Assignment 7

Due Friday, October 30

1.

Consider the system

$$x' = 2y - 3z, \qquad y' = 3x - y - 3z, \qquad z' = -2x + 2y - z.$$

(a) Write the matrix of this system, and find and factor its characteristic polynomial. Then find an eigenvector for each eigenvalue.

(b) Find the solution with $x(0) = 1, y(0) = 0, z(0) = 0$.

(c) Describe what happens to solutions as $t \to \infty$. Which initial states give solutions that approach the origin? What happens to every other solution, and how can you tell from the initial state which way it heads?

2.

Consider the system

$$x' = 2y + 2z, \qquad y' = x - y - 2z, \qquad z' = -2x - y.$$

Let A be the matrix of this system. In Chapter 9, a quadratic factor with no real roots led us to an invariant plane. Here is the procedure. First complete the square to write the factor as $(r - a)^2 + \omega^2$ with $\omega > 0$. Then find a nonzero vector v solving

$$\big((A - aI)^2 + \omega^2 I\big)v = 0,$$

and set

$$w = -\frac{1}{\omega}(A - aI)v.$$

Then $Av = av - \omega w$ and $Aw = \omega v + aw$. So v and w span a plane that the flow never leaves, and in the basis v, w the matrix of A on this plane is

$$\begin{pmatrix} a & \omega \\ -\omega & a \end{pmatrix}, \qquad \text{with flow} \qquad e^{at}\begin{pmatrix} \cos \omega t & \sin \omega t \\ -\sin \omega t & \cos \omega t \end{pmatrix}.$$

On this plane, states rotate at angular speed ω while scaling by e^{at}.

(a) Write the matrix of this system, and find and factor its characteristic polynomial. What motion does each factor describe? For the linear factor, give the exponential rate along its line. For the quadratic factor, give the scaling rate and the time for one full turn in its plane.

(b) Find an eigenvector u for the linear factor. Then use the procedure above to find vectors v and w spanning the invariant plane.

(c) Find the solution with $x(0) = 2, y(0) = -1, z(0) = 0$.

(d) Describe what happens as $t \to \infty$ to solutions starting on the invariant line, solutions starting in the invariant plane, and solutions starting anywhere else.

3.

In each part, write the matrix as a sum of two pieces that commute, and use this to compute its exponential.

(a) Compute e^{tB}, where

$$B = \begin{pmatrix} -2 & 1 & 0 \\ 0 & -2 & 1 \\ 0 & 0 & -2 \end{pmatrix}.$$

(b) Consider

$$C = \begin{pmatrix} 0 & 2 & 1 & 0 \\ -2 & 0 & 0 & 1 \\ 0 & 0 & 0 & 2 \\ 0 & 0 & -2 & 0 \end{pmatrix} = \begin{pmatrix} R & I \\ 0 & R \end{pmatrix}, \qquad R = \begin{pmatrix} 0 & 2 \\ -2 & 0 \end{pmatrix},$$

where I is the 2×2 identity and 0 is the 2×2 zero matrix.

4.

A 6×6 matrix A has characteristic polynomial

$$(r+3)(r-1)(r^2+4)(r^2+2r+5).$$

We do not need the matrix itself to understand the motion of $X' = AX$.

(a) Make a table with one row for each factor. In each row, record whether the factor gives an invariant line or an invariant plane, whether the motion there grows, decays, or neither, and the period of any oscillation.

(b) Describe what happens as $t \to \infty$ to the solution starting from each of these states:

1. a state on the invariant line from $r + 3$;
2. a state in the invariant plane from $r^2 + 4$;
3. a state with components only in the two invariant planes;
4. a state with a nonzero component on the invariant line from $r - 1$.

5.

Every cell carries instructions for building proteins in its genes. To make a protein, the cell copies a gene into a molecule called mRNA, then builds the protein from that copy. Some proteins are **repressors**: a repressor binds to the DNA at the start of another gene and blocks that gene from being copied. The more repressor there is, the less of the other protein gets made. Proteins don't last forever, either. The cell breaks them down, and they are diluted as the cell grows and divides.

In 2000, Michael Elowitz and Stanislas Leibler used these ingredients to build a biological clock from scratch in the bacterium *E. coli*. They chose three repressor genes that occur in no natural clock and arranged them in a ring:

- the protein LacI represses the gene for TetR;
- the protein TetR represses the gene for CI;
- the protein CI represses the gene for LacI.

They called the circuit the **repressilator**. To watch it, they added a gene for a green fluorescent protein that TetR also represses, so a cell glows when its TetR level is low. Under a microscope, individual cells blinked on and off, with a period of around 150 minutes. That is about three times as long as it takes the cells to divide.

Why would this ring oscillate? Suppose a cell has a little extra LacI. Extra LacI shuts down TetR production, so TetR falls. With less TetR, the gene for CI is released, so CI rises. Extra CI

shuts down LacI production, so LacI falls. The original excess of LacI has come back around the ring as a *shortage* of LacI. Each step takes time, because proteins are built and removed gradually, so the levels keep overshooting. Whether these swings die away or grow depends on how strongly each repressor acts. That is what we can decide with linear algebra.

Here is a simplified model, which tracks only the proteins. In a steady state, all three proteins sit at the same level, with production exactly balancing removal. Let x, y, and z be the deviations of LacI, TetR, and CI from that steady level. We measure time in units of a protein's lifetime, so each protein is removed at rate equal to its own deviation. Each production rate is a decreasing function of the repressor upstream of it. For small deviations, we replace that curve by its tangent line, whose slope we write as $-K$. This gives

$$x' = -x - Kz, \qquad y' = -y - Kx, \qquad z' = -z - Ky.$$

For example, the term $-Kx$ in the equation for y' says that extra LacI ($x > 0$) lowers TetR production. The constant $K > 0$ measures how sharply production responds to its repressor.

(a) Write the matrix of this system, and find and factor its characteristic polynomial. Don't multiply out $(r+1)^3$. Instead, write $s = r + 1$ and use the identity

$$s^3 + K^3 = (s + K)(s^2 - Ks + K^2),$$

which you can check by multiplying out the right side. Then complete the square in the quadratic factor.

(b) The quadratic factor describes oscillation in an invariant plane. Find its frequency and its scaling rate in terms of K.

(c) If the oscillations in the invariant plane die out, the protein levels settle back to their steady state, and the clock stops ticking. For the circuit to work as a clock, the oscillations must grow, so that they become large enough to notice and measure. For which values of K does this happen?