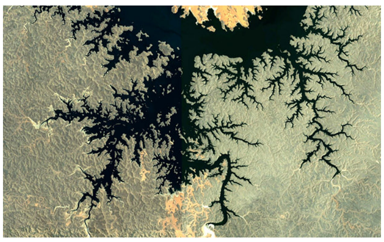
1 Pattern Formation

The last two examples of spatially distributed oscillators serve as a good intro to one of the most important aspects in complex systems: pattern formation. By pattern formation we mean that certain systems have the ability to self-organize into spatially structured states from intitially unstructured or spatially homogenous states. This behavior takes place all over the place, in physics in chemistry in biology in social science etc. Here we will discuss the basic ingredient that are necessary for these processes to occur. One of the patterns that we see in any desert or any beach are ripples in the sand:

One can understand the basic ingredients for pattern formation in this system. Laminar flows of wind move accross the sand and move individual sand grains with it. Slight pertubations in the surface have a higher likelihood of collecting these grains increasing the magnitude of the pertubation and thus increasing the likelihood of catching more sand. This is a positive feedback effect which is necessary in almost all pattern forming systems. This example also shows that one needs to put energy into pattern forming systems, in this case wind. Right behind the pertubation a dip forms, as the probability of grains collecting there becomes lower. Of course the increasing hills cannot increase forever and will be eroded at the top. This is the negative feedback that is also required in pattern formation.

The same thing happens when river beds are formed. There's a continuous precipitation that falls onto the land and the water streams it forms follows gravity downhill. Small streams carve a path and the following water will preferentially follow those paths, too digging deeper into the soil. Of course this can't go on foverever. The process can produce valleys that collapse and new valleys will form:

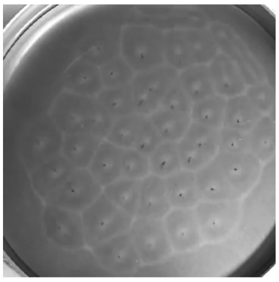


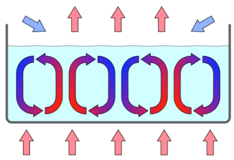
Let's discuss a few examples that all show these type of ingredient.

1.1 Examples of pattern forming in nature

1.1.1 Physics

The most known example of spontaneous pattern formation in physics is probably Benard convection. This happens when a liquid is heated from below at such a high rate that the heat cannot dissipate through the system fast enough. In this case convetion rolls or cells emerge that transport the heat to the cooler regions of the liquid where heat is given off. The cooled liquid then gets pushed to the bottom to be reheated:





This experiment can be easily done by heating oil on the stove and adding metal dust to the oil. Again we have to add energy to the system and once certain parts of the liquid start moving upwards this process will be accelerated and other regions have to move downward to keep the liquid in place. Images of the suns surface show granules which are exactly these kind of convetion pockets.

1.1.2 Chemistry

There's an abundance of chemical reactions that, if they occur in a not-well-stirred scenario, have the potential of generating patterns. One such reaction, the most famous one, is the Belousov–Zhabotinsky reaction. This reaction uses essentially five reactions,

	Reaction	Rate
(O1)	$A + Y \to X + P$	$k_3 = k_{R3}[H^+]^2 AY$
(O2)	$X + Y \to 2P$	$k_2 = k_{R2}[H^+]XY$
(O3)	$A + X \to 2X + 2Z$	$k_5 = k_{R5}[H^+]AX$
(O4)	$2X \to A + P$	$k_4 = k_{R4}X^2$
(O5)	$B + Z \to \frac{1}{2} f Y$	$k_0 BZ$

in which particular chemicals in it start oscillating in their concentration. If the reaction takes place in a petri dish, spiral and target wave form. This is because in its essence this reaction is an activator inhibitor system in which an autocatalytic reaction increases the abundance of a chemical which in turn increases the abundance of a chemical that turns this reaction off. Here's a snapshot of a pattern that the BZ reaction can generate:

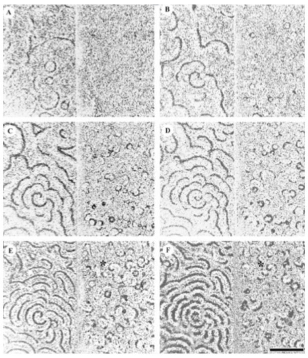
This looks very similar to the patterns we generated with the spatially distributed pulse-coupled oscillators. And in fact the mechanisms in both systems are very similar. We will come back to this later.

