MORPHOGENESIS

Abstract

In this essay we will investigate nonlinear evolution equations used to model morphogenesis and examine their linear stability. We will do this by using simplified models to find both stable and unstable solutions to first order and then second order differential equations by graphical analysis. We will also derive stability conditions for solutions.

1 Introduction

Morphogenesis describes the changing shapes of animals embryos and explains how biological patterns arise during growth [1]. Analysis into linear stability of a uniform state was first carried out by Alan Turing [2] where he suggested that a chemical reaction-diffusion system could explain morphogenesis. The reaction and diffusion gradient of two chemicals, known as morphogens, dictates the formation of cells, tissues and organ systems produces a cascade of pattern formation and is observed in nature for example in sea shells, fish, butterflies patterns and the skeletal system[3].

Morphogenesis is responsible for the print on animals such as leopard and tigers; where two chemicals spread over the animal inducing a non-uniform concentration of chemicals with one causing pigment and the other stopping pigment[4]. For example to create the colouring of cheetah two sets of chemical reactions criss-cross one another to produce spots. On the cheetahs tail the spotted pattern becomes rings towards the end as there is not enough room in the tail for the 2 pairs chemicals to cross over, so instead one set produces stripes. Melanin is produced to represent the spatial pattern of the morphogen gradient produced by the diffusion-reaction gradient.

In this essay will use Turing Model [2] to study morphogenesis. This simplified 1D model demonstrates the majority of the properties of the more complex models. We will examine the stability and characteristics of this model through using graphs, deriving equations and homogeneous tests.

2 Diffusion

In diffusion when there will be regions of high and low concentration of the chemicals, typically the two would spread evenly down the concentration gradient to equilibrium.This can be modelled using the following equation,

$$\frac{\partial u}{dt} = D\frac{\partial^2 u}{\partial x^2}, \tag{1}$$

where u is the density of the material, t represents time passed, D is the diffusion constant which dictates how fast particles diffuse. If the chemicals were left to diffuse there would be an even spread of the morphogens and, when producing pigment, no pattern would be produced. Therefore in this essay we will use Reaction-Diffusion equations which is a combination of the two morphogens and results in a clear morphogen gradient. Melanoblasts which are genetically determined cells, migrate to the surface of the embryo to become eventually specialized pigment cells known as melanocytes. Melanin is produced in pigment cells from morphogenesis synthesis which passes into hair follicles to give them their colour (4). The amount of melanin produced by the cells is dependent on the concentration of the morphogens.

3 Reaction-Diffusion Equations

The Turing model for a system of equations which describe the chemical reaction and diffusion between 2 chemicals u and v is as follows,

$$\begin{aligned} \frac{\partial u}{\partial t} &= f_1(u,v) + D_u \frac{\partial^2 u}{\partial x^2}, \\ \frac{\partial v}{\partial t} &= f_2(u,v) + D_v \frac{\partial^2 v}{\partial x^2}. \end{aligned} \tag{2}$$

Similarly to (1) $D_{u,v}$ represents the diffusion gradient. The functions f_1 and f_2 are non-linear functions which describe the reaction rate.

The Brusselator is a model of (2) for f_1 and f_2,

$$\begin{aligned} f_1(u,v) &= a - (b+1)u + u^2 v, \\ f_2(u,v) &= bu - u^2 v. \end{aligned} \tag{3}$$

We can express this in vector form as

$$\frac{\partial \mathbf{u}}{\partial t} = f(\mathbf{u}) + \mathbf{D}\frac{\partial^2 \mathbf{u}}{\partial x^2}, \tag{4}$$

where $\mathbf{D}$ is a diagonal diffusion matrix such that,

$$\mathbf{D} = \begin{pmatrix} D_u & 0 \\ 0 & D_v \end{pmatrix}. \tag{5}$$

These equations represent no specific reaction but we will use them to model the reactions throughout this essay. They are simplified models however demonstrate the fundamental characteristics of morphogenesis chemical reaction and diffusion.

4 Stationary Solutions

In this section we will carry out linear stability analysis, determine if solutions are stable or not and determine the conditions for stability. This is important because in morphogenesis spatially uniform state is stable is the absence of diffusion however becomes unstable due to diffusion, in our example this would effect the animals patterning. We must first assume there **Q1**
exists homogeneous static solutions to (3) independent of x and t. As this is a static solution all derivatives set to 0 therefore (3) becomes;

$$\begin{aligned} f_1(u_0, v_0) &= 0 \\ f_2(u_0, v_0) &= 0. \end{aligned} \tag{6}$$

