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On the Interplay of Geometrical Shapes and the Analysis of a Dispersal Model for Pattern Formations

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Abstract

A reaction-diffusion model is put forward which is capable of generating chemical maps whose concentration contours are similar to the patterns seen on the flanks of zebras, leopards and other mammals. Initially, this type of reaction diffusion kinetics model was introduced by Turing and later Murray applied it to animal coat patterns. Among many chemical reaction mechanism, we consider Schnackenberg reaction mechanism in details and show that the geometry and scale of the domain, the relevant part of the integument, during the time of laying down plays a crucial role in the structural patterns which result. Patterns which exhibit a limited randomness are obtained for a selection of geometries. Finally the system was solved numerically using finite difference method.

Keywords: Pattern formation; Turing pattern; reaction-diffusion; numerical analysis.

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1 Introduction

People are always be fascinated and enthralled with the wealth, diversity and beauty of pattern in biology. How such patterns and millions of others, were laid down is still unknown although considerable progress has been made in several different areas. Among these patterns, a rich and varied spectrum of coat patterns is exhibited by mammals. Patterned coats are typical of many mammalian groups, whose spots, stripes and other markings have been hypothesized to play important adaptive roles in camouflage, predator evasion, and social communication, see [1, 2, 3, 4, 5] and references therein.

It is generally accepted that color patterns in animals are genetically determined but the mechanism is not known and a study of genetics alone cannot provide a mechanistic understanding of how physical and chemical processes within a developing system conspire to produce the complex spatio-temporal cues to which cells respond and interact. In these cases, a number of complex mechanical and biochemical processes interact in a highly nonlinear way. Such systems are amenable to mathematical modelling and the role of the modeller is to suggest explanations, based on biologically plausible mechanisms, of observed behaviour and to make experimentally testable predictions.

Since Turing's pioneering paper in 1952, many applications have been suggested for reaction-diffusion mechanisms in biology; a chemical mechanism for generating coat patterns [1]. The original article does not take into account changes in geometry, yet the roles that pattern formation plays in biology are so versatile, demand to study this topic in greater detail has surfaced in recent years. Except for circumstantial evidence, still the existence of morphogens is widely conjectural. But Turing's model continue to exist and engaging because it appears to interpret a huge number of experimental results with simple notions.

Turing's initial work has been developed by a number of authors, including Murray, into a more complete mathematical theory [3, 6, 7, 8]. Murray proposed that a single pattern formation mechanism could underlie the wide variety of animal coat markings found in nature. The study suggested that a reaction-diffusion system which can be diffusively driven unstable could be responsible for the laying down of the pre-pattern for animal coat markings.

Spatial instabilities close to this homogeneous equilibrium produce patterns in the concentrations of the chemicals in the system [1, 7, 9, 10, 11, 12]. These spatial instabilities are known as Turing instabilities, or diffusion-driven instabilities.

Initially, let us consider the Alan Turing proposed model such as [1, 7, 13, 14]

$$\frac{\partial c}{\partial t} = f + \nabla \cdot (D \nabla c) \tag{1.1}$$

Note that (1.1) is a system of non-linear differential equations for the chemical concentrations. Equation (1.1) is the general form of the reaction-diffusion system, where $c \equiv c(x,t)$, a vector of morphogen concentrations and f is a function of c, $\mathbf{x}$ and t and known as reaction kinetics. The parameter D is a diagonal matrix of positive diffusion coefficients and may be spatially distributed. The resulting equation with constant D and Laplacian operator Δ is

$$\frac{\partial c}{\partial t} = f + D\Delta c \tag{1.2}$$

Since Turing's [1] classic paper proposed a reaction-diffusion theory of morphogenesis, a number of specific two-reactant model mechanisms have been proposed, studied extensively and applied, with varying degrees of plausibility, to a wide spectrum of problems in developmental biology. There is almost an embarrassing richness of spatial and temporal patterns which can be exhibited by such mechanisms. The steady state heterogeneous patterns are diffusion-driven in the Turing sense.

