Physics 414: Linear stability analysis of two coupled reaction-diffusion equations

December 10, 2018

I give here key details of what I discussed briefly in class. These details should give you enough understanding and context that you can read and understand the Segel-Jackson 1972 paper, where many insights about the Turing instability are derived and discussed.

The main insight is that one can sometimes determine analytically, and often rather easily numerically, when a constant solution of a set of evolution equations, either in the form of ordinary differential equations (odes) or of partial differential equations (pdes), is linearly stable. "Linear stability" means that all tiny perturbations of the constant solution decay over time, leading asymptotically back to the constant solution. Determining when a constant solution of an evolution equation is linearly stable as a function of parameters is an important and widely used technique in many branches of science and engineering, including biophysics.

If a constant solution is linearly unstable, there is at least one small perturbation of the constant solution that will grow instead of decay (usually with exponential growth). However, the mathematical method for studying linear instability of a constant solution is not capable of predicting what the small perturbation will grow into, this requires a nonlinear analysis which generally is difficult mathematically. Much of our knowledge of what a small perturbation of an unstable constant solution evolves into comes from laboratory experiments and from computer simulations.

Linear stability analyses of states of evolution equations are useful in two ways. First, by predicting when a given state loses stability and so will no longer be observable as some experimental parameter is varied in small successive steps, they can identify when some new dynamical behavior will appear. (For example, Turing was able to predict when a spatially uniform set of two reacting chemicals will become unstable to the appearance of some new pattern.) When a constant solution just becomes unstable as a parameter is changed in small successive steps, a linear stability analysis can further predict whether will be a new length scale (leading to a spatial pattern) or time scale (leading to a temporal pattern) associated with the new dynamics that replaces the now unstable constant state.

The following discussion is organized into four cases of increasing mathematical sophistication, leading up to the case of the Turing instability, two chemicals that react and undergo diffusion in a one-dimensional domain. The key details you need to understand for this course are

1. How to use linearization (low-order Taylor series) to obtain the linear evolution equations for a small perturbation $\delta u(t, x)$ of some constant solution.

2. How to convert the linearized constant-coefficient evolution equations to a set of linear non-differential equations for the growth rates σ of exponential time dependence. For two or more reacting chemicals, the linear equations constitute an eigenvalue-eigenvector problem.

3. How to predict linear stability of the constant solution based on when the real parts of all of the eigenvalues σ are negative.

4. Finally, how the growth rate $\sigma = \sigma(k)$ also depends on the wavenumber k of a spatial perturbation, and how this dependence leads to cellular pattern formation with a preferred wavelength λ_c. Typically, $\sigma(k)$ will have a global maximum at $k_c = 2\pi/\lambda_c$ and so σ first becomes positive (linear instability) for spatial perturbations with wavelengths close to λ_c.

Case 1: linear stability of a constant solution for one-variable autonomous ode (ordinary differential equation)

The first and easiest case to discuss of the linear stability of a constant solution for some evolution equation is a single ordinary differential equation (abbreviated as "ode" and pronounced as "oh-dee-ee") describing

the evolution over time of a single variable $u(t)$:

$$\frac{du}{dt} = f(u). \tag{1}$$

Here $f(u)$ is some general function (e.g., $f = kx$ for some constant k, or f could be the function $a \tanh(bu)$). To obtain a unique solution of Eq. (1), an initial condition $u_0 = u(t_0)$ at some particular time t_0 has to be given. Because Eq. (1) is *autonomous* (the function $f(u)$ does not depend on time explicitly), the origin of the time coordinate is arbitrary so we can take the initial time t_0 to be $t_0 = 0$ without losing any generality

$$\text{initial condition:} \;\; u(t = 0) = u_0. \tag{2}$$

For most functions $f(u)$, one can not find explicit mathematical solutions $u(t)$ satisfying Eqs. (1) and (2). But for any general function f, one can try to find and then study the linear stability of the simplest possible mathematical solutions, which would be a constant solution $u_\star$: if you start the dynamical system Eq. (1) with value $u_0 = u_\star$, the value never changes over time. (Some vocabulary: a constant solution of ode evolution equations is often called a "fixed point" since, in the state space of the evolution equations, a constant solution is an initial state that never changes (is fixed) under the dynamics.)

If $u_\star$ is a constant solution of Eq. (1) and since the time derivative of any constant is zero, it follows that

$$\frac{d}{dt} u_\star = 0 = f(u_\star). \tag{3}$$

So any constant solution $u_\star$ of Eq. (1) must be a zero of the right-hand-side (rhs) function $f(u)$. There may be no constant solutions (for example, for $f(u) = 1 + u^2$), finitely many solutions (say for $f(u) = au(b - u)$ with a and b constants, then $u_\star = 0$ or b), or infinitely many constant solutions (say for $f(u) = a \cos(bu)$, with $u_\star = (n + 1/2)\pi/b$ for any integer n).

To carry out a linear stability analysis of a constant solution $u_\star$ we add an arbitrary *tiny* perturbation $\delta u(t)$ to the constant solution and try to determine whether the magnitude of the perturbation δu will grow over time (instability) or decay over time (stability).

A "linear stability analysis" is the analysis of tiny perturbations of a given dynamical state and is the easiest class of mathematical problems to solve for a constant solution since the stability analysis lead to linear constant-coefficient evolution equations for the perturbation. One can also study the stability of constant solutions to perturbations that are not small in magnitude but the mathematics is much harder since one cannot then use a Taylor series expansion to obtain a linear problem. People sometimes use the phrase "finite-amplitude stability theory" to describe studying the stability of a dynamical state to perturbations that are not small.