To begin to find the homogeneous solutions u_0 and v_0 we will substitute (3) into (6) to give the following

$$a - (b+1)u_0 + u_0^2 v_0 = 0 \tag{7}$$

$$bu_0 - u_0^2 v_0 = 0. \tag{8}$$

Then (8) rearranges to $bu_0 = u_0^2 v_0$ which when divided through by u_0 gives us

$$b = u_0 v_0. \tag{9}$$

Substituting (9) rearranged as $u_0 = \frac{b}{v_0}$ into (7) and rearranging as follows gives,

$$\begin{aligned} a - (b+1)u_0 + bu_0 &= 0, \\ u_0 &= a. \end{aligned} \tag{10}$$

This gives our first part of the homogeneous solution (10) and we can now substitute this into (9) and rearrange to obtain a solution for v_0 as seen below

$$\begin{aligned} ba - a^2 v_0 &= 0 \\ a^2 v_0 &= ba \\ v_0 &= \frac{b}{a}. \end{aligned} \tag{11}$$

5 Stability of Solutions

Q2

Having found simple stationary solutions we must now examine their stability, this can be done by an infinitesimally small arbitrary perturbation of (u, v),

$$u = u_0 + \delta u(x,t) \qquad\qquad v = v_0 + \delta v(x,t), \tag{12}$$

substituting (12) into (2) gives us

$$\begin{aligned} \frac{\partial(u_0 + \delta u(x,t))}{\partial t} &= f_1(u_0 + \delta u(x,t), v_0 + \delta v(x,t)) + D_u \frac{\partial^2 (u_0 + \delta u(x,t))}{\partial x^2}, \\ \frac{\partial(v_0 + \delta v(x,t))}{\partial t} &= f_2(u_0 + \delta u(x,t), v_0 + \delta v(x,t)) + D_v \frac{\partial^2 (v_0 + \delta v(x,t))}{\partial x^2}. \end{aligned} \tag{13}$$

Considering what we know about the homogenous stationary solutions we can simplify (13) as we can separate derivatives and due to the nature of stationary solutions $\frac{\partial u_0}{\partial t} = 0$, $\frac{\partial v_0}{\partial t} = 0$, $\frac{\partial^2 u_0}{\partial x^2} = 0$ and $\frac{\partial^2 v_0}{\partial x^2} = 0$. Therefore (13) reduces to,

$$\begin{aligned} \frac{\partial u_0}{\partial t} &= f_1(u_0 + \delta u(x,t), v_0 + \delta v(x,t)) + D_u \frac{\partial^2 u_0}{\partial x^2}, \\ \frac{\partial v_0}{\partial t} &= f_2(u_0 + \delta u(x,t), v_0 + \delta v(x,t)) + D_v \frac{\partial^2 v_0}{\partial x^2}. \end{aligned} \tag{14}$$

Where $\delta \mathbf{u} = \left(\begin{smallmatrix} \delta u \\ \delta v \end{smallmatrix}\right)$, $\mathbf{D} = \left(\begin{smallmatrix} D_u & 0 \\ 0 & D_v \end{smallmatrix}\right)$ and $\mathbf{f}(\mathbf{u})$ represents (3) in vector form. To calculate the solution to this we must use a jacobian matrix and consider from (12) that we are calculating a small perbutation about stationary points such that

$$\mathbf{f}(\mathbf{u}) = \mathbf{A}\delta\mathbf{u}, \tag{15}$$

where the jacobian matrix is,

$$\mathbf{A} = \begin{pmatrix} \frac{\partial f_1}{\partial u_0} & \frac{\partial f_1}{\partial v_0} \\ \frac{\partial f_2}{\partial u_0} & \frac{\partial f_2}{\partial v_0} \end{pmatrix}. \tag{16}$$

Substituting (3) into (16) gives,

$$\mathbf{A} = \begin{pmatrix} 2u_0 v_0 - b - 1 & u_0^2 \\ b - 2u_0 v_0 & -u_0^2 \end{pmatrix}, \tag{17}$$

then given that we know $u_0 = a$ and $v_0 = \frac{b}{a}$ from (10) and (**??**) we can obtain a matrix in terms of a and b only,

$$\mathbf{A} = \begin{pmatrix} b - 1 & a^2 \\ -b & -a^2 \end{pmatrix}. \tag{18}$$

Therefore we have the final expression for our system after a small perturbation about the stationary points

$$\frac{\partial \delta \mathbf{u}}{\partial t} = \mathbf{A}\delta\mathbf{u} + \mathbf{D}\frac{\partial^2 \delta \mathbf{u}}{\partial x^2}. \tag{19}$$

5.1 Homogeneous Stability of Solutions

Q3

For simplicity in the following calculations to examine stability we will compute solutions which do not depend on x, therefore the $\mathbf{D}\frac{\partial^2 \delta \mathbf{u}}{\partial x^2}$ component of (19) disappears,this reduces the problem we are solving for to

$$\frac{\partial \delta \mathbf{u}}{\partial t} = \mathbf{A}\delta\mathbf{u}. \tag{20}$$