One particularly widely studied system is Schnackenburg model [13, 15, 16, 17]. In this paper we limit our discussion on this model since Schnackenberg model can be used to describe the emergence of patterns on the animal skin. In addition, like most activator-substrate system, the Schnakenberg model tends to develop wider, comparatively less sharp wavefronts in contrast to its counterpart inhibitor-activator system. It is well known that dispersion of chemical or biochemical populations can produce a variety of spatial patterns. This type of reaction-diffusion problems includes some important pattern formation equations arising either from the modeling of kinetics of chemical or biochemical reactions and from the formation theory in biological pattern. To present various types of pattern formations, the four mathematical models are typically important; instantly for examples,

- Schnackenberg model,
- Brusselator model,
- Glycolysis model, and
- Gray-Scott model

and serve as mathematical models in biology as well as in physical chemistry. It is remarked that very complicated patterns are described for a parabolic system known as the GrayScott system [18] and similar exploration can be found for Brusselator and Glycolysis equations in [17, 19].

In this study, we are interested to consider the first one, Schnackenberg model, due to it's important significance. The non-dimensional Schnackenburg model involving four positive parameter a, b, β and d_1 with homogeneous Neumann boundary conditions is defined as

$$\begin{cases} \frac{\partial u}{\partial t} = \Delta u + \beta f(u,v), \ t>0, \ x \in \Omega \\ \frac{\partial v}{\partial t} = d_1 \Delta v + \beta g(u,v), \ t>0, \ x \in \Omega \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, \ \ x \in \partial\Omega \\ u(0,x) = u_0, \ v(0,x) = v_0, \ x \in \Omega. \end{cases} \tag{1.3}$$

In the system (1.3), a and b are positive parameters and u and v are the activator and substrate terms, respectively. The activator-substrate system arises when uncompetitive prohibition is achieved via more than one substrate compulsion to an active site at the same time [18, 20, 21]. In dimensionless form, the constant d_1 is the ratio of the diffusion coefficients of u and v. The key parameter β represents a relative strength of reaction terms. The functions $f(u,v)$ and $g(u,v)$ are the reaction kinetics, which will always be nonlinear and n is the outward normal to the boundary. It is remarked that the appropriate selection is the Neumann boundary conditions to ensure no leakage of material out of the domain. Hence zero flux boundary conditions are appropriate for flat region while periodic boundary conditions are appropriate for surface that represent spherical or cylindrical regions. The reaction kinetics functions $f(u,v)$ and $g(u,v)$ are given by

$$\begin{aligned} f(u,v) &= a - u + u^2 v \\ g(u,v) &= b - u^2 v \end{aligned} \tag{1.4}$$

where a is a source of u, $-u$ is exponential decay, and u^2v represents the autocatalysis creating u while v acts as the substrate, necessary to facilitate the autocalytic reaction.

The main novelty of this study is that we analyzed the effect of parametric values on pattern formation. For this purpose, in section 2 we discuss about the stability analysis of Schnackenburg model. In section 3, we consider different values of parameter β while the others are fixed. Also it is shown the significance change of the domain size x, and various values of time, t that satisfy the stability conditions as long as $\beta = 800$. Finally using these values, we simulate the numerical result of the solution of our considered model.