1.1.3 Biology

Biology is full of pattern forming systems, so we are going to look at numerous examples.

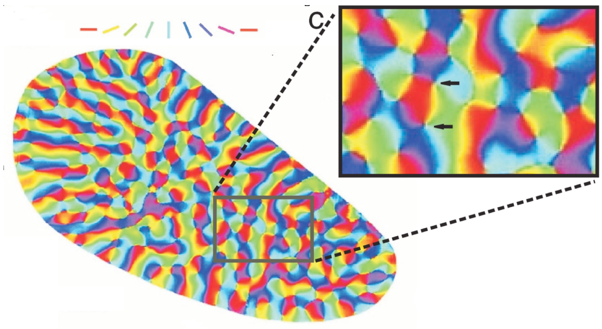
1.1.3.1 cAMP signaling in Dictyostelium discoideum

Dictyostelium discoideum is an interesting organism. It's a single cell amoeba that, when nutrient run low excretes a signalling molecule called cAMP which other individuals in the neighborhood respond to in two ways. 1.) they move up the gradient towards the source, getting closer to the orignator of the signal and, 2.) the start excreting cAMP, too. This is positive feedback. Eventually this leads to the aggregation of thousands of these organisms into a multicellualr organism, a slug like creature that crawls away and develops into a differentiated mold that forms a fruiting body and a stem, spores that get carried away by wind. If one measures the concentration of cAMP one sees spiral waves, just like in the BZ reaction and the pulse coupled oscillators:



1.1.3.2 Orientation Maps in the visual cortex of primates

An interesting pattern is seen on the visual cortex of primates and other higher mammals that have binocular vision. In the visual cortex signals that come in from the receptors in the eyes are processed. It turns out that the visual cortex has a bunch of cells that respond best to stimuli of a particular orientation, for instance contrast contours that are horizontal or vertical etc. If one records response strengths from neurons in the visual cortex one can color code the locations in the visual cortex according to the prefered stimulus orientation and this is what one gets:



We see a pattern that is reminiscent of the pinwheel pattern we saw in the phase coupled oscillator lattice. We see singularties, the pinwheels where all orientation meet. The cool part about thes visual maps is that animals aren't born with them. These maps develop after birth and in response to visual stimuli.

1.1.3.3 Patterns on sea shell

Here's a picture of natural patterns of different snail shells. These shells grow slowly over time by continuous deposits of material and the distribution of types of material and interactions between regions in the organism that make the hard material generate different patterns. This is an example of a growth process that yields complex patterns. Something we will come back to.

This is an interesting example because not only the patterns on the shels are interesting but the patterns of the shells themselves which appear to be following some very basic formation rules. In fact, a whole book was written by one of the pioneers of pattern formation in developmental biology: Hans Meinhardt. He developed a model for pattern formation which we will discuss in detail.

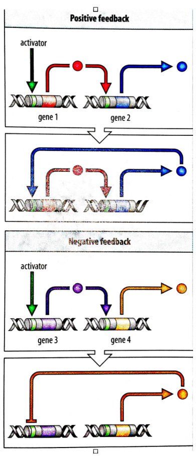
1.1.3.4 Patterns in animal fur

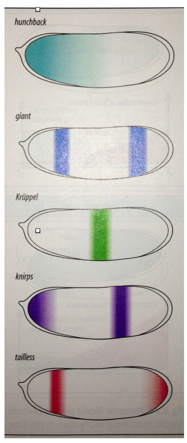
And of course, when we think of patterns in organism we have to mention animal fur:

This picture shows different types of animal fur. Some patterns are spotty, some consist of stripes of different wavelength. It turns out that will very few dynamic ingredient one can devise a model that is capable of generating all these patterns at different parameter values.

