\mathbf{u}(x)$.

Domain growth in Finite Element form

The matrix representation of the discrete weak formulation (12) and (13) becomes

$$\mathbf{M}\frac{d}{dt}\mathbf{c}^{(\mathbf{u})} + \frac{1}{L^2(t)}\boldsymbol{\Psi}\mathbf{c}^{(\mathbf{u})} = \gamma\mathbf{b}^{(\mathbf{f})} \tag{17}$$

$$\mathbf{M}\frac{d}{dt}\mathbf{c}^{(\mathbf{v})} + \frac{d}{L^2(t)}\boldsymbol{\Psi}\mathbf{c}^{(\mathbf{v})} = \gamma\mathbf{b}^{(\mathbf{g})} \tag{18}$$

Numerical Integration

To numerically integrate (17) and (18) with respect to time, we combined Crank-Nicolson Method and Adams-Bashforth Method:

$$\mathbf{M}\frac{\mathbf{U^{k+1}}-\mathbf{U^{k}}}{\Delta t}+\frac{1}{L^2(k\Delta t)}\boldsymbol{\Psi}\frac{\mathbf{U^{k+1}}+\mathbf{U^{k}}}{2}=\gamma\left(\frac{3}{2}\mathbf{F^{k}}-\frac{1}{2}\mathbf{F^{k-1}}\right) \quad (19)$$

$$\mathbf{M}\frac{\mathbf{V^{k+1}}-\mathbf{V^{k}}}{\Delta t}+\frac{d}{L^2(k\Delta t)}\boldsymbol{\Psi}\frac{\mathbf{V^{k+1}}+\mathbf{V^{k}}}{2}=\gamma\left(\frac{3}{2}\mathbf{G^{k}}-\frac{1}{2}\mathbf{G^{k-1}}\right) \quad (20)$$

k is the index of iteration and Δt denotes the time step.

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k is the index of iteration and Δt denotes the time step.
By rearranging (19) and (20), we can solve $\mathbf{U^{k+1}}$ and $\mathbf{V^{k+1}}$ for each iteration in Matlab. ☺

Outline

Fix reaction functions

In order to not get drowned in the vast parameter space, we fixed the parameters within the reaction functions.

- Schnakenberg Kinetics:
  $a = 0.1,\ b = 0.9$ (Crampin et al, 1999)

$$f(u,v) = a - u + u^2 v \tag{2}$$
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- Gierer-Meinhardt Kinetics:
  $a = 0.1$, $b = 1$ (Murray, 2003), $k = 0$ or $k = 0.05$

$$f(u,v) = a - bu + \frac{u^2}{v(1+ku^2)} \tag{4}$$
$$g(u,v) = u^2 - v \tag{5}$$

Cool...we have killed some parameters.

Parameters of primary interests

Mainly, we are interested in varying the following parameters and observe the corresponding pattern formation:

- r: the growth rate
- d: the diffusivity ratio between u and v
- γ: the relative strength of reaction vs. diffusion

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Still a lot for someone who has decision anxiety.

Fix the initial fastest growing mode

Let (u^*, v^*) be the homogeneous equilibrium solution of the system **without** diffusion: $\frac{\partial \mathbf{u}}{\partial t} = \gamma \mathbf{f}(\mathbf{u}) = 0$.
We linearize the system near (u^*, v^*):

$$\mathbf{w_t} = \mathbf{D}\nabla^2\mathbf{w} + \gamma\mathbf{A}\mathbf{w}, \quad \mathbf{w} = \begin{bmatrix} u - u^* \\ v - v^* \end{bmatrix}, \mathbf{A} = \begin{bmatrix} f_u & f_v \\ g_u & g_v \end{bmatrix}_{u^*,v^*} \tag{21}$$

Let $\mathbf{W}$ be the time-independent solution of the spatial eigenvalue problem $\nabla^2\mathbf{W} = -k^2\mathbf{W}$, e.g. $\mathbf{W} \propto cos(kx)$ where $k = \frac{n\pi}{L}$. We call k the ***mode***.
We look for solution of the form $\mathbf{w} = \sum_k c_k e^{\lambda t}\mathbf{W_k}$. Then the ***fastest growing mode*** k^* correspond to the largest $\lambda > 0$.
By fixing k^*, we can put an additional constraint on the relationship between d and γ.