So let's carry out a linear stability analysis of some constant solution $u_\star$ of the evolution equation Eq. (1). We do this by adding some arbitrary small perturbation $\delta u(t)$ to the constant solution

$$u(t) = u_\star + \delta(u)(t), \qquad |\delta u| \ll |u_\star|, \tag{4}$$

and require that $u(t)$ evolves according to (satisfies) Eq. (1). Substituting Eq. (4) into Eq. (1) gives

$$\frac{d}{dt}(u_\star + \delta u) = f(u_\star + \delta u). \tag{5}$$

Because $u_\star$ is a constant, the left side becomes $d\delta u/dt$:

$$\frac{d}{dt}(u_\star + \delta u) = \frac{d\delta u}{dt}. \tag{6}$$

Because $\delta u(t)$ is assumed to be always small compared to $u_\star$, we can Taylor expand $f(u_\star + \delta u)$ about the point $u_\star$ to lowest power in the small quantity δu like this:

$$f(u_\star + \delta u) \approx f(u_\star) + f'(u_\star)\delta u. \tag{7}$$

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Because $u_\star$ is not just a constant but a constant solution of Eq. (1), it satisfies $f(u_\star) = 0$ and so (7) simplifies to

$$f(u_\star + \delta u) \approx f'(u_\star)\,\delta u. \tag{8}$$

Substituting Eq. (6) and (8) into Eq. (5), we discover an evolution equation for the perturbation $\delta u(t)$

$$\frac{d\delta u}{dt} = f'(u_\star)\,\delta u. \tag{9}$$

This is a constant-coefficient linear differential equation, and note how the constant coefficient $f'(u_\star)$ depends on the choice of the constant solution $u_\star$. In principle, one has to carry out a separate linear stability analysis for each constant solution that satisfies $f(u_\star) = 0$.

The solution of all constant-coefficient differential equations can be written as a superposition of exponential solutions. We can confirm this claim for Eq. (9) by assuming that the solution $\delta u(t)$ has the form of a constant times an exponential in time

$$\delta u = a e^{\sigma t}, \tag{10}$$

where σ is the growth rate of the exponential. Substituting Eq. (10) into Eq. (9) and dividing both sides by the non-zero term $\exp(\sigma t)$ after carrying out the derivative leads to the conclusion that Eq. (10) is a solution of Eq. (9) provided that the growth rate σ is chosen to have the value

$$\sigma = f'(u_\star), \tag{11}$$

which can always be done. We conclude that any sufficiently tiny perturbation $\delta u(t)$ of a constant solution $u_\star$ must grow or decay exponentially with this specific form

$$\delta u(t) = a \exp\left[f'(u_\star)\,t\right]. \tag{12}$$

This will decay over time giving linear stability provided that

$$f'(u_\star) < 0, \qquad u_\star \text{ is linearly stable}, \tag{13}$$

and will grow exponentially over time (instability) if the growth rate is positive:

$$f'(u_\star) > 0. \qquad u_\star \text{ is linearly unstable}. \tag{14}$$

The in-between case $f(u_\star) = 0$ corresponds to what is called "marginal stability" of the constant solution $u_\star$. To determine if $u_\star$ is linearly stable when $f'(u_\star) = 0$, one has to expand $f(u_\star + \delta u)$ to second or higher power in δu and substitute the resulting expansion into Eq. (5) to get a new evolution equation for $u_\star$.

As a simple concrete example, consider the evolution equation with reaction kinetics $f(u) = au(b - u)$:

$$\frac{du}{dt} = au(b - u), \tag{15}$$

where a and b are constant parameters and we assume $b > 0$. As you can verify, this evolution equation has two constant solutions

$$u_{1\star} = 0 \quad \text{and} \quad u_{2\star} = b. \tag{16}$$

According to Eq. (13), the constant solution $u_{1\star} = 0$ is linearly stable if

$$f'(u_{1\star}) = \left.\left(ab - 2au\right)\right|_{u=0} = ab < 0. \tag{17}$$

Since we assume that b is positive, the zero solution $u_{1\star} = 0$ is linearly stable only if $a < 0$ and linearly unstable if $a > 0$. We cannot say anything about linear stability of $u = 0$ for the marginal case $a = 0$ without doing a Taylor expansion to higher order and studying a new evolution equation for δu.

Physically, if $a < 0$ and $b > 0$ and we start the dynamical system off with the value $u = 0$, then tiny perturbations of the zero will decay so we expect that $u = 0$ is a robust observable state. But as soon as a

becomes positive, $u = 0$ becomes linearly unstable and there is at least some tiny perturbation that will grow exponentially in which case we do *not* expect to observe the solution $u = 0$ experimentally since there are always perturbations around in a finite temperature macroscopic system, arising from the randomness of molecular collisions that slightly alter the concentration at any small region of space.

Note the important point that $u = 0$ is always a solution of the evolution equation Eq. (15), whether or not it is linearly stable. But only for the parameter regime $a < 0$ will the solution $u = 0$ be experimentally observable since only stable solutions can be observed in experiments.

Similarly, the second constant solution $u_{2\star} = b$ is linearly stable if

$$f'(u_{2\star}) = \left. \left(ab - 2au \right) \right|_{u=b} = -ab < 0. \tag{18}$$

Since again $b > 0$, the second constant solution $u = b$ is linearly stable if $a > 0$, which is the opposite of the condition for $u_{1\star} = 0$.