Solutions to (20) are of the form

$$\delta \mathbf{u} \quad = \mathbf{w}e^{\sigma t} \tag{21}$$

where $\mathbf{w}$ is a constant vector, σ is a constant we will solve for and $\mathbf{w}$ is a vector of arbitrary length specifying direction. Substituting (21) into (19) gives,

$$\mathbf{Aw} \quad = \sigma \mathbf{w}. \tag{22}$$

We can see clearly that σ is an eigenvalue of the matrix, therefore we can solve the following equation for a solution of σ

$$\det(\mathbf{A} - \mathbb{1}\sigma) = 0. \tag{23}$$

we can solve this to find the eigenvalue solutions, first by expanding (23), substituting in A and rearranging give the characteristic polynomial of $\mathbf{A}$,

$$det(\mathbf{A} - \mathbb{1}\sigma) \quad = \quad \sigma^2 + \sigma(a^2 + 1 - b) + a^2. \tag{24}$$

Now using the quadratic formula we can now solve (24) for σ,

$$\sigma^{\pm} \quad = \quad \frac{(b - 1 - a^2) \pm \sqrt{(-(b-1-a^2))^2 - 4a^2}}{2}. \tag{25}$$

Next we will consider the following components of a matrix and use them to simplify (25), where tr$\mathbf{A}$ is trace of matrix A and det$\mathbf{A}$ is the determinant of matrix A,

$$tr\mathbf{A} \quad = \quad b - 1 - a^2 \tag{26}$$

$$det\mathbf{A} \quad = \quad a^2. \tag{27}$$

Then substituting (26) and (27) into (25) gives our final solutions for σ

$$\sigma^{\pm} = \frac{tr\mathbf{A} \pm \sqrt{(tr\mathbf{A}^2) - 4det\mathbf{A}}}{2}. \tag{28}$$

Now we can solve this equation generally and specifically for (3) when a=2 , we will also examine the stability of the solutions graphically. Q4

Solutions $\sigma^{\pm}$ are of the following forms:

- We can see that if (28) has a complex component then

$$tr\mathbf{A}^2 - 4det\mathbf{A} \qquad < 0, \tag{29}$$

$$tr\mathbf{A}^2 \quad < 4det\mathbf{A}. \tag{30}$$

  Substituting in (27) and (26) for $a = 2$, this condition implies $1 < b < 9$.

- Furthermore can see that if $Re(\sigma) < 0$ then $tr\mathbf{A} < 0$ which corresponds to $b < 5$ for our specific solutions, and likewise when $Re(\sigma) < 0$, $tr\mathbf{A} < 0$ and $b > 5$.

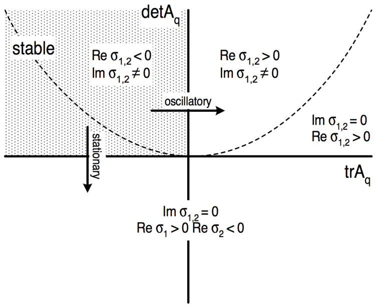

Figure 1:
Graph summarizing the stability of solutions of σ and shows the general solutions for (28) in terms of det**A** and tr**A** [5].

- On the boundaries when $tr\mathbf{A}^2 = 4det\mathbf{A}$ and $b = (1 or 9)$ then the solutions are of the form $\sigma^+ = \sigma^-$, negative or positive depending on which side of $tr\mathbf{A}$ they lie.
- Finally when $tr\mathbf{A} = 0$, $b = 5$ then the solutions are of the form $\sigma+ = -\sigma^+$ and have no real component.

Q5

As we can see clearly in the table below that our calculations discussed previously correspond to the type σ solutions for certain b values.

a	b	u_0	v_0	trA	$\sqrt{trA^2 - 4det\mathbf{A}}$	σ^+	σ^-
2	0	2.0	0.0	-5.0	± 3.0	-1.0	-4.0
2	1	2.0	0.5	-4.0	0.0	-1.0	-1.0
2	3	2.0	1.5	-2.0	$\pm 3.46i$	-1.0+1.73i	-1.0-1.73i
2	5	2.0	2.5	0.0	$\pm 4i$	2i	-2i
2	8	2.0	3.0	3	$\pm 2.65i$	1.5+1.3i	1.5-1.3i

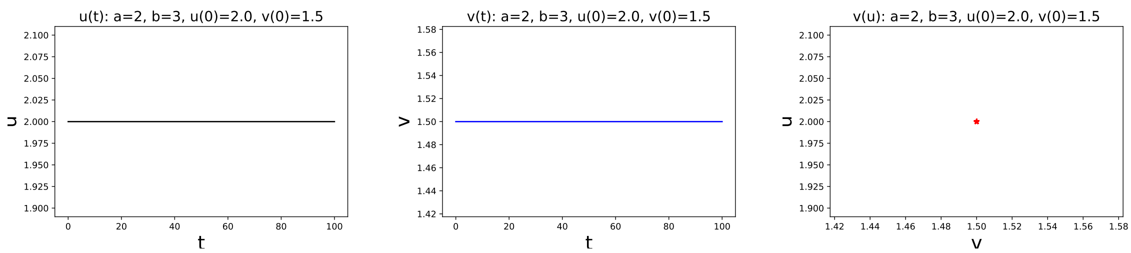

Figure 2:
Graphs showing homogeneous static solutions v_0 and u_0 before the perturbation in (12). Equations are clearly stable as do not evolve over time and remain constant. Confirms the calculations for (10) and (11) are correct.