Fix the initial fastest growing mode

To specify the constraint, we need to find the eigenvalues of the matrix:

$$\mathbf{J} = -k^2\mathbf{D} + \gamma\mathbf{A} = \begin{bmatrix} \gamma f_u - k^2 & \gamma f_v \\ \gamma g_u & \gamma g_v - k^2 d \end{bmatrix}_{u^*,v^*} \quad (22)$$

which are

$$\lambda = \frac{1}{2}\{tr\mathbf{J} \pm \sqrt{(tr\mathbf{J})^2 - 4det\mathbf{J}}\} \quad (23)$$

We know that $tr\mathbf{J} = \gamma(f_u + g_v) - k^2(d+1) < 0$. To have some positive λ, we need $det\mathbf{J} < 0$ for some value of k, and the minimum of $det\mathbf{J}$ correspond to the largest λ.

Fix the initial fastest growing mode

In other words, k^* minimize the function

$$h(k^2) = dk^4 - \gamma k^2(df_u + g_v) + \gamma^2(f_u g_v - f_v g_u) \qquad (24)$$

which is

$$(k^*)^2 = \gamma \frac{df_u + g_v}{2d} \qquad (25)$$

If we want to fix k^* and d, the choice of γ is unique:

$$\gamma = \frac{2d(k^*)^2}{df_u + g_v} = \frac{2d(n^*)^2\pi^2}{L^2(df_u + g_v)} \qquad (26)$$

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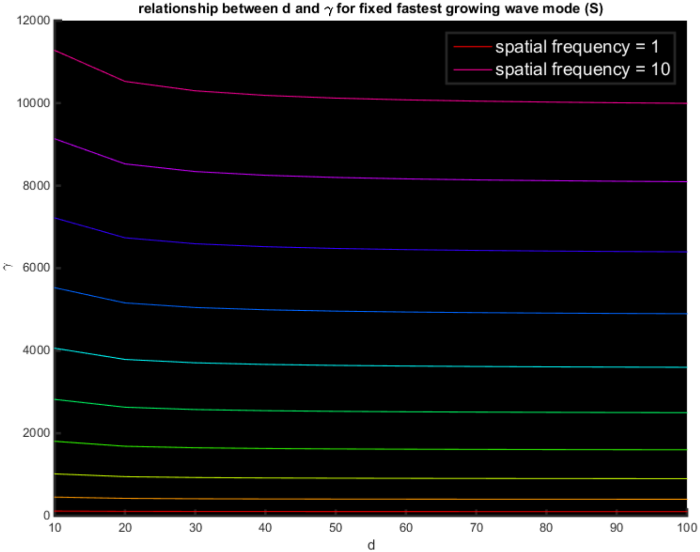
What to choose as initial spatial frequency on L_0?

Relationship between γ and d for fixed k^*



Pick a number

"If oneness isn't present in the others, the others are neither many nor one." - from *Parmenides*, Plato

Determine γ by the choice of d

That was just to say, we chose the initial frequency as 1 cycle per unit distance, and initial domain size $L_0 = 1$, then

$$\gamma = \frac{8d\pi^2}{d f_u + g_v} \tag{27}$$

Allowable number of periods

Since Turing Patterns only exists for $det\mathbf{J} < 0$, i.e. for discrete values of k's bounded by the roots, say k_1, k_2, of $h(k^2)$:

$$k_{1,2}^2 = \frac{\gamma}{2d}\{(df_u + g_v) \pm \sqrt{(df_u + g_v)^2 - 4d(f_u g_v - f_v g_u)}\} \quad (28)$$

We define the **allowable number of periods** on a domain of given size are those that satisfies

$$k_1^2 < k^2 < k_2^2 \quad (29)$$

Thus we have also determined the allowable number of periods for each point in time.
Warning: all we have been talking about are near homogeneous equilibrium conditions.

