Engsci 711

Assignment 2

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Question 1

Consider the system:

$$\dot{x} = y + \mu x$$
$$\dot{y} = -x + \mu y - x^2 y$$

where μ is a control parameter.

a) For what parameter values do you expect a Hopf bifurcation to occur at the origin?
b) Check the stability and type of the fixed point at the origin on either side of the bifurcation.
c) Use XPPAut to explore the neighbourhood this bifurcation and determine whether the Hopf bifurcation is subcritical, supercritical or degenerate (periodic solution appears at bifurcation but disappears for all other parameter values). Plot some typical solutions in the phase plane for these cases.
d) Verify *analytically* that the Hopf bifurcation is non-degenerate, i.e. that it has a *non-zero crossing speed* as the parameter varies.

Question 2

This question is motivated by the study of *biochemical switches*. These arise in the study of gene regulation and pattern formation problems such as 'how did the zebra get its stripes?'.

Here we look at a simple model of gene regulation developed by Lewis et al. (1977). In this model, a gene G is activated by a biochemical signal substance S. The idea is that the gene may normally be inactive but can be 'switched on' to produce a gene product (protein etc) when S exceeds a certain threshold. In pattern formation models the gene product could be e.g. a pigment molecule leading to striped patterns.

Let $p(t)$ be the concentration of the gene product and assume the concentration of the signal substance S, denoted by s_0, is a control parameter. The model is then

$$\dot{p} = k_1 s_0 - k_2 p + \frac{v_m p^2}{K_m^2 + p^2}$$

This model is based on simple 'reaction kinetics'-style modelling. It includes: a linear production term for how S leads to an increase in p, a linear decay term for how the product is removed from the system and a nonlinear *autocatalytic* (positive self-feedback) production term. Here the $k_i > 0$ are positive first-order rate constants, v_m is a fixed positive constant representing the maximum 'reaction velocity' of the autocatalytic term and K_m is a Hill constant with the same units as p. Note that when $p = K_m$, the autocatalytic term is equal to half the maximum reaction velocity, i.e. $v_m/2$.

a) Our first step here will be to non-dimensionalise this system. In particular, for this part you should show that the system can be put in the non-dimensional form

$$\frac{dx}{d\tau} = s - rx + \frac{x^2}{1+x^2}$$

where $r > 0$ and $s \geq 0$ are dimensionless combinations of parameters (i.e. of the k_i, v_m, s_0 and K_m).

You should have done this sort of thing before, and Richard will cover this in more detail, but here is a brief guide:

- Introduce non-dimensional variables x, τ, for product and time respectively, by writing:

$$p = P_0 x$$
$$t = T_0 \tau$$

Here P_0 and T_0 are arbitrary scale factors that we are *free to choose* in order to simplify our problem or to emphasise the relative importance of various terms.

The art of choosing the scale factors to balance various terms is sometimes called *scaling analysis*, *the method of dominant balances*, and/or *order-of-magnitude analysis*. Inevitably this sort of analysis requires some subjective judgement - in principle we are free to choose any non-dimensionalisation we like (e.g. we can measure the same length in cm or metres etc).

- Here we are lucky: we know what we want the final simplified form to look like. Thus you should choose P_0 and T_0 to be combinations of k_1, k_2, K_m, v_m, s_0 so that the system takes the given non-dimensional form. Make sure to state what your choices are and also what s and r are in terms of the problem parameters.

b) Now we will analyse the non-dimensional form

$$\frac{dx}{d\tau} = s - rx + \frac{x^2}{1+x^2}$$

where $r > 0$ and $s \geq 0$.

- Sketch or plot various graphs of $rx - s$ and $\frac{x^2}{1+x^2}$, considered as functions of x, to indicate how the number of fixed points depends on the values of r and s. You do not need to given any numerical values (i.e. you just need to indicate *qualitative* behaviour here).

c) Show *analytically* that if $s = 0$:

- $x = 0$ is a solution.
- There are also two positive (> 0) solutions if $r < r_c$ for some r_c that you should determine.

d) Assuming that r is fixed at $r < r_c$, sketch or plot the functions $rx - s$ and $\frac{x^2}{1+x^2}$ in order to illustrate how the existence of fixed points varies with s. What sort of bifurcations would you expect to occur?

e) Evaluate the stability of the origin for $s = 0$. Use this information and the information from the previous part to construct a *qualitatively correct* bifurcation diagram illustrating how the *existence and stability* of the fixed points vary with s (still assuming r is fixed below r_c).

