Two-dimensional differential equations and phase planes

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The phase plane

For systems of two equations in two unknowns, the state of the system can be represented as a point in the *phase plane*. As with the phase line, the phase plane does not explicitly show the time dependent behaviour of the system. Provided the system is *autonomous* (i.e. time does not explicitly appear on the right hand side of the equations), the instructions for how the state of the system is evolving is contained in the equations. Graphically, in the phase plane, these directions are interpreted as horizontal and vertical components of a vector that shows the direction of "motion". By motion, I mean where the state of the system is going, which may or may not be physical motion – to give this its own term, we call the movement of solutions in the phase plane "the flow" (technically, this is not the precise definition of flow but it is close enough and often used informally).

Let's consider the example of the *lac* operon, described in class. The equations for the concentration of intracellular lactose and LacY are given by:

$$\frac{dl}{dt} = \beta l_{ext} LacY - \gamma l \tag{1}$$

$$\frac{dLacY}{dt} = \delta + p\frac{l^2}{l_0^2 + l^2} - \sigma LacY \tag{2}$$

To draw the phase plane, we must calculate and plot the nullclines, fill in enough direction-field arrows to see how solutions move through the phase plane, identify steady states and determine their stability graphically (if possible) and plot a few example solution curves. See Figure 1 for an illustration of this procedure. The following list explains each panel of the figure.

(A) The $LacY$ nullcline has a horizontal asymptote (horizontal dashed line) at $(\delta + p)/\sigma$ and near $l = 0$ it is shaped like the parabola $(\delta + p\frac{l^2}{l_0^2})/\sigma$ (i.e. it is flat at $l = 0$). At $l = l_0$, the nullcline is exactly halfway between δ/σ and $(\delta + p)/\sigma$ (vertical dashed line).

(B) The l nullcline is a straight line through the origin with slope $\gamma/(\beta l_{ext})$. For l_{ext} large (e.g. l_{ext1}), the two nullclines cross only once (at a relatively large value of l and $LacY$ close to $(\delta + p)/\sigma$) – off the right edge of the diagram. For intermediate values of l_{ext} (e.g. l_{ext2}), there are three crossings. For small values of l_{ext} (e.g. l_{ext3}), these is a single crossing at low l and low $LacY$ concentrations.

(C) Consider the case $l_{ext} = l_{ext2}$. Add horizontal and vertical direction vectors (arrow heads omitted for now) to the appropriate nullclines. Because $LacY$ is the vertical variable, any solution that sits directly on the the $LacY$ nullcline at some moment in time has $dLacY/dt = 0$ at that moment so the vertical component of the vector at that point is zero (hence horizontal