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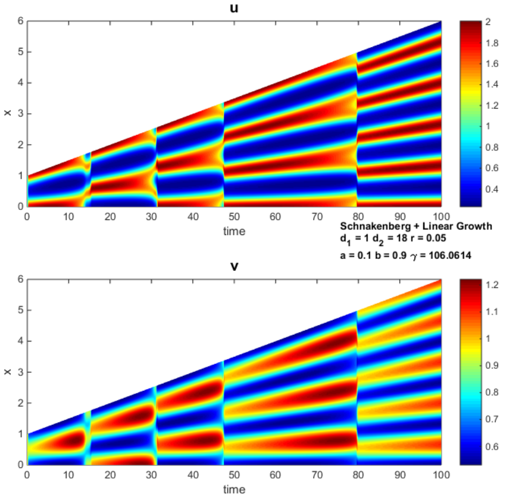
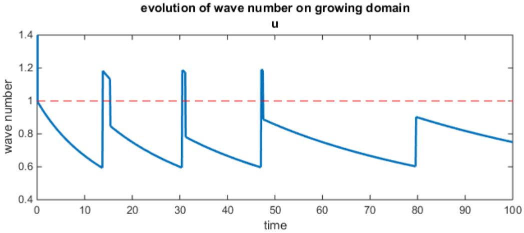
Linear Growth Example

Schnakenberg Kinetics with fixed the final domain length 6 for 100 unit time's growth. For linear growth **r** = 0.05.



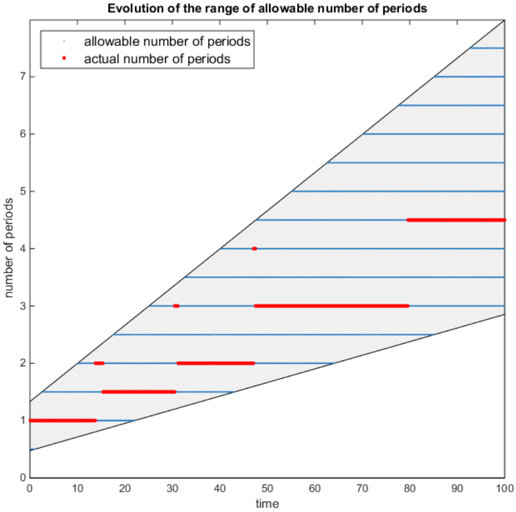
Linear Growth Example

The evolution of spatial frequency (cycle/unit distance):



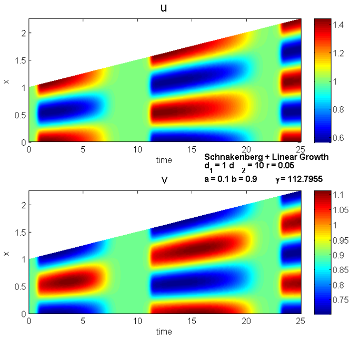
Linear Growth Example

Allowable number of periods and actual number of periods:



Effect of diffusivity in linear grow

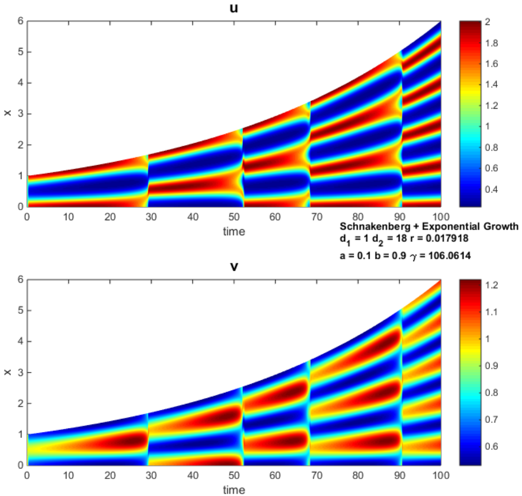
Changing d with fixed k^*. d influence the pattern formed and the transitions in the growth sequence.



Contingent on grid resolution (100 pts) and time step (5×10^{-5}), we used $d = 18$ for most occasions.

Exponential Growth Example

Schnakenberg Kinetics with fixed the final domain length 6 for 100 unit time's growth. For exponential growth **r** ≈ 0.018.