Note: you *do not need to do any more analytical justification of the stabililities.* Just give a reasonable explanation instead (hint: although $s \geq 0$, if you are having trouble justifying the stabilities, you *may* find it helpful to also think about what happens for negative s values as well).

f) Assume that initially there is no gene product, i.e. $p(0) = 0$, and hence $x(0) = 0$. Suppose s is slowly increased from zero (i.e. the activating signal is turned on), giving x time to equilibrate for each s value. Again assume r is held fixed below r_c.

- How does the qualitative behaviour of x vary with s under this scenario.

- What happens if s is *subsequently* reduced back to zero? Does the gene turn off again? What sort of phenomenon does this represent (hint: look at the most recent version of the tutorial 3 worked answers).

Question 3

Consider the system

$$\dot{x} = x^2 y - x^5$$
$$\dot{y} = -y + 3x^2$$

where $x, y \in \mathbb{R}$.

a) Verify that the origin is a fixed point of this system.

b) Find the Jacobian derivative - first as a function of x and y and then evaluated at the origin $(0,0)$.

c) Find the eigenvalues of the linearisation about the origin and - if they exist - the associated stable, unstable and centre eigenspaces, E^s, E^u and E^c respectively. Sketch the eigenspaces in the (x, y) plane. You do not (yet) need to show any nearby trajectories.

d) Use a power series expansion to calculate an expression for the centre manifold $W^c_{loc}(0,0)$ that is correct up to and including quartic order.

e) Use the previous expression to determine the dominant dynamics on the centre manifold, again correct up to and including quartic order, and thus determine whether these dynamics are (asymptotically) stable or unstable.

f) Sketch the local phase portrait of the system near the equilibrium.

Question 4

Consider the system

$$\dot{x} = y$$
$$\dot{y} = -xz$$
$$\dot{z} = -z + x^2 + xy$$

a) Linearise the system about the origin and hence determine that there is a *two-dimensional* centre (slow) manifold. State which variables are the slow variables and which is the fast.

b) Before carrying out a systematic centre manifold reduction we'll first consider a more naive form of *quasi-steady-state* approximation. We need to describe this a bit first!

The key to this sort of argument is suppose that z 'rapidly reaches its steady state' and hence assume

$$\dot{z} \approx 0$$

therefore

$$z = x^2 + xy$$

Let's call this the 'quasi-steady state manifold' to distinguish it from the centre/slow manifold. To see the implications of this assumption for a stability analysis we'll need a general nonlinear method for determining the stability of the origin in our resulting two-dimensional quasi-steady and/or slow systems.

In particular, in order to analyse the *nonlinear stability* of the origin in terms of the remaining x and y dynamics we can use a so-called Lyaponuv or 'energy-like' function, $E(x, y)$. This is a scalar-value, continuously-differentiable function that satisfies $E(x, y) > 0$ for all $x, y \neq 0$ (at least in some neighbourhood of interest).

If we can show that this function is *strictly decreasing along model trajectories*, then it follows that the origin is a *stable* equilibrium (see e.g. Strogatz 7.2 for more discussion). If it is *strictly increasing along model trajectories* then the origin is *unstable*.

Here we can use (magic):

$$E(x, y) = x^4 + 2y^2$$

Its rate of change along trajectories follows from the chain rule:

$$\dot{E} = \frac{\partial E}{\partial x}\dot{x} + \frac{\partial E}{\partial y}\dot{y}$$

Now, the tasks:

- First substitute in the expressions for the energy function $E(x, y)$ and the dynamics $\dot{x}, \dot{y}$ into the above expression for $\dot{E}$.
- Next substitute in the quasi-steady-state assumption $z = x^2 + xy$ and deduce whether the origin is stable or unstable on the 'quasi-steady manifold'.

c) Now, carry out a systematic centre manifold reduction instead.

- Use the usual procedure to find that the centre (slow) manifold is given by

$$z = x^2 - xy + O(x^4 + y^2)$$

Note: If your centre manifold is two-dimensional then you need to expand in two variables. An example of expanding an arbitrary two-variable function in variables u and v to quadratic order is:

$$f(u, v) \approx a + bu + cv + du^2 + euv + fv^2$$

- Repeat the calculation of the rate of change of the energy function along the slow manifold and show that the result is the opposite to that found from the naive quasi-steady state approximation.