2 Stability Analysis

Before starting the analysis of this model, we place a short note on biological constraints posed on this model. Since the model is used to describe the evolution of concentrations of chemicals, we must consider that u and v are positive. It is also noted that the parameters a, b, β and d_1 are positive, which are more realistic in the physical sense. In order to analyses the reaction diffusion, we consider initial conditions and boundary conditions to make the problem well-posed. In this paper, we consider no flux boundary conditions. A good starting point analysing a system of equation like (1.3) is to look for homogeneous steady state solution, i.e. a state where all spatial and temporal derivatives vanish, and thus to look for solutions to $f(u, v) = g(u, v) = 0$. In case of Schnakenberg model, we get only one such state

$$u^* = a + b, \quad v^* = \frac{b}{(a+b)^2}.$$

Since a and b are positive u^* and v^* are also positive. The crucial idea of Turing was that it is possible to have such steady states which are stable in the absence of diffusion, but which turn unstable in the presence of diffusion and form spatially heterogeneous patterns. Now we have to determine conditions on which these pattern occur. Since we are concerned with diffusion-driven instability, we are interested in linear instability of this steady state that is solely spatially dependent. So, in the absence of any spatial variation the homogeneous steady state must be linearly stable: we first determine the conditions for this to hold.

If there is no spatial variations of u and v then

$$u_t = \beta f(u, v), \quad v_t = \beta g(u, v) \tag{2.1}$$

To look at the steady states u^* and v^*, we perform a linear stability analysis. We perturb the steady state by a small perturbation i.e. $u = u^* + \widetilde{u}$ and $v = v^* + \widetilde{v}$, where the perturbations satisfied $|\widetilde{u}| \ll 1$, $|\widetilde{v}| \ll 1$. The growth of these perturbations determines the stability and the result is a linearised system of equations around the steady state.

Linearizing about the steady state at $u = u^*$ and $v = v^*$, we set

$$\mathbf{w} = \begin{pmatrix} u - u^* \\ v - v^* \end{pmatrix} \tag{2.2}$$

For small $|\mathbf{w}|$, u and v are small and the quadratic terms in u and v are extremely small. Hence the perturbation of Equation (2.1) is locally governed by the equation

$$\mathbf{w}_t = \beta A \mathbf{w} \tag{2.3}$$

where A is the stability matrix and defined as

$$A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}_{(u^*, v^*)} \tag{2.4}$$

We now take the partial derivatives of f and g to be evaluated at the steady state unless stated otherwise. The solutions can be found in the following form

$$\mathbf{w} = e^{\lambda t} \tag{2.5}$$

where λ is the eigenvalue. The steady state $\mathbf{w} = 0$ is linearly stable if $Re(\lambda) < 0$, since in this case the perturbation $\mathbf{w} \to 0$ as $t \to \infty$. Substitution of Equation (2.5) into Equation (2.3) we get

$$\begin{aligned} \lambda e^{\lambda t} &= \beta A e^{\lambda t} \\ \Rightarrow \lambda I &= \beta A \\ \Rightarrow \beta A - \lambda I &= \mathbf{0} \end{aligned}$$

To obtain non-trivial solution, it is required that

$$\begin{aligned} det(\beta A - \lambda I) &= 0 \\ \Rightarrow \begin{vmatrix} \beta f_u - \lambda & \beta f_v \\ \beta g_u & \beta g_v - \lambda \end{vmatrix} &= 0 \\ \Rightarrow \lambda^2 - \beta(f_u + g_v)\lambda + \beta^2(f_u g_v - f_v g_u) &= 0 \end{aligned} \tag{2.6}$$

Linear stability, that is, $Re(\lambda) < 0$, is guaranteed if

$$(i)\, trA = f_u + g_v < 0\ ,\ (ii)\, |A| = f_u g_v - f_v g_u > 0 \tag{2.7}$$

Since $u = u^*, v = v^*$ are functions of the parameters of kinetics, these inequalities thus impose certain constraints on the parameters.