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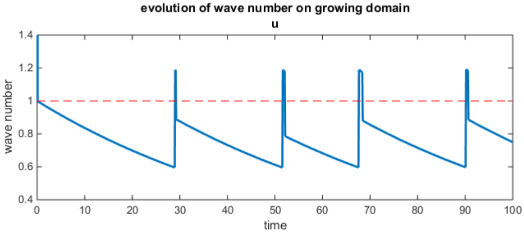

Exponential Growth Example

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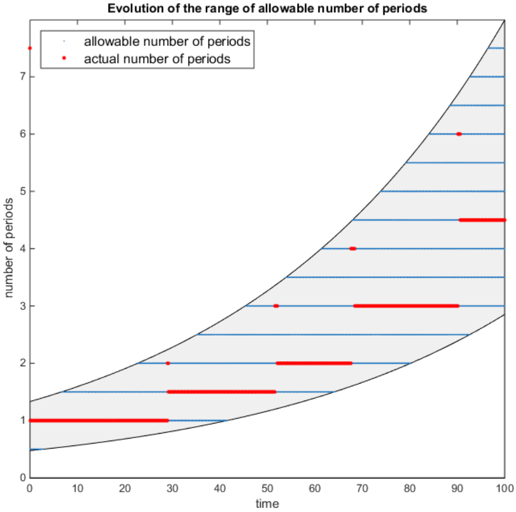
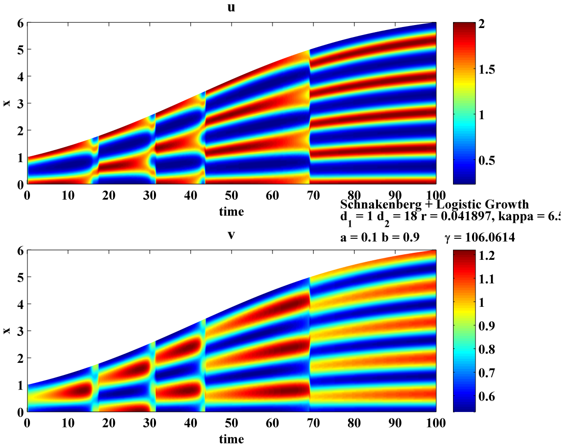


Logistic Growth Example

Schnakenberg Kinetics with fixed the final domain length 6 for 100 unit time's growth. For Logistic growth **r** ≈ 0.042.



Logistic Growth Example

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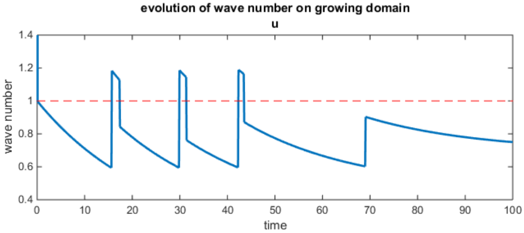

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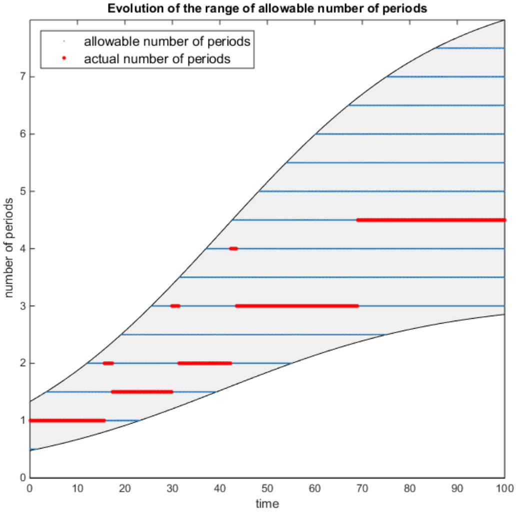