So the evolution equation Eq. (15) has two constant solutions (and many other non-constant solutions). For fixed $b > 0$, the zero solution is linearly stable when $a < 0$ and becomes unstable when $a > 0$, which is when the second constant solution $u = b$ changes from unstable to stable. A reasonable guess (which I will let you confirm on your own by numerical exploration using a numerical ode integrator) is that, as the parameter a is increased slowly from negative to positive values, the constant solution $u = 0$ becomes no longer observable and only the solution $u = b$ is observable (robust to perturbations).

Case 2: linear stability of a constant solution for one-variable autonomous reaction-diffusion partial differential equation (pde) in one space dimension

Let us now study the next simplest case of linear instability, a reaction-diffusion equation in one spatial variable x with one single concentration $u(t, x)$. The evolution equation then has the form

$$\partial_t u(t, x) = D \partial_{xx}^2 u + f(u), \tag{19}$$

which we can describe verbally as a "one-variable reaction-diffusion evolution equation in one space dimension". This evolution equation is similar to the ode case Eq. (1) except that $u = u(t, x)$ now depends on space and time and the concentration u can diffuse as well as undergo a chemical reaction described by $f(u)$. Indeed, if the concentration $u(t, x) = u(t)$ is spatially uniform and so does not vary with x, the spatially uniform state evolves exactly like the ode Eq. (1). (So for pde evolution equations, a fixed point—a solution that does not change with time—does not have to be a constant solution since it can vary spatially. You saw an example of this when we discussed the steady-state Bicoid concentration for a fly embryo.)

Again, the simplest case of linear stability to investigate is a constant solution $u_\star$ that is constant in time and constant in space. Since the derivatives ∂_t and ∂_{xx}^2 acting on a constant are zero, the condition for $u_\star$ to be a constant solution of Eq. (19) is exactly the same as Eq. (3)

$$f(u_\star) = 0. \tag{20}$$

Eq. (20) again might have zero, finitely many, or infinitely many solutions $u_\star$ and one has to study the linear stability of each constant solution separately.

We use the exact same strategy as case 1 above to determine whether some constant solution $u_\star$ of Eq. (19) is linearly stable by asking whether the magnitude of an arbitrary *tiny* perturbation $\delta u(t, x)$, that can now vary with space x as well as with time t, will decay over time (linear stability) or grow over time (linear instability). So we write

$$u(t, x) = u_\star + \delta u(t, x), \qquad |\delta u| \ll |u_\star|, \tag{21}$$

and require that $u(t, x)$ satisfy the evolution equation Eq. (19). Substituting Eq. (21) into Eq. (19) gives:

$$\partial_t \left[u_\star + \delta u(t, x) \right] = D \partial_{xx}^2 \left[u_\star + \delta u \right] + f \left(u_\star + \delta u \right). \tag{22}$$

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Using the fact that $u_\star$ is a constant that satisfies Eq. (20) and using the same lowest-order Taylor expansion in δu as Eq. (7), we find that an arbitrary tiny perturbation $\delta u(t, x)$ of a constant solution $u_\star$ evolves over time according to this evolution equation

$$\partial_t \delta u(t, x) = D\partial_{xx}^2 \delta u + f'(u_\star)\, \delta u. \tag{23}$$

Equation (23) is again a constant-coefficient linear evolution equation and we again expect the general solution to be a superposition of exponentials. But there is one new detail, which is that the solution must be written as an exponential in time times an exponential in space like this:

$$\delta u(t, x) = a\, e^{\sigma t}\, e^{ikx}, \tag{24}$$

where σ is again a growth rate, where $i = \sqrt{-1}$ is a square root of -1, where $k \geq 0$ is a wavenumber, and where a is some nonzero constant.

In Eq. (24), I hope you remember from your math, wave, or quantum courses Euler's important and remarkable identity

$$e^{ix} = \cos(x) + i\sin(x), \tag{25}$$

that relates the exponential of an imaginary argument ix (where x is a real number) to a complex number $a+ib$ consisting of the two trigonometric functions cos and sin. This identity tells us that we should think of the term e^{ikx} in Eq. (24) as trig functions in space. That is, e^{ikx} represents spatial sinusoidal oscillations with wavenumber k or with wavelength $\lambda = 2\pi/k$.

Physically, we can think of decomposing an arbitrary tiny spatiotemporal perturbation $\delta u(t, x)$ at any given time t into a sum of sinusoidal perturbations e^{ikx} of different wavenumbers, that is we can Fourier analyze an arbitrary tiny perturbation into a sum of Fourier terms like Eq. (24). If for any wavenumber $k > 0$ the growth rate σ is positive, the magnitude of that Fourier mode will grow exponentially and the constant solution $u_\star$ will be linearly unstable.

We can verify that Eq. (24) is a solution of Eq. (23) by substituting Eq. (24) into Eq. (23). Upon doing this, evaluating the derivatives, and canceling common terms from both sides, we find that Eq. (24) is a solution provided that the growth rate σ depends on the wavenumber k like this (please verify this for yourself)

$$\sigma = f'(u_\star) - Dk^2. \tag{26}$$

Note how the result Eq. (26) is almost the same as the result Eq. (11) for the evolution equation Eq. (1) without diffusion, diffusion adds a term $-Dk^2$ to the growth rate. Since the diffusion constant D is positive, $D > 0$, the term $-Dk^2$ is always negative and so we see that diffusion decreases the growth rate σ (slows the growth) of any spatial oscillation with wavenumber k. Further, the more rapidly the perturbation varies spatially (the large the wavenumber k, the shorter the wavelength $\lambda = 2\pi/k$), the more negative the term $-Dk^2$. So a perturbation with rapid spatial variations will decay more rapidly than perturbations that vary less rapidly in space.