Now consider the governing reaction-diffusion Equations of (1.3)

$$\begin{aligned} u_t &= \beta f(u,v) + \Delta u \\ v_t &= \beta g(u,v) + d_1 \Delta v \end{aligned}$$

For steady states

$$\begin{aligned} \beta f(u,v) + \Delta u &= 0 \\ \beta g(u,v) + d_1 \Delta v &= 0 \end{aligned}$$

To formulate the problem mathematically, we require boundary and initial conditions. Here we consider a rectangular domain $0 \le x \le p,\ 0 \le y \le q$ where x, y are cartesian co-ordinates and $p,\ q$ are constants. We consider the zero flux boundary conditions for the rectangular domain. After tedious mathematical simplification, one can show that the conditions of spatial pattern in the presence of diffusion are [1, 6]

$$(iii)\ d_1 f_u + g_v > 0,\ \ (iv)\ (d_1 f_u + g_v) - 4d_1\,(f_u g_v - f_v g_u) > 0 \tag{2.8}$$

Now we state the following theorem and the similar result can be found in [13].

Theorem 2.1. *If (u^*, v^*) is the equilibrium point of (1.3) then the conditions for Turing pattern to form are*

$$(i)\ f_u + g_v < 0,\ (ii)\ f_u g_v - f_v g_u > 0,\ (iii)\ d_1 f_u + g_v > 0$$

and

$$(iv)\ (d_1 f_u + g_v) - 4d_1\,(f_u g_v - f_v g_u) > 0$$

We will derive conditions on the parameters of Schnackenberg model (1.3) by using Turing conditions. The first three Turing conditions become

$$(i)\ f_u + g_v < 0 \Rightarrow 1 - \frac{2a}{u^*} - (u^*)^2 < 0 \Rightarrow a > \frac{u^*}{2}\left(1 - (u^*)^2\right)$$

Next

$$(ii)\ f_u g_v - f_v g_u > 0 \Rightarrow (u^*)^2 > 0$$

$$(iii)\ d_1 f_u + g_v > 0 \Rightarrow d_1 - (u^*)^2 - a\frac{2d_1}{u^*} > 0 \Rightarrow a < \frac{u^*}{2}\left(1 - \frac{(u^*)^2}{d_1}\right)$$

From the above conditions, we see that the second condition is trivially true. Since $d_1 > 1$ the first and third conditions do not contradict. For the last one, we have a quadratic equation in a such that

$$(iv)\ (d_1 f_u + g_v) - 4d_1\,(f_u g_v - f_v g_u) > 0 \Rightarrow m_1(d_1)\,a^2 - m_2(d_1)\,a + m_3(d_1) > 0$$

where we have

$$m_1(d_1) = 4d_1^2, \;\; m_2(d_1) = 4d_1u^*\left(d_1 - (u^*)^2\right)$$

and

$$m_3(d_1) = (u^*)^2\left(d_1 - (u^*)^2\right)^2 - 4d_1(u^*)^4.$$

Since condition (iv) gives a quadratic equation in a, there are two possibilities on a: either

$$a < \frac{m_2(d_1) - \sqrt{m_3(d_1)^2 - 4m_1(d_1)m_3(d_1)}}{2m_1(d_1)}$$

or

$$a > \frac{m_2(d_1) - \sqrt{m_3(d_1)^2 - 4m_1(d_1)m_3(d_1)}}{2m_1(d_1)}.$$

Using the value of $m_1(d_1)$, $m_2(d_1)$ and $m_3(d_1)$ we have

$$a < \frac{u^*}{2}\left(1 - \frac{2u^*}{\sqrt{d_1}} - \frac{(u^*)^2}{d_1}\right), \;\; a > \frac{u^*}{2}\left(1 + \frac{2u^*}{\sqrt{d_1}} - \frac{(u^*)^2}{d_1}\right)$$

the second of these two conditions is conflicting with (iii) and thus can not be satisfied. The first makes (iii) superfluous and we end up with two boundary curves in the $(a, b)-$plane which bound the turing space.

3 Numerical Examples

In this section, we solve Schnackenberg model by using finite difference method and simulate the result using MATLAB language platform. In order to find pattern from Schnackenberg model in two dimensional coordinates, we have to choose parameter values that satisfy the four conditions we have derived in the previous section. In this case, we consider (fix) the parametric values, $a = -0.55$, $b = 1.9$, $d_1 = 4.8$ while the domain size, parameter β and time are varies in different diagrams in the following subsections. Since β is a key factor, we always listed this scaler factor in captions.