When our solution is unstable $\delta\mathbf{u}$ can become very unstable and large, and contradict our initial assumption (12). This is one limitation of our analysis as we do not know with complete certainty that (12) remains true. To calculate the real solution we want to take $D_u = D_v = 0$ (which essentially assumes u and v are independent of x to solve the system of equations (2) and (3). This gives us the pair of ordinary differential equations that can be easily solved numerically,

$$\frac{\partial u}{\partial t} = a - (b+1)u + u^2 v \qquad \frac{\partial v}{\partial t} = bu - u^2 v. \tag{31}$$

The following graphs discuss the stability of the solutions to (31) for b=(3,5,8) when perturbed from the homogeneous static solutions by 0.1. All produce graphs identical to (2) for the homogeneous static values and therefore have been omitted for b=(5,8).

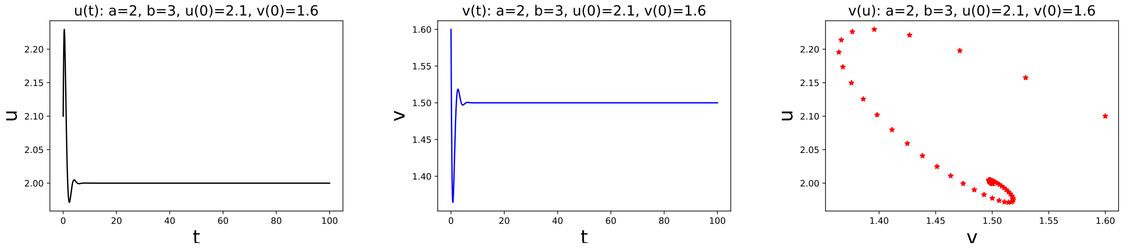

Figure 3:
Graph shows u and v initially displaced from the stable solutions by 0.1 and then decreases exponentially to the homogeneous u_0 and v_0 values shown in the table. We can see in the v(u) plot that the values converge in a spiral to our solution.

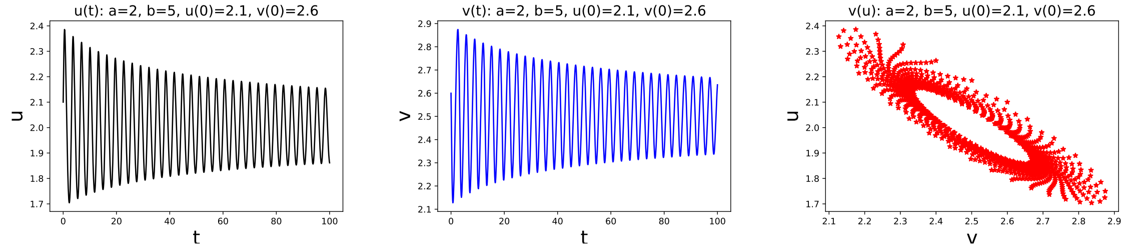

Figure 4:
Graphs show u and v initially displaced from the stable solutions by 0.1 and then oscillating with decreasing amplitude about the homogeneous solutions. The functions do not converge, this can be seen in the plot v(u) which shows the value of u and v spiralling to a circle and never becoming stationary. The increasing thickness of the red line shows the v and u spiral inwards at a decreasing rate of convergence. It is unclear from this graph whether it converges to a solution or not so we will produce another plot with different conditions, see fig(5) .

Examining (21) the generally linear solutions of $\delta\mathbf{u}$ can be given by,

$$\delta\mathbf{u} = C^{+}\mathbf{w}^{+}exp(\sigma^{+}t) + C^{-}\mathbf{w}^{-}exp(\sigma^{-}t), \tag{32}$$

Q4

where $\mathbf{w}^{\pm}$are solutions of (22) corresponding to $\sigma^{\pm}$, $C^{\pm}$ are complex coefficients such that$\delta\mathbf{u}$ is real. From this we can make the following conclusions, which correspond to what is observed in fig(3), fig (4), fig(5) and fig(6);

- If $\sigma^{\pm}$ are both complex then they must be conjugates. This will introduce trigonometric functions as $e^{i\theta} = cos(\theta) + isin(\theta)$, in this case they will correspond to rotations in the complex plane. $\delta\mathbf{u}$ will converge exponentially to 0 if Re($\delta\mathbf{u}$)<0 and diverge if Re($\delta\mathbf{u}$) > 0. This can be observed in fig(6).
- If either σ^{-} or σ^{+} is positive then $\mathbf{u}$ diverges exponentially from the static solution after a small perturbation and $\delta\mathbf{u}$ increases rapidly.
- If $\sigma^{\pm}$ are both real and negative then homogeneous solution is stable even when perturbed, and $\delta\mathbf{u}$ decreases exponentially to 0. This can be observed in fig(3).