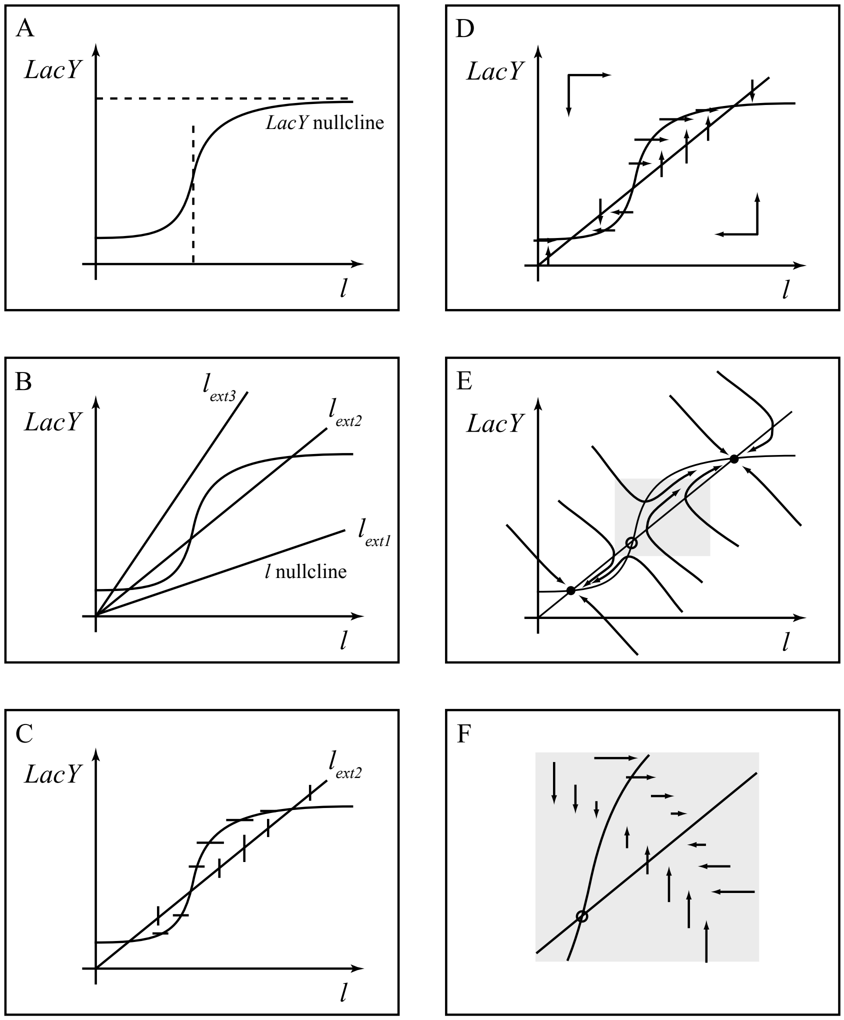

Figure 1: See text for explanation.

vectors on the $LacY$ nullcline). This means that as solutions cross the $LacY$ nullcline, they must run horizontally. Similarly, the vectors right on the l nullcline are vertical.

(D) Filling in arrow heads on the nullclines requires looking at the equations above. Anywhere above the $LacY$ nullcline, $LacY$ must be decreasing (imagine plugging in a large value of LacY and a small value of l to the $LacY$ equation). Similarly, below the Lac nullcline, $LacY$ is increasing. A similar conclusion can be drawn for above and below the l nullcline. This same arrow-estimating approach tells us that above and left of the two nullclines, flow is down and right and below and right of both nullclines, flow is up and left. On the diagram, there is not enough space to include vectors between the nullclines but they can be inferred from the vectors on the nullclines. Note that if you think of the nullclines as chopping the plane into distinct regions, if you know the direction of flow at one point in a particular region, the flow at all other points in the same region have horizontal and vertical components with the same sign as the known point. Also, provided the nullclines represent zeros of multiplicity one (i.e. the zero appeared on the right hand side of the differential equation as a factor $(x-a)$ rather than $(x-a)^2$), crossing a nullcline means either the horizontal or vertical component of the

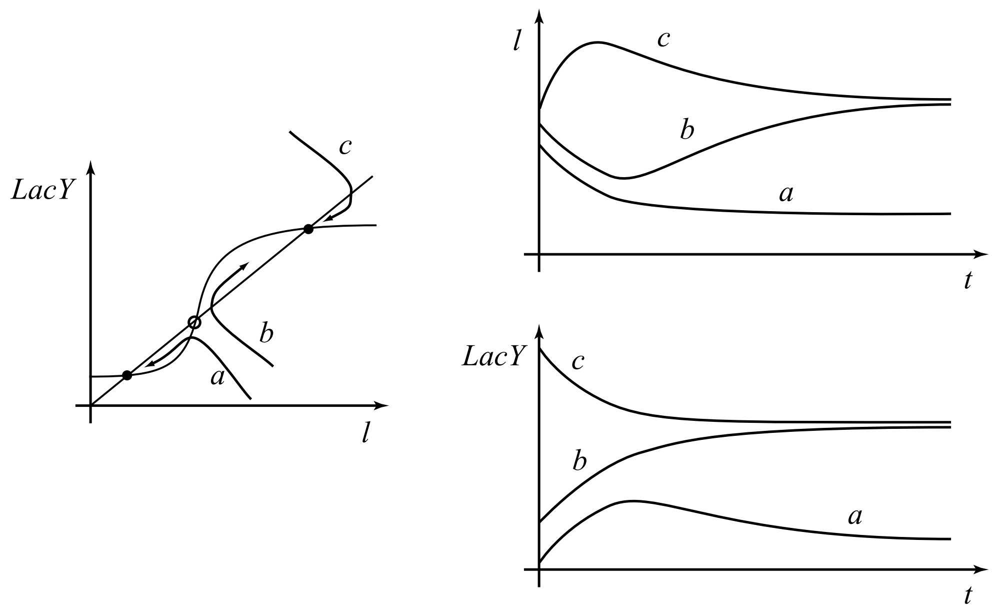

Figure 2: See text for details.

flow changes sign. This is illustrated in (F) which is a blow-up of the shaded region shown in (E).