We can use Eq. (26) to make an interesting prediction that is helpful for appreciating the Turing instability: **a single constant concentration $u = u_\star$ undergoing reaction and diffusion cannot produce a pattern by becoming linearly unstable as some parameter is varied**. That is, a Turing instability, in which a uniform set of concentrations become linearly unstable, cannot produce a pattern (first become unstable at some finite wavenumber) unless there are at least two reacting chemicals.

To understand why, appreciate that Eq. (26) says that, if the quantity $f'(u\star)$ is negative then necessarily the growth rate $\sigma = f'(u_\star) - Dk^2$ is also negative for any choice of the wavenumber k. This implies that every tiny spatial periodic perturbation of the constant state $u_\star$ will decay exponentially over time (a superposition of decaying terms is itself a decaying expression). A negative growth rate $\sigma < 0$ for all k is the same as saying that the constant state $u_\star$ is linearly stable: all tiny perturbations of the constant solution $u_\star$ will decay over time.

But now imagine that, as some parameter p of the reaction diffusion system Eq. (19) is varied, the quantity $f'(u_\star)$ changes from being negative to just becoming positive. (The parameter p would be some parameter

inside the expression $f(u)$, like the parameter a in Eq. (15).) Then the growth rate $\sigma(k) = f'(u_\star) - Dk^2$ first becomes positive for wavenumbers k close to zero. That is, only small-wavenumber long-wavelength perturbations that are nearly constant spatially can start growing. These correspond to an approximately uniform (same everywhere in space) change of the constant solution $u_\star$ so no new spatial structure appears, say in the form of a localized bump or sinusoidal spatial variation.

The linear stability analysis of a constant solution $u_\star$ for the 1d single-variable reaction-diffusion system Eq. (19) thus predicts that, as some parameter p in the term $f(u)$ is slowly varied, any constant solution will first become unstable to long-wavelength and so approximately constant spatial perturbations, which means that a pattern (novel spatial structure) does not form.

As a specific example, we can again look at the case of the reaction term $f(u) = au(b - u)$ but now with diffusion included, Eq. (19). The constant solution $u_{1\star} = 0$ becomes linearly unstable when a changes from negative $a < 0$ to positive $a > 0$, the same as before, but now we know that, just as a becomes slightly positive, only spatial perturbations with nearly constant long wavelengths (wavenumbers k close to zero) will start growing in magnitude. The constant solution $u_{2\star} = b$ is unstable for $a < 0$ and becomes stable just as the parameter a becomes slightly positive. Again, a reasonable guess is that the unstable spatially uniform solution $u = 0$ for $a < 0$ simply evolves into a new spatially uniform solution $u = b$ as a is slowly increased from just negative to just positive. Computer solutions indeed support this guess, and I encourage you to explore this.

Case 3: linear stability of a constant solution for two coupled autonomous odes

The next step up in mathematical complexity is to study two coupled chemical reactions without diffusion. This would correspond physically to studying two reacting chemical solutions in a beaker that is stirred (mixed) so rapidly (say by a spinning magnetic rod) that spatial gradients do not form. In this case, two concentrations $u_1(t)$ and $u_2(t)$ react and evolve according to these two coupled odes

$$\frac{du_1}{dt} = f_1(u_1, u_2),\tag{27}$$

$$\frac{du_2}{dt} = f_2(u_1, u_2),\tag{28}$$

where $f_1(u_1, u_2)$ and $f_2(u_1, u_2)$ are two general functions of two variables.

Again, the simplest kinds of solutions whose linear stability can be studied are the constant solutions $\mathbf{u}_\star = (u_{1\star}, u_{2\star})$ which satisfy these two coupled nonlinear equations

$$0 = f_1(u_1, u_2),\tag{29}$$

$$0 = f_2(u_1, u_2).\tag{30}$$

Just like the one variable case Eq. (3), there can be no solutions, finitely many solutions, or infinitely many solutions and finding even one solution can be difficult.

Let us assume that we somehow have identified a constant solution $\mathbf{u}_\star = (u_{1\star}, u_{2\star})$ of Eqs (29) and (30). Then just as we did in the two previous cases, we can investigate whether this constant solution becomes unstable to tiny (small magnitude) perturbations by deriving and studying linear constant-coefficient evolution equations for the perturbations of each constant concentration. But now we need to introduce a separate perturbation $\delta u_1(t)$ and $\delta u_2(t)$ for each constant concentration $u_{1\star}$ and $u_{2\star}$. That two separate perturbations are needed should make sense to you physically since there is no reason why the statistical fluctuations arising from molecular collisions that change $u_{1\star}$ slightly in some small region should be the same as the fluctuations that change $u_{2\star}$ in the same small region, i.e. the u_1 and u_2 molecules random walk and so diffuse independently of one another.

So for two reacting chemicals, Eq. (4) generalizes to

$$u_1(t) = u_{1\star} + \delta u_1(t), \qquad |\delta u_1(t)| \ll |u_{1\star}|, \tag{31}$$

$$u_2(t) = u_{2\star} + \delta u_2(t), \qquad |\delta u_2(t)| \ll |u_{2\star}|. \tag{32}$$

We substitute Eqs. (31) and (32) into Eqs. (27) and (28) to get:

$$\frac{d}{dt}\left[u_{1\star} + \delta u_1(t)\right] = \frac{d\delta u_1}{dt} = f_1(u_{1\star} + \delta u_1, u_{2\star} + \delta u_2), \tag{33}$$

$$\frac{d}{dt}\left[u_{2\star} + \delta u_2(t)\right] = \frac{d\delta u_2}{dt} = f_2(u_{1\star} + \delta u_1, u_{2\star} + \delta u_2). \tag{34}$$

Because the perturbations $\delta u_i(t)$ for $i = 1, 2$ are assumed to be tiny, we can Taylor-expand the right sides of Eqs. (33) and (34) to lowest-order in powers of the δu_i like we did in Eq. (7) above, but now we need to carry out a two-variable Taylor expansion.