This gives us conditions for homogeneous stability as we saw previously that when $\sigma^{\pm}$ are both real and negative are both real and negative then,

$$tr\mathbf{A} < 0. \tag{33}$$

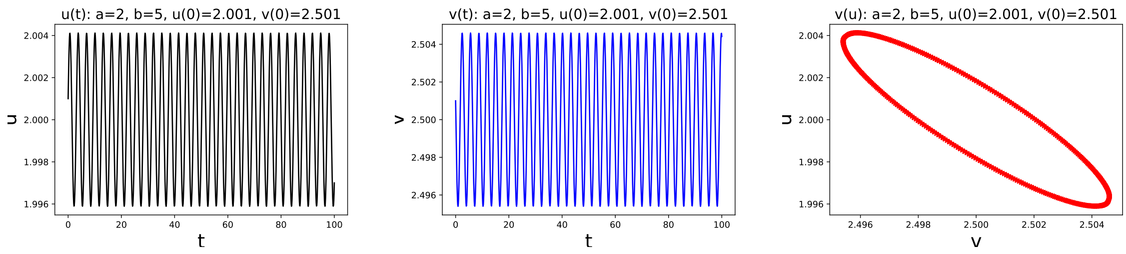

Figure 5:
Graphs show same a b values as in (4) however the perturbation is 100 times smaller. These diagrams clearly show that the functions do not converge so are unstable solutions. The plot of v(u) shows a bold red circle as the values repeatedly oscillate with the same amplitude.

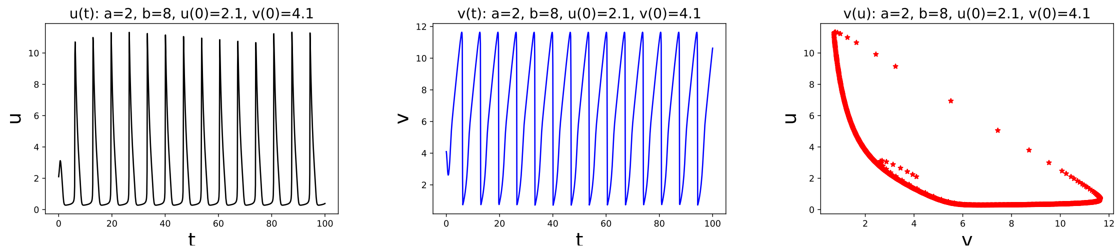

Figure 6:
Graphs showing u and v values diverging exponentially once perturbed so are not stable. The plot of u(v) shows a bold red curve from (u_{max}, v_{min}) to (u_{min}, v_{max}) which corresponds to the oscillations shown in the first two graphs.

Also when $\sigma^{\pm}$ are complex conjugates then,

$$det\mathbf{A} > 0, \tag{34}$$

this condition also requires $Re(\sigma) < 0$ which implies $tr\mathbf{A} < 0$ again.

5.2 General Stability Analysis

The particular solution $\delta\mathbf{u}$ is time and spatially dependent and for a more general solution it can be expressed as,

$$\delta\mathbf{u} = \delta\mathbf{u}_q e^{\sigma_q t} e^{iqx}, \tag{35}$$

where $\delta\mathbf{u}_q$ is a constant vector and σ_q and q are also constants representing growth rate and wave number respectively. We can now substitute (35) into (19) and simplify to give,

$$\begin{aligned} \frac{\partial(\delta\mathbf{u}_q e^{\sigma_q t} e^{iqx})}{\partial t} &= \mathbf{A}(\delta\mathbf{u}_q e^{\sigma_q t} e^{iqx}) + \mathbf{D}\frac{\partial^2 \delta(\delta\mathbf{u}_q e^{\sigma_q t} e^{iqx})}{\partial x^2}, \\ \sigma_q(\delta\mathbf{u}_q e^{\sigma_q t} e^{iqx}) &= \mathbf{A}(\delta\mathbf{u}_q e^{\sigma_q t} e^{iqx}) + q^2(\delta\mathbf{u}_q e^{\sigma_q t} e^{iqx}), \\ \sigma_q \delta\mathbf{u} &= \delta\mathbf{u}(\mathbf{A} - \mathbf{D}q^2). \end{aligned} \tag{36}$$