3.1 Effects of Schnackenburg parameter on pattern formation

In Figs. 1, 2, 3 and 4, we show the effect of β on pattern formation of u and v. From these Figures, we have seen that if we increase the value of β, then the number of spots increases although other conditions remain same.

3.2 Effects of domain size on pattern formation

It is observed that in Figs. 5 and 6, the effect of domain size on pattern formation has significance change for both u and v. From these diagrams one can check that if we increase domain size, the number of spots increases while other conditions has no change.

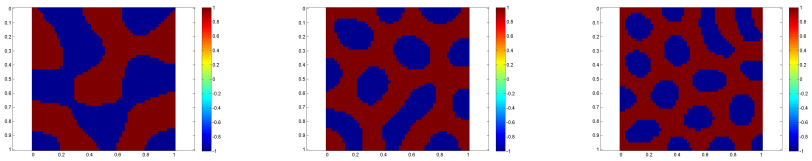

Fig. 1. Effect of β on pattern formation of u for (left) $\beta = 300$, (middle) $\beta = 600$ and (right) $\beta = 900$.

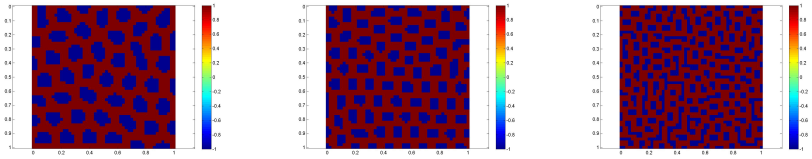

Fig. 2. Effect of β on pattern formation of u for (left) $\beta = 3000$, (middle) $\beta = 5000$ and (right) $\beta = 10000$.

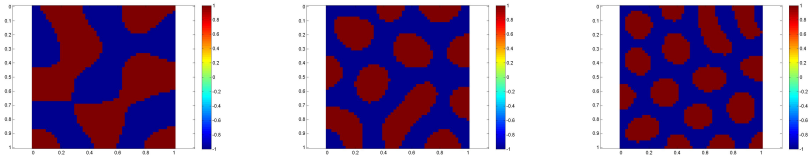

Fig. 3. Effect of β on pattern formation of v for (left) $\beta = 300$, (middle) $\beta = 600$ and (right) $\beta = 900$.

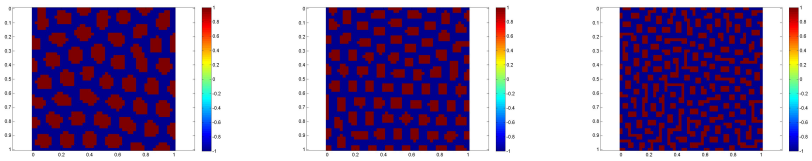

Fig. 4. Effect of β on pattern formation of v for (left) $\beta = 3000$, (middle) $\beta = 5000$ and (right) $\beta = 10000$.

3.3 Effects of time variation on pattern formation

In Figs. 7 and 8, we show the effect of time duration on pattern formation of u and v. By observing these figures it is seen that if we increase interval then the number of spots approximately remain same.

Remark 1. *It is noted that we have chosen all values of the parameters that satisfy turing stability conditions.*

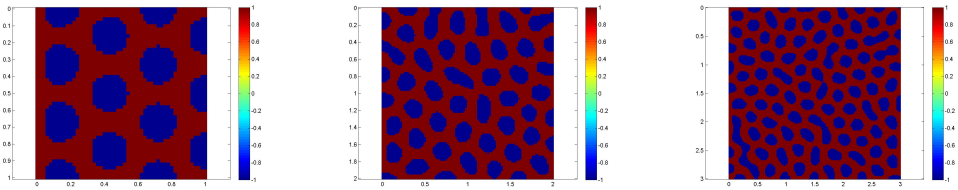

Fig. 5. Effect of domain size on pattern formation of u for $\beta = 800$ and (left) $x = 1$, (middle) $x = 2$ and (right) $x = 3$.