1.1.3.5 Biological Morphogenesis

The above pattern in animals are a special case of something a lot more fundamental. The problem of how multicelluar organisms with a great diversity of function and cell morphology can develop from a single, homogeneous fertilized egg. First, all cells in a multicellular organism have the same genome despite the variety in shape and function. This can be the case because these cells differ in what genes are expressed, i.e. active or repressed, i.e. inactive. On the way towards an adult organsism, cells differentiate by a sequential switching off an on of genes. This mechanism is responsible for spontaneouly introducing differences in embryos. For example in the drosophila melanogaster (fruitfly) embryo, different genes are expressed in different regions. The combination of expression levels introduces different cell fates for the cells in specific locations which eventually governs the development of a full blown fly:



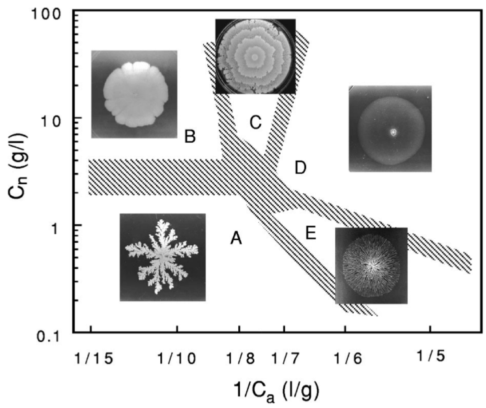


This process is very autonomous. If one disturbs gene expression in certain locations one can generate interesting effects, for instance a fruit fly that has a full functioing middle segment with additional wings:

Or mice with additional digits:

1.1.3.6 Growth of bacterial colonies

Here's another interesting example of a growing colony of the bacterium bacillus subtilis in a petri dish of nutrients. The control parameters are the physical properties of the agar in which the bacteria can move around and the concentration of nutrients. As a function of motility and nutrient concentration different growth patterns emerge. We will discuss these types of patterns later when we talk about diffusion limited aggregation and growth processes:



1.1.4 Alan Turing

The guy who first thought and published about the origins of spontaneous pattern formation was Alan Turing, who published a seminal paper called "The chemical basis of morphogenesis". In this paper, published only shortly before his death, Turing argued that an abundance of patterns observed in nature, many of the ones mentioned above, can be generated by the interaction of three different ingredients.

1. Activation
2. Inhibition
3. Diffusion

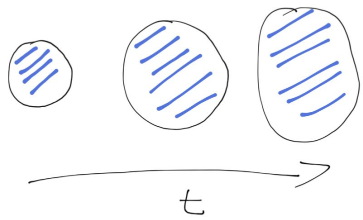
The basic idea being that essentially two types of agents (e.g. molecules, animals or other dynamical quantities) interact. An activator that does autocatalysis, which means this activator generates more of itself. Also, the activator triggers the generation of an inhibitor. The action of the inhibitor decreases the abundance of the activator. We have seen examples of such dynamical systems. The clue is that both, activator and inhibitor can move in space diffusively. So imagine you have a small concentration of an activator that subsequently generates more of itself and diffuses which may trigger a travelling wave of activation. However, the inhibitor is also generated and if that inhibitor diffuses faster it will eventually stop the activator. Activator can diffuse beyond the wall of inhibitor and generate a new activator nucleation and the process repeats causing a systems of stripes or rings to emerge. We will discuss how generic this process is by looking at numerous representative examples.

1.2 Transient and stable patterns

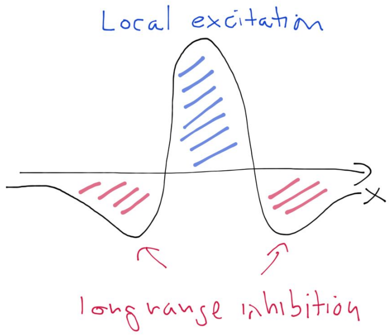
We've seen a couple of examples of patterns so far. It's reasonable to make the distinction between transient patterns that come and go, and those that stabilize. For instance, in one if we have a pattern that can be described by a fisher equation

$$\partial_t u = \lambda u(1-u) + D\partial_x^2 u$$

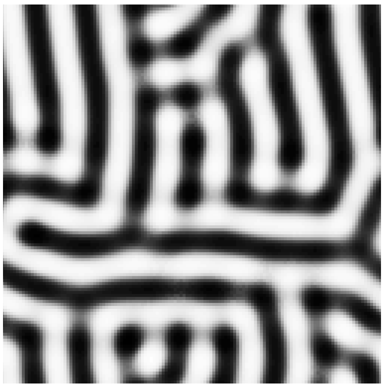
then for the appropriate initial condition we can observe a propagating wave that will spread throughout the entire system.