From your multivariate calculus course or from some other physics course, you hopefully know that if you have a function $f(x, y)$ of two variables x and y and two small quantities Δx and Δy, one can expand the function f about the point (x, y) as a sum of powers of the small quantities like this:

$$f(x + \Delta x, y + \Delta y) = f(x, y) + \partial_x f(x, y)\,\Delta x + \partial_y f(x, y)\,\Delta y \tag{35}$$

$$+ \frac{1}{2}\partial_{xx}^2 f(x, y)\,\Delta x^2 + \partial_{xy}^2 f(x, y)\,\Delta x \Delta y + \frac{1}{2}\partial_{yy}^2 f(x, y)\,\Delta y^2 \tag{36}$$

$$+ \text{higher-order-terms.} \tag{37}$$

If Δx and Δy are sufficiently tiny, we can ignore all higher-order powers of these quantities (e.g., terms involving $\Delta x^2, \Delta x \Delta y, \Delta y^3, \Delta x^2 \Delta y$, etc except the first-order ones and so get this lowest-order two-variable approximation to a function that is linear in the small quantities Δx and Δy:

$$f(x + \Delta x, y + \Delta y) \approx f(x, y) + \partial_x f(x, y)\,\Delta x + \partial_y f(x, y)\,\Delta y. \tag{38}$$

If we apply Eq. (38) to the right sides of Eqs. (33) and (34), if we introduce the abbreviations

$$a_{11} = \left.\frac{\partial f_1}{\partial u_1}\right|_{\mathbf{u}_\star}, \quad a_{12} = \left.\frac{\partial f_1}{\partial u_2}\right|_{\mathbf{u}_\star}, \tag{39}$$

$$a_{21} = \left.\frac{\partial f_2}{\partial u_1}\right|_{\mathbf{u}_\star}, \quad a_{22} = \left.\frac{\partial f_2}{\partial u_2}\right|_{\mathbf{u}_\star}, \tag{40}$$

and if we use the fact that $\mathbf{u}_\star$ is a solution of the evolution equations so that Eqs. (29) and (30) hold, you should verify that Eqs. (33) and (34) become the following two coupled evolution equations that describe how the perturbations $\delta u_i(t)$ evolve in time:

$$\frac{d\delta u_1}{dt} = a_{11}\delta u_1 + a_{12}\delta u_2, \tag{41}$$

$$\frac{d\delta u_2}{dt} = a_{21}\delta u_1 + a_{22}\delta u_2. \tag{42}$$

These are yet again constant-coefficient linear differential equations, with the constant coefficients being given by Eqs. (39) and (40), which means that they depend on the choice of constant solution $\mathbf{u}_\star$. Again, we expect the general solution $\delta u_i(t)$ to be a superposition of particular solutions that consist of exponentials.

But we need to be a bit more careful or more clever in choosing how to solve Eqs (41) and (42) in terms of exponentials. Some thinking and trial and error leads to the insight that we want to solve these evolution equations by using the *same* growth rate σ for both perturbations $\delta u_i(t)$. That is, we want to write

$$\delta u_1(t) = \delta u_{10}\, e^{\sigma t}, \tag{43}$$

$$\delta u_2(t) = \delta u_{20}\, e^{\sigma t}, \tag{44}$$

where σ is the growth rate and where the δu_{i0} are constants. Substituting Eqs. (43) and (44) into Eqs. (41) and (42) and dividing out the common exponentials on both sides leads to these two non-differential linear equations:

$$\sigma \, \delta u_{10} = a_{11}\delta u_{10} + a_{12}\delta u_{20} \tag{45}$$

$$\sigma \, \delta u_{20} = a_{21}\delta u_{10} + a_{22}\delta u_{20}. \tag{46}$$

From previous math and physics courses, you should recognize these two coupled linear equations as representing an eigenvalue-eigenvector problem. This can be made more clear by rewriting these equations in a matrix form like this:

$$\mathbf{A} \, \delta \mathbf{u}_0 = \sigma \, \delta \mathbf{u}_0, \tag{47}$$

where the 2×2 matrix $\mathbf{A}$ is defined by

$$\mathbf{A} = \left(\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array} \right), \tag{48}$$

and where the 2×1 constant column vector $\delta \mathbf{u}_0$ is defined to be

$$\delta \mathbf{u} = \left(\begin{array}{c} \delta u_{10} \\ \delta u_{20} \end{array} \right). \tag{49}$$