We can see that $\delta\mathbf{u}$ is an eigenvalue of the matrix $\mathbf{B}$, therefore similarly to (23) to find a solution we must impose the following condition,

$$\det(\mathbf{A} - \mathbf{D}q^2 - \mathbb{1}\sigma) = 0. \tag{37}$$

For simplicity in further calculations let,

$$\mathbf{B} = \mathbf{A} - \mathbf{D}q^2 = \begin{pmatrix} \mathbf{A}_{11} - D_u q^2 & \mathbf{A}_{12} \\ \mathbf{A}_{21} & \mathbf{A}_{22} - D_v q^2 \end{pmatrix}, \tag{38}$$

then by following similar calculations to (23), (24) and (25) we have

$$\sigma_{q^{\pm}} = \frac{tr\mathbf{B} \pm \sqrt{(tr\mathbf{B}^2) - 4det\mathbf{B}}}{2}. \tag{39}$$

From (36) we can deduce that the constant vector $\mathbf{u}_q$ and growth rate σ_q form an eigenvalue pair for $\mathbf{B}$. For a given q there are 2 linearly independent eigenvectors denoted by $\delta\mathbf{u}_{iq}$ and corresponding eigenvalues σ_{iq}, for $i = 1, 2$. The particular solution with wave number q will be;

$$(c_{1_q}\delta\mathbf{u}_{1q}e^{\sigma_{1q}t} + c_{2_q}\delta\mathbf{u}_{2q}e^{\sigma_{2q}t})e^{iqx}, \tag{40}$$

where c_{iq} are complex coefficients. Using (39) we can refine our conditions for stability in (34) and (33) as they now become,

$$tr\mathbf{B} = \mathbf{A}_{11} + \mathbf{A}_{22} - (D_u + D_v)q^2 < 0 \tag{41}$$

$$det\mathbf{B} = (\mathbf{A}_{11} - D_u q^2)(\mathbf{A}_{22} - D_v q^2) - \mathbf{A}_{12}\mathbf{A}_{21} > 0. \tag{42}$$

Remembering that diffusion constant D_i and q^2 are positive we can simplify (41) to ,

$$\mathbf{A}_{11} + \mathbf{A}_{22} < 0. \tag{43}$$

Setting D_i to 0 in (41) and (42) we can calculate the conditions for linear stability in the absence of diffusion,

$$\begin{aligned} \mathbf{A}_{11} + \mathbf{A}_{22} &< 0, \\ \mathbf{A}_{11}\mathbf{A}_{22} - \mathbf{A}_{12}\mathbf{A}_{21} &< 0. \end{aligned} \tag{44}$$

We now need to determine when $\det(\mathbf{A})$ changes sign from positive to negative for all q. As seen in (42) $\det\mathbf{B}$ is a parabola in q^2 and is positive when q is large. Now to find the minimum we can do the following calculation,

$$\frac{\mathrm{d}det(\mathbf{B})}{\mathrm{d}(q^2)}|_{q=q_m} = 2D_u D_v q^2 - D_u\mathbf{A}_{22} - D_v\mathbf{A}_{11} = 0, \tag{45}$$

therefore,

$$q^2_{min} = \tfrac{D_u\mathbf{A}_{22} + D_v\mathbf{A}_{11}}{2D_u D_v}. \tag{46}$$

Substituting (46) back into (42) gives,

$$det(\mathbf{B}(q_m)) = \mathbf{A}_{11}\mathbf{A}_{22} - \mathbf{A}_{21}\mathbf{A}_{12} - \left(\frac{(D_u\mathbf{A}_{22} + D_v\mathbf{A}_{11})^2}{4D_u D_v}\right) < 0, \tag{47}$$

therefore,

$$D_u\mathbf{A}_{22} + D_v\mathbf{A}_{11} < 2\sqrt{D_u D_v(\mathbf{A}_{11}\mathbf{A}_{22} - \mathbf{A}_{21}\mathbf{A}_{12})}. \tag{48}$$

Due to (44) we know that the term inside of the square root of (48) is always positive. From the Brusselator model we have $\mathbf{A}_{22} < 0$ and $\mathbf{A}_{11} > 0$. The condition (48) can be expressed as diffusion lengths,

$$\begin{aligned} l_1 &= \sqrt{\frac{D_u}{\mathbf{A}_{11}}}, \\ l_2 &= \sqrt{\frac{D_v}{-\mathbf{A}_{22}}}. \end{aligned} \tag{49}$$

Now dividing (48) by D_vD_u and substituting in (49) gives us,

$$q_m^2 = \frac{1}{2}\Big(\frac{1}{l_1^2} - \frac{1}{l_2^2}\Big) < 2\sqrt{\frac{\mathbf{A}_{11}\mathbf{A}_{22} - \mathbf{A}_{21}\mathbf{A}_{12}}{D_vD_u}}, \tag{50}$$