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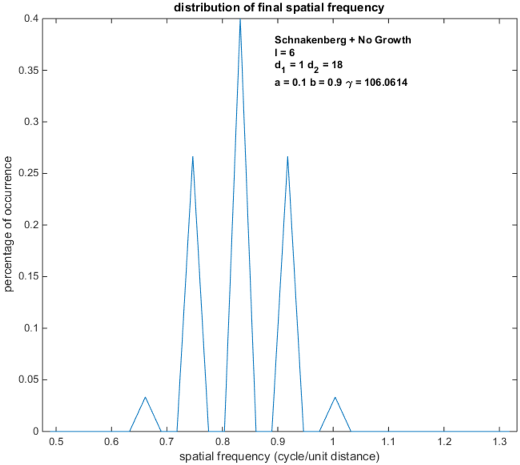
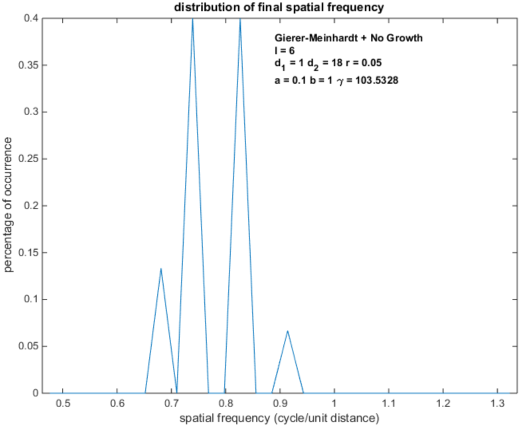
Distribution of final pattern for stationary domain

The distribution reflects 30 runs of Schnakenberg Model, with small random perturbation near equilibrium.



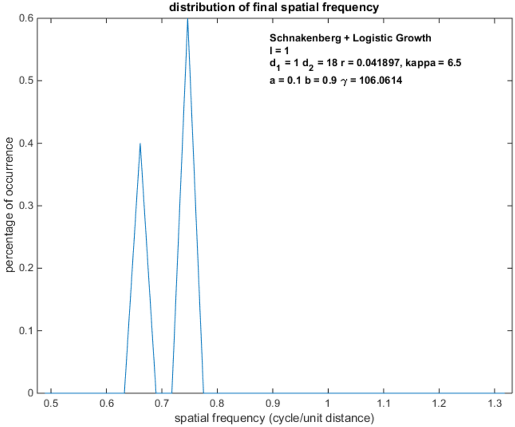
Distribution of final pattern for stationary domain

30 runs of Gierer-Meinhardt Model with no growth.



Distribution of final pattern for growing domain

30 runs of Schnakenberg Model with Logistic growth.



Robustness?

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- For Logistic growth, the modes are biased towards the lower bound of the allowable frequencies.
- More parameter tuning might be required to produce *unique* mode as reported by previous studies.

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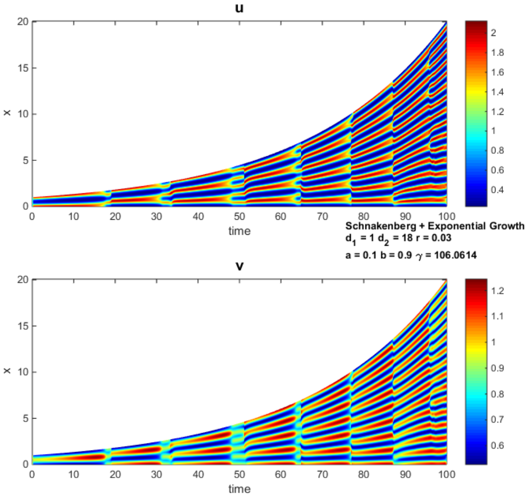
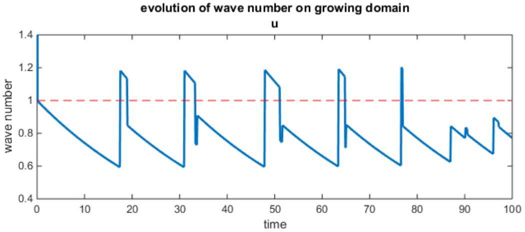
Manipulate growth rate r in exponential growth

Schnakenberg reactions, with **r** = 0.03, show *tendencies* of period doubling, i.e. transient doubling.