Equation (47) is a 2×2 eigenvalue-eigenvector problem where σ is an eigenvalue and $\delta \mathbf{u}_0$ is the corresponding eigenvector. Your linear algebra and physics textbooks then tell you that you can find the values of the eigenvalues σ by finding the roots of the so-called characteristic polynomial $p(\sigma)$, which in turn is obtained by setting the following determinant to zero:

$$0 = p(\sigma) = \det\left[A - \sigma I\right] \tag{50}$$

$$= \det\left[\left(\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array} \right) - \sigma \left(\begin{array}{cc} 1 & 0 \\ 0 & 1 \end{array} \right) \right] \tag{51}$$

$$= \det\left[\left(\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array} \right) - \left(\begin{array}{cc} \sigma & 0 \\ 0 & \sigma \end{array} \right) \right] \tag{52}$$

$$= \det\left[\left(\begin{array}{cc} a_{11} - \sigma & a_{12} \\ a_{21} & a_{22} - \sigma \end{array} \right) \right] \tag{53}$$

$$= (a_{11} - \sigma)(a_{22} - \sigma) - a_{21}a_{12} \tag{54}$$

$$= \sigma^2 - \tau\sigma + \Delta, \tag{55}$$

where I have defined

$$\tau = \mathrm{Tr}(\mathbf{A}) = a_{11} + a_{22},$$

$$\Delta = \det(\mathbf{A}) = a_{11}a_{22} - a_{12}a_{21},$$

and where I hope you remember that the trace of a matrix $\mathrm{Tr}(\mathbf{A})$ is the sum of its diagonal elements, and that $\det(\mathbf{A})$ denotes the determinant of a matrix. That is, the growth rate σ of the solution Eqs (43) and (44) is a zero of the quadratic characteristic equation

$$\sigma^2 - \tau\sigma + \Delta = 0, \tag{56}$$

A quadratic equation has generally two distinct roots and so there are two eigenvalues σ_1 and σ_2 associated with the linear stability problem of Eqs (41) and (42). Since it is possible (and rather common) for the roots of a quadratic equation (or more generally for any eigenvalue) to be complex numbers, we have to consider writing the growth rate σ as a complex number:

$$\sigma = a + ib = \mathrm{Re}[\sigma] + i\mathrm{Im}[\sigma], \tag{57}$$

where a is the real part of σ and b is the imaginary part of σ. Since

$$e^{\sigma t} = e^{(a+ib)t} = e^{at}\,e^{ibt},\tag{58}$$

we further see that it is the real part a of the growth rate that determines whether some perturbation grows or decreases in magnitude over time. The imaginary part simply contributes an oscillation of fixed magnitude (since $|e^{ibt}| = \cos^2(bt) + \sin^2(bt) = 1$ has a fixed magnitude of 1 for all b).

To give you some practice thinking about real parts of complex numbers and thinking about the implications of some algebra, I finish this section by deriving a key result mentioned in the Segel-Jackson paper, that a constant solution $\mathbf{u}_\star$ of the two coupled evolution equations (27) and (28) is linearly stable if and only if

$$\tau = a_{11} + a_{22} < 0 \qquad \text{and}\tag{59}$$
$$\Delta = a_{11}a_{22} - a_{21}a_{12} > 0.\tag{60}$$

These are necessary and sufficient conditions for the two eigenvalues σ_1 and σ_2 that are roots of Eq. (56) to both have negative real parts. If either of these two conditions are violated, the constant solution becomes linearly unstable and will evolve into some new solution.

The starting point is to remember that we can use the quadratic formula to write the roots of Eq. (56) explicitly in terms of the coefficients of the quadratic[1]

$$\sigma = \frac{\tau}{2} \pm \frac{\sqrt{\tau^2 - 4\Delta}}{2}.\tag{61}$$

There are then two cases to consider, depending on whether the quantity $\tau^2 - 4\Delta$ under the square root (the discriminant) is negative or non-negative.

1. **negative discriminant** Let's assume that $\tau^2 - 4\Delta < 0$. Then the two roots Eq. (61) are complex numbers $a \pm ib$ that are complex conjugates of each other:

$$\sigma = \frac{\tau}{2} \pm i\frac{\sqrt{4\Delta - \tau^2}}{2}.\tag{62}$$

   Since Eq. (58) shows that only the real part of a growth rate can change the magnitude of $e^{\sigma t}$, and the two complex roots have the same real part $\tau/2$, we conclude that linear stability of the constant solution requires $\tau < 0$. Further, since we assumed that the discriminant $\tau^2 - 4\Delta < 0$ was negative, we also have $\Delta > \tau^2/4 > 0$ so Δ must be positive at the same time. So for the case of complex conjugate roots, the criteria Eqs (59) and (60) are correct.

2. **non-negative discriminant** Let us next assume that $\tau^2 - 4\Delta \geq 0$. Then the two roots Eq. (61) are both real valued and linear stability of the constant solution requires that both roots (growth rates) be negative numbers. The smaller root

$$\sigma = \frac{\tau}{2} - \frac{\sqrt{\tau^2 - 4\Delta}}{2},\tag{63}$$

   will automatically be negative if $\tau < 0$ since adding the negative number $-\sqrt{\tau^2 - 4\Delta}/2$ to a negative $\tau/2$ will also give a negative number. When considering the larger root

$$\sigma = \frac{\tau}{2} + \frac{\sqrt{\tau^2 - 4\Delta}}{2},\tag{64}$$

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[1]A remarkable theorem by 18-year-old Galois in 1830 showed that it is impossible to write the roots of a real polynomial of degree five or higher algebraically in terms of the coefficients of the polynomial. Further, the formulas for the roots of a cubic or quartic in terms of their coefficients that generalizes the quadratic equation are so long so as to be nearly useless for mathematical analysis. So two-reacting chemicals is the mathematical sweet spot of being practical to figure out without too much work. If you get bored sometime, see if you can discover the formula for the roots of a cubic in terms of its coefficients.

we observe that, since $\sqrt{\tau^2 - 4\Delta}/2$ is a non-negative number, this root can only become negative if $\tau/2$ is negative, that is if $\tau < 0$. But for Eq. (64) to be negative, $\tau/2$ has to be more negative than $\sqrt{\tau^2 - 4\Delta}/2$ is positive, and this will hold only if $\Delta > 0$. (If $\Delta < 0$, the quantity $\sqrt{\tau^2 - 4\Delta} = \sqrt{\tau^2 + 4|\Delta|} > \sqrt{\tau^2} = \tau$.) Since both roots must be negative at the same time for linear stability, we again reach the conclusion that a constant solution $\mathbf{u}_\star$ is linearly stable if and only if Eqs. (59) and (60) hold.