It can also be shown by linear superposition of all solutions of the type (36) (similarly as with (32)will giver the general linear solutions of the form,

$$\delta\mathbf{u} = \sum_q \Big[\delta\mathbf{u}_q^+ e^{\sigma_q^+ t}(C_{+q}^+ e^{iqx} + C_{-q}^+ e^{-iqx}) + \delta\mathbf{u}_q^- e^{\sigma_q^- t}(C_{+q}^- e^{iqx} + C_{-q}^- e^{-iqx})\Big]. \tag{51}$$

We can see that $C^{\pm}\pm q$ are Fourier coefficients of the perturbation $\delta\mathbf{u}$, as with (58) we must impose some boundary conditions so specify the solution. We assume there is a finite domain from 0 to L and will impose that chemicals bounce off the edge of the domain when they reach it. This conditions for all times t can be expressed mathematically as,

$$\frac{\partial\delta\mathbf{u}}{\partial x}|_{x=0} = \frac{\partial\delta\mathbf{u}}{\partial x}|_{x=L} = 0. \tag{52}$$

We can consider $\mathbf{w}_q^- = 0$ or $\mathbf{w}_q^+ = 0$ independently as (52) is true for all time. Therefore implementing the conditions of (52) on (58) means that,

$$C_{+q}^+ e^{iq0} - C_{-q}^+ e^{-iq0} = 0, \tag{53}$$

$$C_{+q}^+ e^{iqL} - C_{-q}^+ e^{-iqL} = 0, \tag{54}$$

and similarly for $C_{\pm q}^-$. These conditions also restrictions the values q can take. Therefore (53) implies $C_{+q}^+ = C_{-q}^+$ and (54) implies $iqL = in\pi$ therefore,

$$q_n = \frac{n\pi}{L}, \tag{55}$$

where q is wave number and n is an arbitrary constant. Considering we know similarly that $C_{+q}^- = C_{-q}^-$ substituting (55) into (51) gives,

$$\delta\mathbf{u} = \sum_{n=0}^{\infty} \Big[C_{q_n}^+ \delta\mathbf{u}_{q_n}^+ e^{\sigma_{q_n}^+ t} + C_{q_n}^- \delta\mathbf{u}_{q_n}^- e^{\sigma_{q_n}^- t}\Big] \cos\big(\frac{n\pi x}{L}\big). \tag{56}$$

6 Numerical Integration of the Brusselator

To improve our understand of the Brusselator model we need to solve (2) and (3). We can do this by transforming (2) into discrete system of equation, given that for any $u(x)$

$$\frac{d^2u}{dx^2} \approx \frac{u(x+\Delta x) + u(x-\Delta x) - 2u(x)}{\Delta x^2}, \tag{57}$$

we can approximate (2) to,

$$\begin{aligned} \frac{du_i}{dt} &= D_u\frac{u_{i+1} + u_{i-1} - 2u_i}{\Delta x^2} + f_1(u_i, v_i), \\ \frac{dv_i}{dt} &= D_u\frac{v_{i+1} + v_{i-1} - 2v_i}{\Delta x^2} + f_2(u_i, v_i). \end{aligned} \tag{58}$$

The following graphs examine the solutions to (2) and (3) by solving (58) numerically by the 4^{th} order Runge-Kutta method, using the boundary conditions that $\frac{\partial u}{\partial x}$ and $\frac{\partial v}{\partial x}$ vanish on the edge of the domain. **Q6**

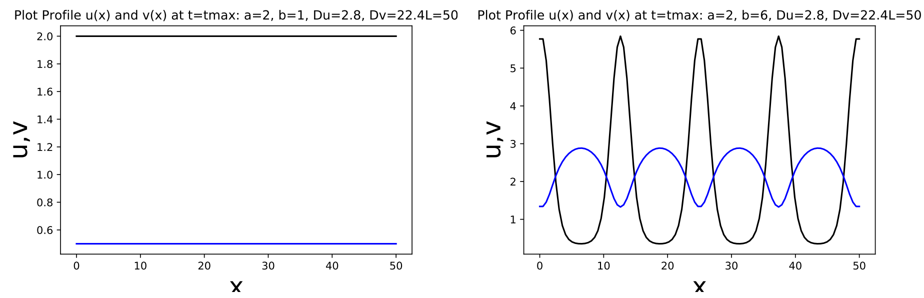

Figure 7:
Graphs showing how concentration of two chemicals u and v evolve over our 1 dimension x. We can see that when $b = 1$ the concentration of the chemicals do not change. Whereas for our unstable solution $b = 6$ the concentration of the two chemicals change across the displacement at t_{max}.