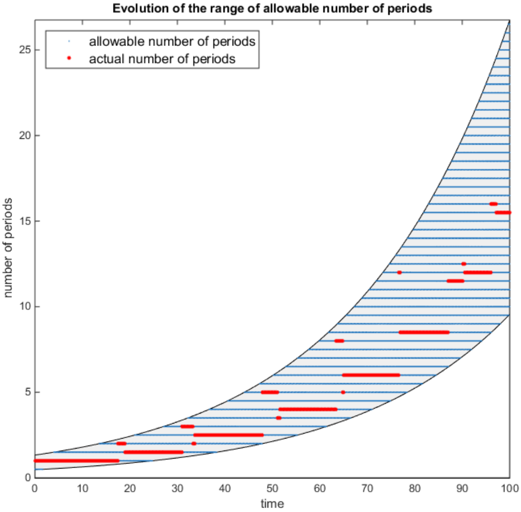
Evolution of spatial frequency for r = 0.03

Comparing to an earlier example (r ≈ 0.018, slower growth), the episodes of transient doubling appear to be longer for r = 0.03.



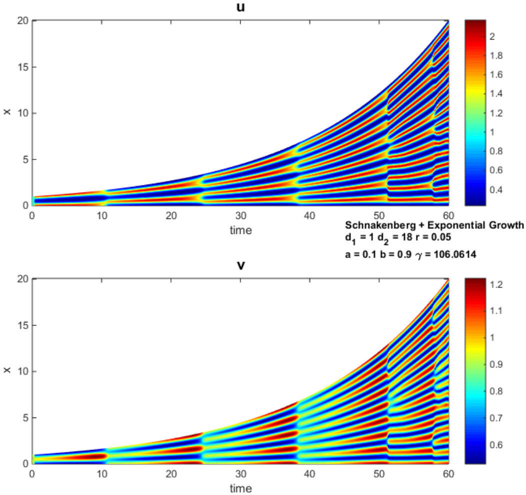
Evolution of number of periods for r = 0.03

A better view of the curious sequence of period changes.



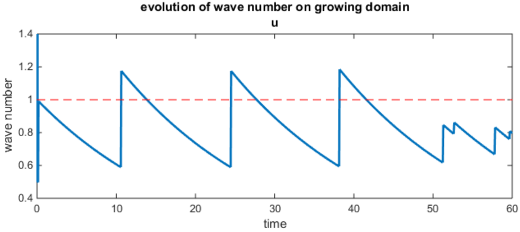
Period doubling found for r = 0.05

Period doubling appeared three times in the sequence, but broke down afterwards.



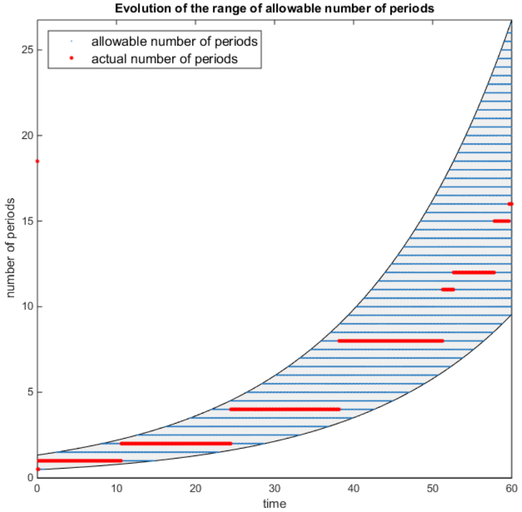
Period doubling found for r = 0.05

The final break-down might be a consequence of insufficient grid resolution or/and increased delicacy of patterns in larger domain.



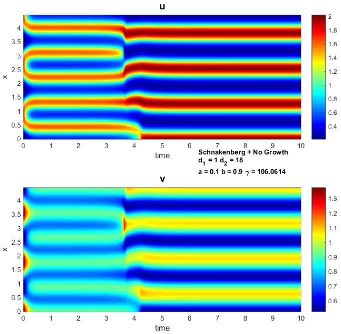
Increased delicacy?

A much greater number of mode options for larger domain.



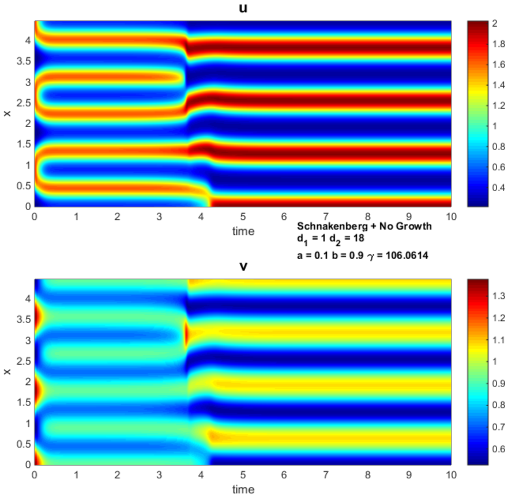
Is it growth or is it special initial conditions?