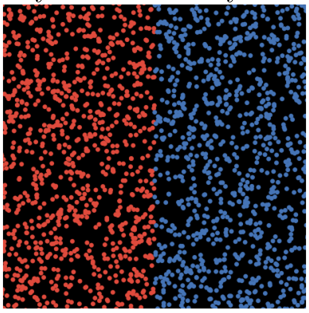
This is an example of a transient pattern.

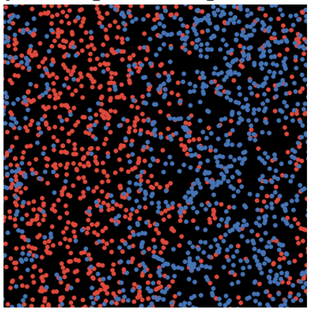


In one of the homework assignments we looked at a system in which the activity at a location was increased by the activity in a smaller radius and decreased by the activity of element in a larger radius. This local excitation and long range inhibition was able to produce stable stripelike patterns.



In that assignment, though, this mechanism was imposed and we need non-local interactions. In many physical systems, e.g. when particles can only move, e.g. diffuse, this non-local interaction doesn't work. A question is now whether diffusion mechanism can effectively yield this type of local excitation and long range inhibition. Intuitively we would expect that this isn't possible because diffusion usually enhances homogeneous patterns, i.e. distributions which are initially non-homogeneous go to a more homogeneous state. E.g. in the picture below, we've got diffusive particles of two types intitally separated spatially and when they diffuse they mix, yielding a homogeneous distribution.





1.2.1 Ad-hoc stable patterns

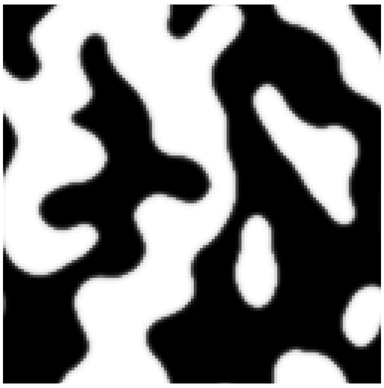
Let's try to construct a system that can potentially generate spatial patterns. Let's look at a dynamical system

$$\dot{u} = u - u^3$$

this is a dynamical system that has three fixedpoints, the unstable fixed point $u = 0$ and stable fixed points at $u = \pm 1$. Let's be experimental and look at this system, but spatially extended.

$$\partial_t u = u - u^3 + \partial_x^2 u.$$

This is what this system generates:



A nice pattern of regions that are either black or white ($u = \pm 1$). However, this is not such a surprise because the local dynamics already has two stable solutions and the diffusion only amplifies the initial condition. In fact these patterns change continuously and will eventually go into a homogeneous state. More importantly, the question is whether diffusion can introduce the emergence of a pattern in a system which otherwise would be homogeneous.

1.3 The Turing mechanism

It turns out that diffusion can also generate pattern in a system that without diffusion would be going to a stable homogeneous state. The idea is the following. Essentially many systems consist of an activator and an inhibitor. Let's for instance look at

$$\begin{aligned}\partial_t u &= u^2 w - u \\ \partial_t w &= \beta - u^2 w\end{aligned}$$

In this dynamical system u is an autocatalytic chemical that is activated by itself and ω and degrades spontaneously. When it increases it inhibits w by removing it. This system has a stationary solution

$$u^\star = \beta \quad \text{and} \quad w^\star = 1/\beta.$$

Let's see if this state is stable we need to compute the Jakobian

$$A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}\Bigg|_{u^\star, v^\star} = \begin{pmatrix} 1 & \beta^2 \\ -2 & -\beta^2 \end{pmatrix}$$