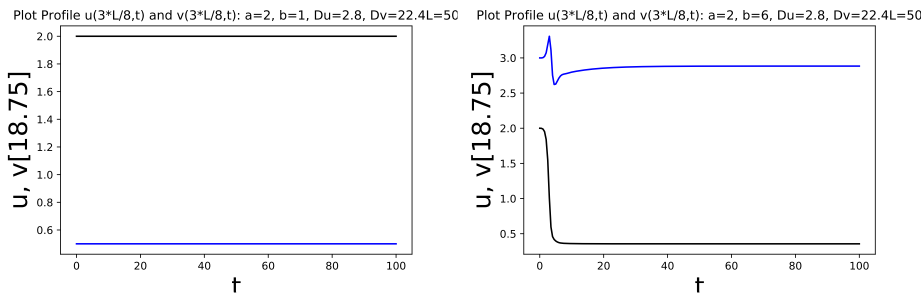

Figure 8:
Graphs showing how concentration of two chemicals u and v evolve over time. As shown previously when $b = 1$ this is an stable solution and we can see clearly the concentrations of each chemical remains constant. Where as when $b = 6$ the values fluctuate and then settle over time, to a solution different to their initial value.

The results shown in (7) and (8) demonstrate why we are interested in finding the unstable solution for (2) in this essay as change in concentration of the two chemicals produces the pattern on animals, such as a zebras stripes. If the equation was stable then no pattern would be produced. The graphs in (7) and (8) also show that as the name suggests, the homogeneous stable solutions remain constant as they evolve over time whereas the unstable solutions develop to other values, andD_v fluctuate over local maximum and minimum values at t_{max}. Calculating the difference between maximum and minimum values of u and v gives us the amplitude of the spacial oscillations of the solutions as shown below,

$$\begin{aligned} A_u &= \max(u(x)) - \min(u(x)), \\ A_v &= \max(v(x)) - \min(v(x)). \end{aligned} \tag{59}$$

The graphs in fig(9) generate figures of (59) as functions of shows plots of A_v and A_u from (59) as a function of b for different D_u values. We can observe that as the difference between D_u and D_v decreases the the stability of the solutions also decrease.

Examining fig(9) we can see that for $D_u = 1$ the $A_v A_v$ solutions are static and equal to zero while the value of b satisfies the conditions (48) and (33). When colouring the points according to stability or instability we have this conditions, but in fact the solutions of $A_v A_v$ are stable whilst they equal 0. We can see from the second two graphs that as D_u increases the accuracy of the stability conditions for decrease. For example when $D_u = 7$ the solutions are stable until $b = 4$ however they no longer satisfy the stability conditions. This highlights an inaccuracy with the theoretical predictions.

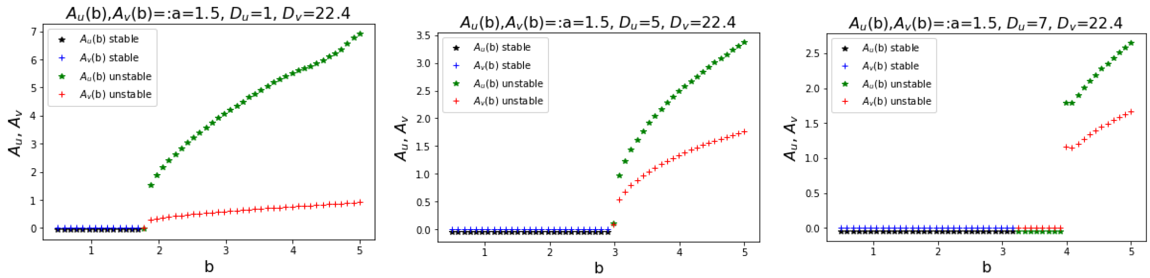

Figure 9: Plots of A_v and A_u from (59) as a function of b for different D_u values

7 Conclusions

In this project we used the Brusselator model of morphogenesis to examine stable and unstable solutions of first and second order differential equations graphically. This enabled us to also analyze the stability conditions for solutions, both generally and specifically for our model. We have shown how in practice the morphogens should be unstable so as to produce a fluctuating concentration gradient. If the morphogens are stable then a pattern will not be made on the animal.

One limitation was that we only studied the chemical reactions in a simplified model in 1D whereas realistically they are occurring in 3D. We could of improved this by using a model where $\mathbf{u}$ was a function of (x, y, z, t). Also we carried out detailed analysis into the solutions of σ however for plotting graphs we used simpler derivations. The result of this inaccuracy can me seen in the discrepancies in fig(9).

Comparing calculations with varying diffusion coefficients, highlights that diffusion can be a destabilizing influence. We can also conclude from (50) that l_2 must be much larger than l_1 to ensure instability, this is known as the Turing condition [2]. Essentially, as observed in fig(9) the greater the difference in diffusion constants, the more unstable the equation is as the diffusion length is therefore longer. When applied in nature in the formation of patterns on animals, as the two chemicals react (one propagating pigment production and the other inhibiting it) the difference of diffusion coefficients of the two chemicals needs to be large in order to ensure instability and therefore pattern formation.

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