A mathematical model for butterfly wing patterns.

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This project deals with the implementation and testing of a model for butterfly wing pattern formation proposed by Murray [1].

In this project we will consider models based on two main mechanisms, the diffusion of a substance called morphogen on the wings, and the corresponding creation of a colour-altering gene-product. We will further show how variation of the models parameters alters the results.

1 The Model

Experiments by Kuhn, Engelhart(1933) and Schwartz(1962) propose that characteristic crossbands of pigment on butterfly wings arise from a wave of morphogen emanating from the edges of the wing [1]. This wave is thought to come from initial concentrations of morphogen that diffuse over the wing in early pupal development. To explain the sharp contrasts in butterfly patterns there was proposed a biological switch mechanism. The thought was that the morphogen concentration on the wing started production of a certain gene-product which controlled the later pigment development in a cell. Once a cell had reached a critical value of morphogen concentration , the gene-product would no longer degrade to zero, but to a positive value. A cell in which the gene product reached such a steady-state is thought to be a coloured cell.

The proposed governing equation for the morphogen concentration, S is:

$$\frac{\partial S}{\partial t} = D\nabla^2 S - K\gamma S, \tag{1}$$

where K is a constant determining the speed of degradation, γ is a size factor and D is a constant determining the speed of diffusion.

The gene product, g, is governed by the equation:

$$\frac{\partial g}{\partial t} = \gamma(k_1 S + \frac{k_2 g^2}{1+g^2} - k_3 g) \tag{2}$$

The equation for the change of g can be chosen rather freely, as long as it has 2 non-negative stable steady-states.This makes g work as a switch.

To test this model one should solve these equations on a domain resembling a butterfly wing. We make the further assumption that there is no diffusion across the veins of a butterfly wing, so

$$\frac{\partial S}{\partial \vec{n}}_{\Omega} = 0 \tag{3}$$

where Ω is the boundary and $\vec{n}$ is the normal vector of the boundary.

2 Difference formula

To solve the equations for the morphogen and gene-product concentrations given the boundary conditions and initial values I have used finite difference schemes. Here a continuous domain is reduced to a set of points in a grid, so that there is only a finite number of values to keep track of. Differentiation then becomes an approximation using finite differences instead of infinitesimals[2].

The form of a derivative depends on the form of the grid, which in turn often reflects a particular set of coordinates used. In cartesian coordinates a laplacian takes the form

$$\nabla^2 = \frac{\partial}{\partial^2 x} + \frac{\partial}{\partial^2 y} \tag{4}$$

which can be approximated using a second order central difference method. It can be shown through Taylor-expansion that this approximation has an error of leading term $\mathcal{O}(h^2)$ where h is the step size between grid-points[2].

Analogously, a laplacian can be solved in a grid based on polar coordinates by changing the infinitesimals in the laplacian in polar coordinates to finite differences.

The boundary condition of no diffusion along veins can be achieved in the numerical solution by using "ghost nodes". These are nodes which lie on the boundary and have values which do not depend on concentration, but are chosen specifically so that the normal derivative of the neighbouring interior node vanishes, thus satisfying the boundary condition[2].

A simple Euler method was used to solve the differential equations, as the primary interest of the results were their qualitative nature.

3 Implementation

Inspired by Murray, his sketched results were reproduced numerically in a grid using polar coordinates. Figure 2 shows the gene product stabilized after an initial concentration of 10 morphogen units was placed in a narrow band on each edge. The green area is where the gene-product has stabilized to a positive value, and the yellow area is a hole, meaning no diffusion could happen through there, and all morphogen flowing into it is lost. Figures 1 and 2 reproduce the results Kuhn and Engelhart got by cauterizing butterfly-wings in different areas in the pupal stage.

The γ parameter in the expression in equation 2 is a measure of the domain size and thus we can simulate domains of varying sizes by altering it. In Figure 3 the parameter γ is altered. An increasing γ artificially increases the size of the domain while not actually enlarging the grid. We can thus see that the coloured cells cover less of the wing for increasing γ, as expected[1].

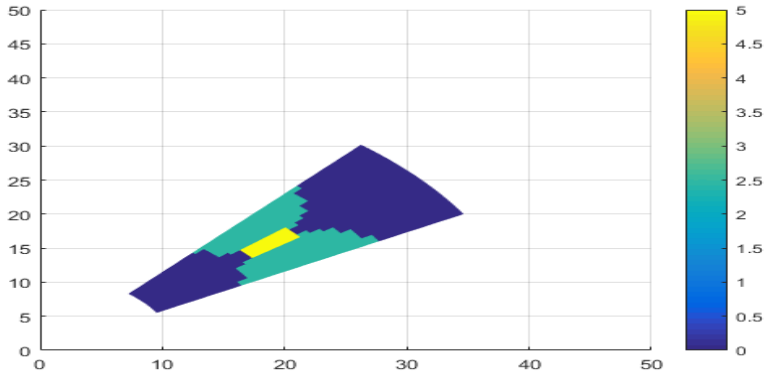

Figure 1: Gene-product after initial concentration of 10 along the edge-cells. The cauterization is here performed such that no band could form.