Setting initial condition to 2.5 periods of cosine wave, run the experiments on *stationary domains* of length about 4. Here period 5 is not the fastest growing mode from near homogeneous initial conditions, but will it occur for this special intial condition?

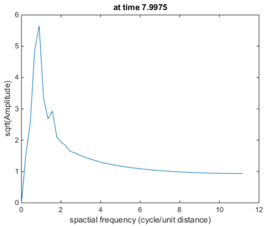


A longer run for $L = 4.478$

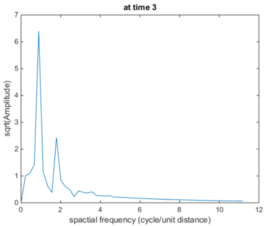
As larger domain used, transient period doubling persisted longer, but still broke down eventually.



A close look at the spectra for $L = 4.478$



(a) From periodic initial condition



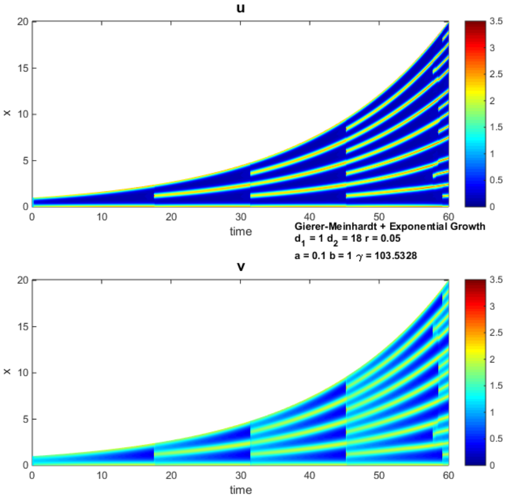
(b) From homogeneous initial condition

Outline

1. Introduction
   - Reaction and Diffusion
   - Why are growing domains fun?
2. Implementation
   - How to program 1-D domain growth?
   - Choosing parameters
3. Results
   - Examples for different growth functions
   - Robustness of final spatial pattern
   - Find period doubling
   - Different reaction models
   - Effect of noise
   - Funkier stuff

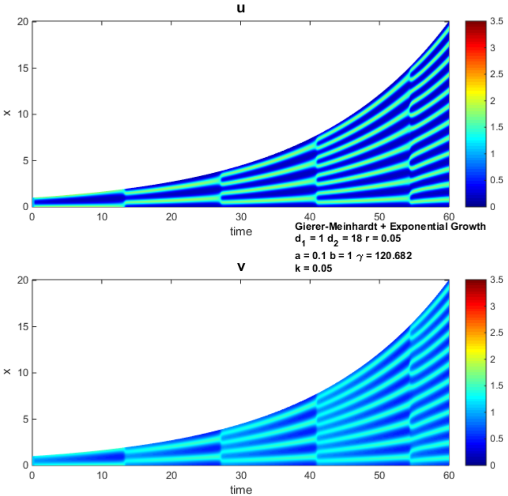
Period doubling for Gierer-Meinhardt Model

For $k = 0$, Gierer-Meinhardt reaction showed period doubling via peak insertion as reported by previous studies.



Period doubling for Gierer-Meinhardt Model

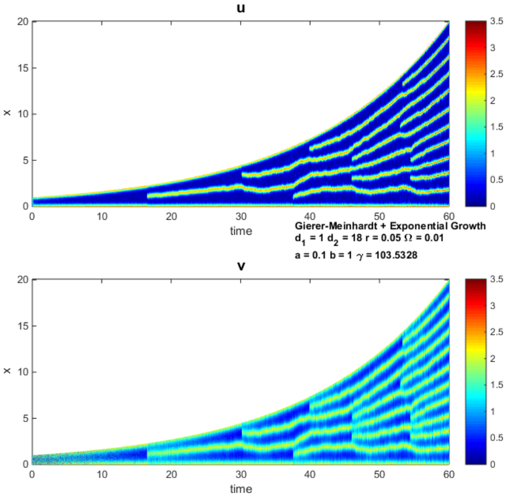
For $k = 0.05$ (saturation factor for u), Gierer-Meinhardt reaction also exhibited peak splitting similar to Schankenberg reaction.