And remember that this is stable if the trace of A is negative and the determinant is positive

$$1 - \beta^2 < 0 \quad \text{and} \quad \beta^2 > 0$$

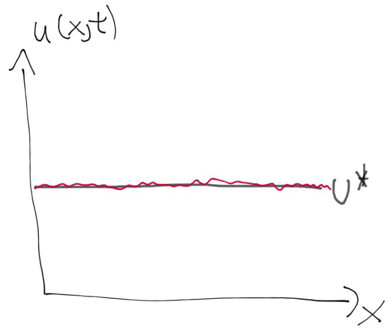
This means, the systems stationary state is stable if $\beta > 1$. Now let's imageing that

$$u = u(x,t) \quad \text{and} \quad v = v(x,t)$$

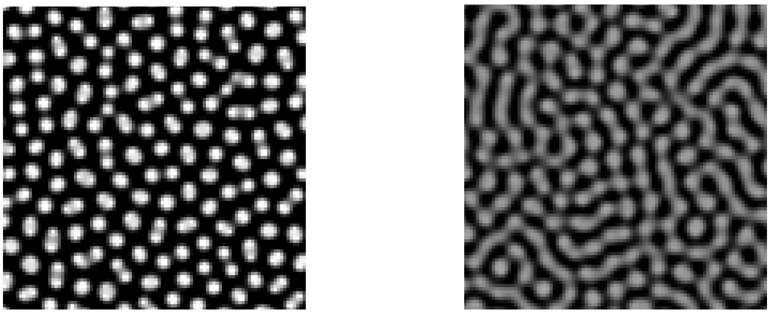
and that both chemicals can also diffuse with different diffusion coeffients. In this case

$$\begin{aligned}\partial_t u &= u^2 w - u + D_u \partial_x^2 u \\ \partial_t w &= \beta - u^2 w + D_w \partial_x w.\end{aligned}$$

Now if we distribute the chemicals uniformly then the partial derivatives with respect to the spatial coordinate vanish and the system behaves like the local system. The question is, what happens to slight pertubations from the stationary state.



. Do they get amplified or are they damped down. Let's see what can happen in the above system when we simulate it. We pick the parameters $\beta = 1.5$ and $D_w/D_u = 4$. What we see if we solve the above system numerically is that everything moves to the globally homogeneous state. However if we increase the diffusion of the inhibitor $D_w = 16$ the homogeneous state beomes unstable and a pattern consisting of spots or stripes emerges.



This is a general effect: If the diffusion of inhibition happens a lot faster than that of the activator, the system undergoes a Turing instability and patterns emerge which are called turing patterns. The come in different flavors some of which we will discuss soon. How can we understand this?

It turns out that with a little math we can and we can in fact derive a set of 4 equations that can tell us for what parameters a Touring instability will occur.

1.3.1 Another Example

Let's look at the following system

$$\begin{aligned}\partial_t u &= \frac{u^2}{w} - \mu u + \rho + \partial_x^2 u \\ \partial_t w &= u^2 - \lambda w + \sigma \partial_x^2 w\end{aligned}$$

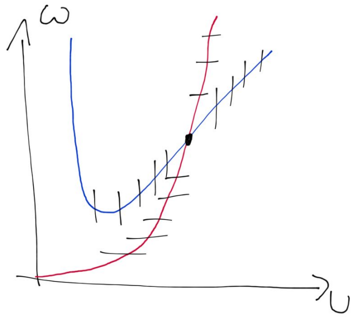
Here u is again an autocatalytic quantity that increases by positive self-coupling. However it also generates w which if it increases decreases the autocatalytic mechanism. Thus w is the inhibitor. Again the local system has one stable fixed point which is where the nullclines

$$w = \frac{u^2}{\mu u - \rho}$$

and

$$w = \frac{1}{\lambda} u^2$$

meet.



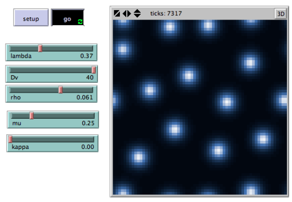
The fixed point is given by

$$u^{\star} = \frac{\rho + \lambda}{\mu} \quad \text{and} \quad w^{\star} = \frac{(\rho + \lambda)^2}{\lambda \mu^2}$$

We also observe in this sytem that when

$$\sigma < \sigma_c$$

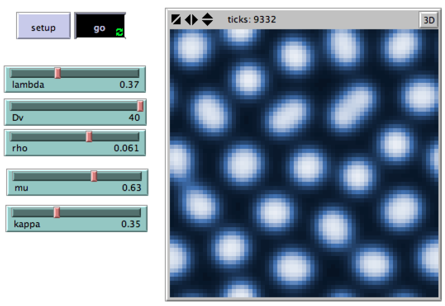
then the sytem goes into a homogeneous state, but when $\sigma > \sigma_c$ a Turing instability occurs and spots form.