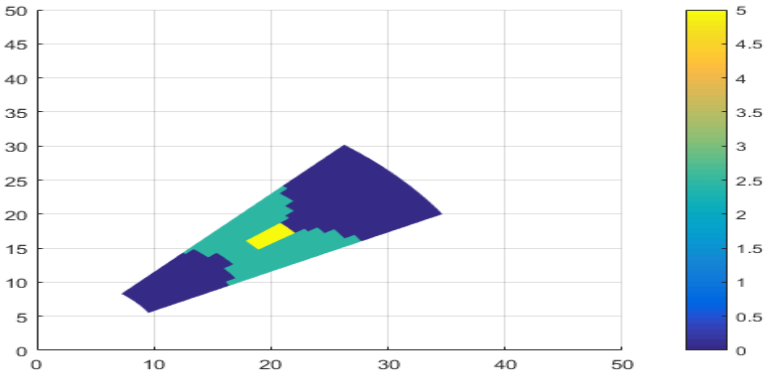

Figure 2: Gene-product after initial concentration of 10 along the edge-cells. The cauterization is here performed farther out in the wing than in figure 1, thus allowing a band to be formed

3.1 New Domain

To show how these cells could be combined to give a whole butterfly wing I chose to etch out a butterfly wing in a square grid. The borders of the domain where obtained by projecting Lagrange Polynomials with chosen interpolation points on the grid. Figure 4 shows the results of this.

Murray theorizes that the process of morphogen diffusion may happen multiple times in the development of butterfly wings with differing morphogen-agents and gene-products. This may result in the mosaic and overlay seen in real butterflies.

In Figure 5 is a model where 2 different morphogen concentrations have been superimposed.

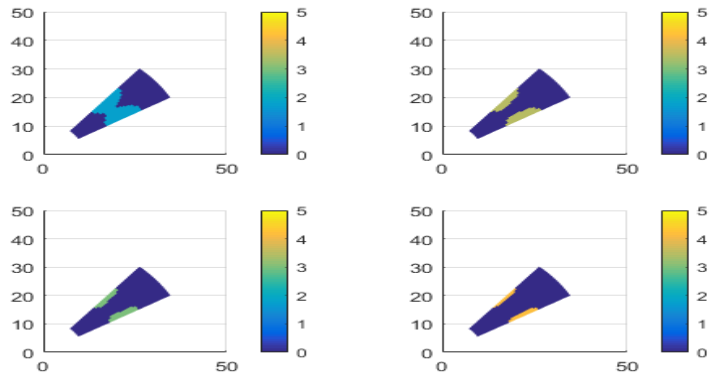

Figure 3: Here the wing is plotted for varying γ, while all other paramters) are fixed. Top left γ=1, top right γ=6, bottom left γ=10 and bottom right γ=40. $k_1 = 10$, $k_2 = 100$, $k_3 = 10$, $K = 0.5$.

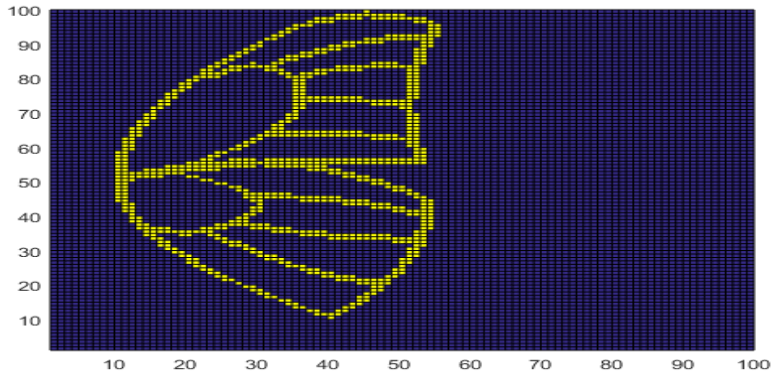

Figure 4: The boundary obtained by interpolation between chosen points

4 Conclusion

The mathematical model proposed by Murray surely has the power to reproduce some patterns of butterfly wings. The diffusion mechanism coincides nicely with the real behaviour of wing-patterns with holes. Through the introduction of more morphogen agents it has the capacity to explain even more complex patterns. By having these morphogens affect each other, which is not unreasonable, it is plausible that even more patterns could be produced. This model is however rather simple in that it treats a butterfly wing as a homogenous domain, as it may in reality have some asymmetries which are better described by a more elaborate mathematical model.

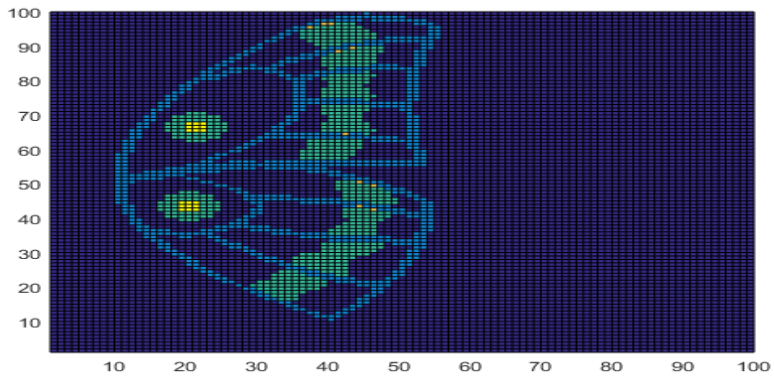

Figure 5: A butterfly wing with 2 different initial concentrations superimposed. The green regions correspond to cells with gene-product from the first morphogen, while the yellow points correspond to gene-product from the second

References

[1] J.D. Murray. Mathematical Biology: 1. An Introduction, Third Edition. 2002.

[2] B. Owren, E. Celledoni. Class notes for: TMA4212 Numerical solution of partial differential equations with finite difference methods.2014. https://folk.ntnu.no/elenac/numdiffdm/notat.pdf