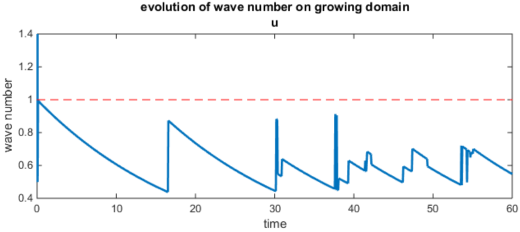
Outline

Noise destroy period doubling sequence

Small noise ($\sqrt{\Omega} = 0.1$) was added in each iteration.



Noise destroy period doubling sequence



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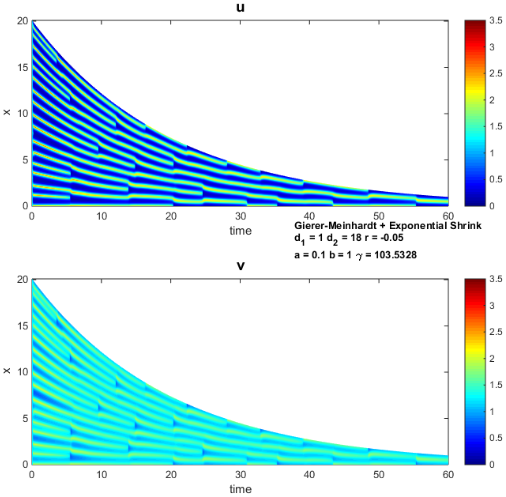
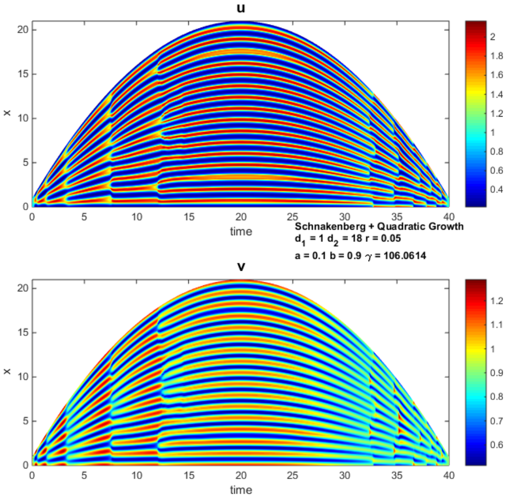
Exponential shrink (decay) ...

Shrinking shows asynchronized local pattern changes.



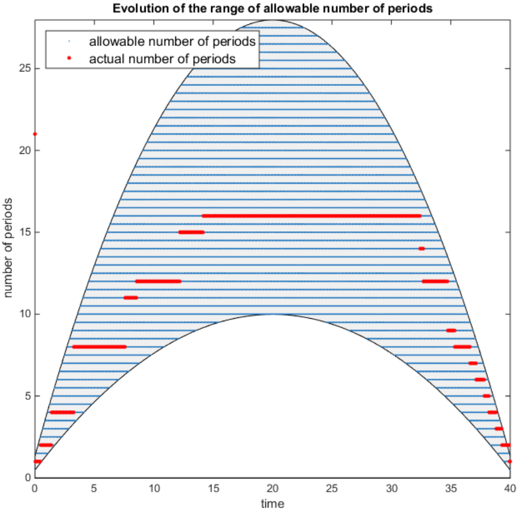
Even funkier ...

Growing then shrinking, $L(t) = L_0 - \mathbf{r}(t - T)t$ with $T = 40$, shows obvious asymmetry.



Even funkier ...

Growing then shrinking show obvious asymmetry.



Summary

- We have found effects of growth similar to preexisting studies.
- Explored the effect of initial conditions and their cooperation with growth.
- Shrinking could be an interesting topic too. ☺

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