For the general case of N chemical concentrations reacting with each other in the absence of diffusion, the evolution equation takes the general vector form $d\mathbf{u}/dt = \mathbf{f}(\mathbf{u})$ where $\mathbf{u} = (u_1(t), \cdots, u_N(t))$ and where the reaction vector is given by N functions involving the N concentrations $\mathbf{f} = (f_1(\mathbf{u}), \cdots f_N(\mathbf{u}))$. A constant solution then satisfies $\mathbf{f}(\mathbf{u}_\star) = \mathbf{0}$, which is N coupled nonlinear differential equations. A given constant solution $\mathbf{u}_\star$ is linearly stable if all of the N eigenvalues σ_i of the $N \times N$ eigenvalue-eigenvector problem $\mathbf{J}\,\delta\mathbf{u}_0 = \sigma\,\delta\mathbf{u}_0$ have negative real part, where $\mathbf{J} = \partial f_i/\partial u_j|_{\mathbf{u}_\star}$ is the $N \times N$ Jacobian matrix of $\mathbf{f}(\mathbf{u})$ evaluated at the fixed point. There is no practical analytical method for finding the eigenvalues of a $N \times N$ matrix for $N > 2$ or for determining when all of the real parts of the eigenvalues are negative, so one needs to turn to a computer to estimate the eigenvalues numerically. Fortunately this is fast and easy to do for most problems of interest and so many linear stability calculations have been carried out numerically.

Case 4: linear stability of a constant solution for two-coupled reaction-diffusion equations in one space dimension

The last case is fairly easy since it is a combination of case 2 and case 3 above, no new ideas are needed. Assume that we have two coupled autonomous (no-explicit time dependence) one-space-dimension reaction-diffusion evolution equations for two concentrations $u_1(t, x)$ and $u_2(t, x)$:

$$\partial_t u_1(t, x) = D_1 \partial_{xx}^2 u_1 + f_1(u_1, u_2), \tag{65}$$

$$\partial_t u_2(t, x) = D_2 \partial_{xx}^2 u_2 + f_2(u_1, u_2), \tag{66}$$

where the general functions $f_i(u_1, u_2)$ represent the reaction kinetics. We will analyze these equations on an infinite domain

$$-\infty < x < \infty, \tag{67}$$

since this simplifies the mathematics by allowing us to ignore the boundary conditions on u_1 and u_2 at the end points of some interval.

Since the space and time derivatives vanish when acting on a constant solution, any constant solution $\mathbf{u}_\star = (u_{1\star}, u_{2\star})$ must be a zero of the two reaction terms:

$$f_1(u_{1\star}, u_{2\star}) = 0, \tag{68}$$

$$f_2(u_{1\star}, u_{2\star}) = 0. \tag{69}$$

It can be difficult to find even one solution of two coupled nonlinear equations but let's assume we know at least one constant solution.

We again study the linear stability of the constant solution $(u_{1\star}, u_{2\star})$ by finding a mathematical criterion that will tell us when the magnitude of an arbitrary tiny perturbation of the constant concentrations $(u_{1\star}, u_{2\star})$ will grow (instability) or decay (stability) over time. As we did for case 3, we assume that a solution of the reaction-diffusion equations Eqs. (65) and (66) can be written as a tiny perturbation of each concentration like this:

$$u_1(t, x) = u_{1\star} + \delta u_1(t, x), \qquad |\delta u_1| \ll |u_{1\star}|, \tag{70}$$

$$u_2(t, x) = u_{2\star} + \delta u_2(t, x), \qquad |\delta u_2| \ll |u_{2\star}|, \tag{71}$$

where the functions δu_1 and δu_2 are assumed to be everywhere tiny in magnitude. Substituting these expressions into the evolution equations Eqs. (65) and (66) and using the same simplifications that we

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carried out for case 3 above leads to the following evolution equations for the two perturbations:

$$\partial_t \delta u_1(t,x) = D_1 \partial_{xx}^2 \delta u_1 + a_{11} \delta u_1 + a_{12} \delta u_2, \tag{72}$$

$$\partial_t \delta u_2(t,x) = D_2 \partial_{xx}^2 \delta u_2 + a_{21} \delta u_1 + a_{22} \delta u_2, \tag{73}$$

where the a_{ij} are again given by Eqs. (39) and (40).