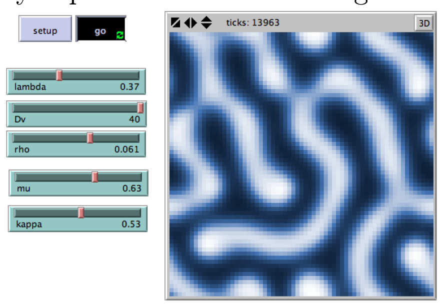


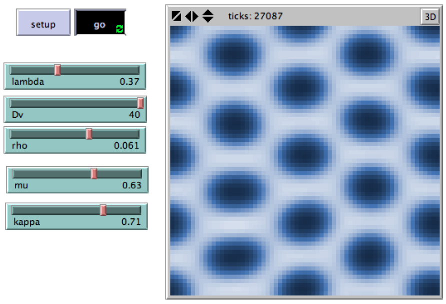
If we modify this dynamical system a little bit by replacing

$$u^2 \to \frac{u^2}{1 + \kappa u^2}$$

which means that the autocalytic process saturates and effect introduced by the new parameter κ the system is able to produce a variety of patters out of the turing instability.







1.3.2 Conditions for a Touring instability.

We can play with these system and will always find that if the inhibitor diffuses faster a turing instability will occur. But it's of course also important to know when. So let's see how far we can get by looking all systems of the form

$$\begin{aligned} \partial_t u &= f(u,w) + D_u \partial_x^2 u \\ \partial_t w &= g(u,w) + D_w \partial_x^2 u \end{aligned}$$

which we can also write as

$$\begin{aligned} \partial_t u &= f(u,w) + \partial_x^2 u \\ \partial_t w &= g(u,w) + \sigma \partial_x^2 u \end{aligned}$$

Now we assume one stable fixed point of the spatially homogeneous system:

$$f(u^\star, w^\star) = g(u^\star, w^\star) = 0$$

We have to compute the Jakobian

$$A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}\Bigg|_{u^\star, v^\star}$$

and the fixed point is stable if

$$s = \mathrm{Tr} A < 0 \quad \Delta = \det A > 0$$

which meanst that

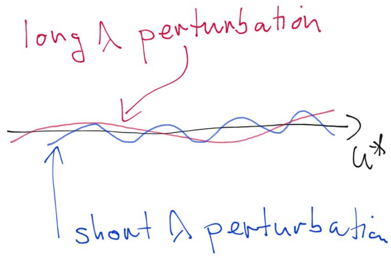
$$f_u + g_v < 0$$

and

$$f_u g_v - f_v g_u > 0$$

These are two conditions on the dynamical system for stability. Now look at spatial system in the vicinity of uniform solution, meaning that we perturb the system with a spatial pertubation:

$$\begin{aligned} u(x,t) &= u^\star + \delta u(x,t) \\ w(x,t) &= w^\star + \delta w(x,t) \end{aligned}$$



Let's pack the two variables into a vector

$$\mathbf{U} = (\delta u, \delta w)$$

Then this vector evolves according to

$$\partial_t \mathbf{U} = A\mathbf{U} + D\partial_x^2 \mathbf{U}$$

with a matrix

$$D = \begin{pmatrix} 1 & 0 \\ 0 & \sigma \end{pmatrix}$$

The question is what happens to the pertubation $\mathbf{U}$, is it going to grow or vanish. Let's make the following ansatz for a solution

$$\mathbf{U}(x,t) = \mathbf{U}_0 e^{\lambda t} \cos(kx)$$

If this is a solution to the equation and if $\mathrm{Re}\lambda > 0$ this solution will grow expontiealy and the pertubation is unstable. If on the other hand $\mathrm{Re}\lambda < 0$ the pertubation will go away. We are looking at a pertubation that's a cosine wave with wavelength $2\pi/k$. We are doing this so we can see if the behavior of pertubations depends on the nature of the pertubation. Plugging this into the above equation we get