(E) Choosing a set of widely spaced initial condition, we can now fill in a few solution curves in the phase plane. We can clearly see that the upper and lower steady states are stable. This follows from the fact that no matter what direction you go from the steady state (taking a small step), the flow forces you back to the steady state. We can also see that the middle steady state is unstable. Notice that by drawing many solution curves near the middle nullcline, you should be able to find one curve on each side (one coming from above-left and one from below-right) that actually makes it to the steady state – all others lead away.

In Figure 2, I've drawn three solutions in the phase plane and translated each of them into a curve for $l(t)$ and $LacY(t)$ drawn as functions of time. Notice that whenever a solution curve in the phase plane crosses a nullcline, one of the curves on the left has a maximum or minimum. If the nullcline being crossed is the $LacY$ nullcline, the max/min is in the $LacY$ variable (similarly for l nullcline crossings). This is due to the fact that upon crossing a nullcline, the solution curve necessarily changes direction with respect to that variable.

To add: - crossing of curves in the phase plane, as functions of time.

Classification of steady states

Steady states in the phase plane come in a limited number of shapes. Except for a few degenerate

Bistability and switches

The *lac* operon is known to underlie bistability in the metabolic activity of *E. coli*. Bistability means that for some environmental conditions, there are two stable modes of distinct behaviour that might be seen. For the *lac* operon, these correspond to using either glucose or lactose as the primary source of energy. In the phase plane, bistability occurs when there are simultaneously (i.e. for a single set of parameter values) two stable steady states. As illustrated in the phase plane above, the *lac* operon demonstrates bistability when the concentration of extracellular lactose is in an intermediate range (e.g. l_{ext2}). In this case, there is a third steady state (an unstable one) sitting between the two stable ones – this is actually common for bistable systems and is a result of topological constraints that exist on vector fields in the plane (and on a line, for that matter).

One important feature of systems that demonstrate bistability is that they can be used to generate a switch. To make a switch from a bistable system, we need several features. First, we give each stable state a behaviour designation; for the *lac* operon, these would be "glucose mode" and "lactose mode". Next, we need to have control of some parameter that allows us to eliminate each of the two modes by moving the parameter across a range of values. For the *lac* operon, this can be done by changing the concentration of extracellular lactose, l_{ext}. Suppose l_{ext} is at a level for which the glucose mode exists (low or intermediate) and the cell is currently in glucose mode. To flip the switch (i.e. change to lactose mode), we must somehow eliminate the glucose mode. This can be accomplished by increasing l_{ext} to a high value (e.g. l_{ext1} as shown in Figure 1B). Once the external lactose concentration is increased, the phase plane changes in such a way that the flow drives the cell to the (only) high steady state. The cell is now in lactose mode. However, this is only half a switch. To have a complete switch, there must be a way of turning it back "off". In this case, decreasing the external lactose concentration does the trick. For l_{ext} small enough, the upper stable steady state disappears and the flow drives the cell back to glucose mode.

One important feature of a bistable switch is that the value l_{ext} for which the switch flips on is different from the value that switches it back off. This means that the process is not reversible (i.e. reversing a parameter change by a small amount at any stage of the switching process does not revert the state of the system to what it was before the original small change). This feature is sometimes called hysteresis. To summarize the terminology, a system can be bistable for a given set of parameter values. If, in addition, there is some way to irreversibly change the current state of the system from one stable state to the other by changing a parameter value, the system is a one way switch. If there is a way of changing a parameter value so that the system can be pushed from one state to the other and back again, the system is a switch. An irreversible switch demonstrates hysteresis.

One common feature of a switch is that as the switching parameter is changed in one direction, one of the stable steady states approaches and collides with the unstable steady state in the middle. This is clearly seen in the *lac* operon as shown in Figure 1B. Other ways of switching from one state to another exist but are more complicated and not as common.