These are constant-coefficient linear partial differential equations and their solutions are a superposition of exponentials. A given exponential solution can be found by combining cases 2 and 3 above by writing

$$\delta u_1(t,x) = \delta u_{10} \, e^{\sigma t} \, e^{ikx}, \tag{74}$$

$$\delta u_2(t,x) = \delta u_{20} \, e^{\sigma t} \, e^{ikx}, \tag{75}$$

where both terms have the *same* growth rate σ and the *same* wavenumber k. Substituting these expressions into the linear pdes Eqs. (72) and (73) leads to the exact same equations Eqs. (41) and (42) as above except the diffusion terms alter the diagonal matrix elements a_{11} and a_{22}, leading to the matrix

$$\mathbf{A}_k = \begin{pmatrix} a_{11} - D_1 k^2 & a_{12} \\ a_{21} & a_{22} - D_2 k^2, \end{pmatrix} \tag{76}$$

We now have an infinity of linear stability cases to solve: for each wavenumber $k > 0$, determine whether both eigenvalues σ_{ik} of the matrix $\mathbf{A}_k$ have negative real parts. Fortunately, given the key result Eqs. (59) and (60) above, the discussion is easy. You should now be well prepared to read and understand the discussion of the Segel-Jackson paper which is what you should read next to complete your understanding of the Turing instability.

There is one more detail worth mentioning. In all of the above discussion (all four cases), I have assumed that the reaction kinetic functions $f_i(\mathbf{u})$ are simple algebraic functions, like a polynomial or ratio of polynomials or possibly involving trig or hyperbolic functions or exponential functions of the concentrations. But it is fairly common when dealing with reaction-diffusion systems like Eq. (19), or like Eqs. (65) and (66), or when dealing with other pattern-forming evolution equations, that the functions $f_i(\mathbf{u})$ might also involve spatial derivatives of the concentrations. For example, in Eq. (19), one might have an expression like

$$f(u) = (\partial_x u) \, u^2, \tag{77}$$

and you saw for the Navier-Stokes equations of fluid dynamics that the nonlinear term was an advective derivative $-(\mathbf{v} \cdot \nabla)\mathbf{v}$ that involves spatial derivatives of the velocity components. The existence of derivatives in the functions $f_i(\mathbf{u})$ raises the question of what does one mean by the derivative $f'(u_\star) = (df/du)_{u_\star}$ in Eq. (23) that is needed to derive the linearized evolution equation.

The answer is that the expression df/du has to be understood as the expression one gets by linearizing $f(u_\star + \delta u$ to lowest (linear) order in the small perturbation δu and in derivatives of δu. Strictly speaking, $f(u) = f(u(t))$ is not a function of a variable but a function of a function $u(t)$, and so one has to compute the so-called functional derivative $\delta f/\delta u$ of f with respect to the function $u(t)$, not an ordinary derivative. We can ignore the distinction between ordinary derivatives and functional derivatives as long as there are no derivatives of u_i present.

It is perhaps easier to show by an example rather than explain verbally how to compute and understand the functional derivative of some expression $f(u(t))$ in the case when derivatives of u appear in the reaction rate. You simply substitute $u + \delta u$ into f and assume that not only δu is small but that all spatial derivatives of δu (of any order) are small. Then one expands $f(u(t) + \delta u)$ in powers of δu and of its derivatives, and finally drop all terms that are not linear in δu or in derivatives of δu.

This leads to the following calculation for the specific expression Eq. (77)

$$f[u(t) + \delta f(t)] = \partial_x [u + \delta u] \, (u + \delta u)^2 \tag{78}$$

$$= (\partial_x u + \partial_x \delta u) \, (u^2 + 2u \, \delta u + \delta u^2) \tag{79}$$

$$= \left[\partial_x u \, u^2\right]_0 + \left[u^2 \partial_x \delta u + 2u \, \partial_x u \, \delta u\right]_1 + \text{higher order terms.} \tag{80}$$

So the functional derivative $\delta f / \delta u$ of Eq. (77) evaluated at the function $u(t)$ is given by

$$\frac{\delta f}{\delta u}[u(t)] = u^2 \partial_x \delta u + 2u \partial_x u \, \delta u. \tag{81}$$

We see that the functional derivative is really a linear operator (much like you learned about in a quantum mechanics course) that acts on a function $u(t)$, and typically the functional derivative has terms involving derivatives of δu as well as δu itself.

For the specific term $f(u) = (\partial_x u)u^2$, the linear evolution equation for δu, Eq. (9), becomes

$$\partial_t \delta u(t,x) = D \partial_{xx}^2 \delta u + u^2 \partial_x \delta u + (2u \partial_x u) \, \delta u. \tag{82}$$

When evaluated at a specific constant solution $u_\star$, this further becomes

$$\partial_t \delta u = D \partial_{xx}^2 \delta u + u_\star^2 \partial_x \delta u, \tag{83}$$

since the last term $(2u \partial_x u)\delta x$ vanishes if u is a constant function. The only new detail compared to the earlier discussions is the appearance of a $\partial_x \delta u$ term. But this doesn't change the discussion in any essential way. For example, when one substitutes $\delta u(t,x) = e^{\sigma t} e^{ikx}$, Eq. (24), into Eq. (83), one finds that Eq. (24) still satisfies the linearized equation Eq. (83) provided that the growth rate is equal to

$$\sigma = -Dk^2 + iku_\star^2. \tag{84}$$

The growth rate is now complex valued because of the ik term that the derivative ∂_x brings in. Since the real part of σ is always negative, a constant solution $u_\star$ is always linearly stable for the reaction term Eq. (77)

Try this yourself, see if you can calculate the following functional derivative to show that

$$\frac{\delta}{\delta u} \left[u \left(\partial_x u \right)^2 \partial_{xx}^2 u \right] = (\partial_x u)^2 \, \partial_{xx}^2 u \, \delta u + 2u \, \partial_x u \, \partial_{xx}^2 u \, \partial_x \delta u + u \, (\partial_x u)^2 \, \partial_{xx}^2 \delta u. \tag{85}$$

This completely vanishes when evaluated at any constant solution $u_\star$, so this term cannot cause linear instability of a constant solution.