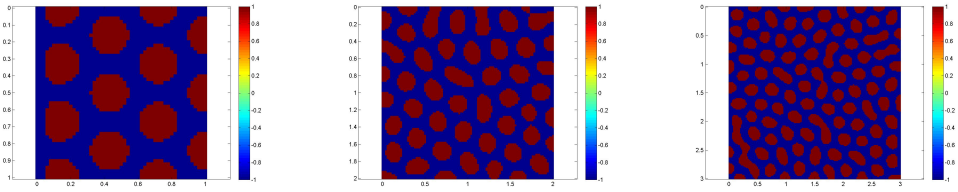

Fig. 6. Effect of domain size on pattern formation of v for $\beta = 800$ and (left) $x = 1$, (middle) $x = 2$ and (right) $x = 3$.

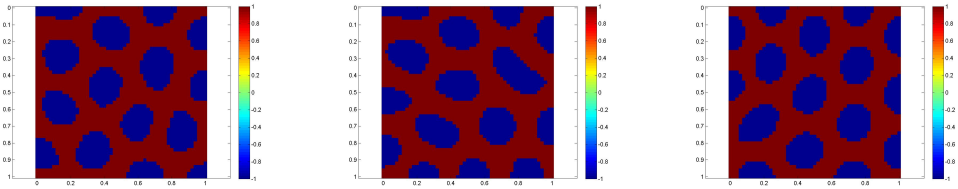

Fig. 7. Effect of time duration on pattern formation of u for $\beta = 800$ and (left) $t = 0.2$, (middle) $t = 0.3$ and (right) $t = 0.4$.

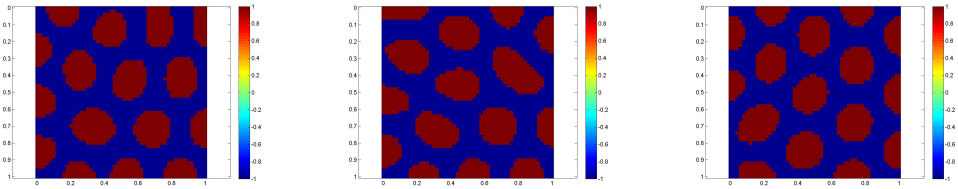

Fig. 8. Effect of time duration on pattern formation of v for $\beta = 800$ and (left) $t = 0.2$, (middle) $t = 0.3$ and (right) $t = 0.4$.

4 Summary and Conclusion

The main purpose of this paper is to present qualitative evidence in support of a reaction-diffusion mechanism for the laying down of the pre-patterns for animal markings. To do this we choose Schnackenberg model, solve this model by using finite difference method for different values of the parameters that used in the model. We have found that the parameter β has a great impact on pattern formation. Domain size has also a influence on pattern formation. There exists an intimate relation between geometry and size and the corresponding time scale for generation of pattern.

The sphere, on the other hand, has a more smooth, constant curvature throughout the surface. This allows the patterns to distribute evenly in comparison to the cone, torue or even cylinder. Thus, aside from the plane, it is easier to see how different kinetics affect the end result on this shape. The present study can be extended for the spherical geometrical shape for further study [13].

However, the role of geometry is shown to be important and the gradation from spots to stripes is an immediate consequence of domain size reduction as on tail and leg extremities. The intimate relation between geometry and size and the corresponding time scale required for generating heterogeneous structure as opposed to homogeneity gives a possible explanation for the uniformity in coat colour in very small animals and very large ones. The patterns discussed here only touch on the wealth of possibilities such simple two species reaction-diffusion systems can exhibit. In such a mechanism the genetic coding involvement could be a simple inhibitor-type switch.

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Competing Interests

Authors have declared that no competing interests exist.

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