$$\lambda \mathbf{U} = \left[A - Dk^2\right] \mathbf{U}$$

so we need to solve this eigenvalue problem and determine the sign of the eigenvalues. We have to understand the eigenvalues of the matrix $B = A - Dk^2$. which is given by

$$\begin{pmatrix} f_u - k^2 & f_v \\ g_u & g_v - \sigma k^2 \end{pmatrix} = B$$

We know that the nature of the eigenvalues are determined by the trace and determinant of the matrix B so the trace is given by

$$(f_u + g_v) - k^2(1+\sigma) = \mathrm{Tr}B$$

and the determinant by

$$\begin{aligned}\left(k^2 - f_u\right)\left(\sigma k^2 - g_v\right) - f_v g_u &= \det B \\ \sigma k^4 - (g_v + \sigma f_u)k^2 + f_u g_v - f_v g_u &= \det B \\ \sigma k^4 - (g_v + \sigma f_u)k^2 + \det A &= \det B\end{aligned}$$

The steady state is unstable either if

$$\mathrm{Tr}B > 0$$

or if

$$\det B < 0$$

The trace, however is always negative, because $TrA = f_u + g_v < 0$. So we have to find conditions when the determinant becomes negative. Since $\det A > 0$ the only way for the determinant to become negative is:

$$g_v + \sigma f_u > 0$$

If, for example

$$g_v < 0$$

at the fixed point then $f_u > 0$ then the requirement is

$$\sigma > 1$$

which means the inhibitor needs to diffuse faster. Let's set

$$\begin{aligned}p &= (g_v + \sigma f_u) > 0 \\ q &= \det A > 0\end{aligned}$$

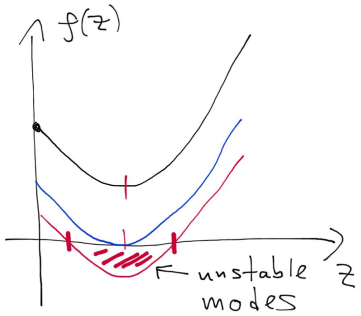
and $k^2 = z$. Then we can write the above equation as

$$\sigma z^2 - pz + q = h(z)$$

and see what it can look like. We have to see where this guy becomes negative. The function is a parabola that has an offset q and a minimum at

$$h_{min} = \frac{p}{2\sigma} = \frac{g_v + \sigma f_u}{2\sigma}$$

and it looks like this:



If we change the parameters we can make this parabola become negativ at a certain value $z_c = k_c^2$ which means that pertubation with this wavelength become unstable. The condition for this happening is when $h(z) = 0$ and this happens when

$$p^2/q \quad > \quad \sigma$$

or

$$\frac{(g_v + \sigma f_u)^2}{4(f_u g_v - f_v g_u)} > \sigma$$

which we can write has

$$(g_v + \sigma f_u)^2 > 4\sigma(f_u g_v - f_v g_u)$$

1.3.2.1 In summary

So that means we have a bunch of conditions:

$$f_u + g_v \quad < \quad 0$$

$$f_u g_v - f_v g_u > 0$$

$$g_v + \sigma f_u > 0$$

$$(g_v + \sigma f_u)^2 - 4\sigma(f_u g_v - f_v g_u) > 0$$

If these conditions are met, then the homogeneous state is unstable and patterns emerge.

1.3.3 Example

Let's look at our example

$$\begin{aligned} \partial_t u &= u^2 w - u + \partial_x^2 u \\ \partial_t w &= \beta - u^2 w + \sigma \partial_x^2 w \end{aligned}$$

We have

$$A = \begin{pmatrix} 2uw - 1 & u^2 \\ -2uw & -u^2 \end{pmatrix} = \begin{pmatrix} 1 & \beta^2 \\ -2 & -\beta^2 \end{pmatrix}$$

and

$$\begin{aligned} f_u + g_v &= 2uw - 1 - u^2 \\ &= 1 - \beta^2 \end{aligned}$$

so the first condition implies $\beta > 1$. The determinant is always positive.

$$\Delta = -\beta^2 + 2\beta^2 = \beta^2 > 0$$

The third condition reads

$$\sigma > \beta^2$$

and finally the fourth condition is

$$\left(\sigma - \beta^2\right)^2 \quad > \quad 4\sigma\beta^2$$

Or

$$\sigma > b^2\left(3 + 2\sqrt{2}\right)$$