2008 Lecture No.4
Bifurcations
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We can observe a complete change in behavior upon crossing the boundary separating the stable and unstable solutions. This observation must be generalized: whenever the solution to an equation changes qualitatively at a fixed value — called a critical value — of a parameter, this will be called a bifurcation. A point in parameter space where such an event occurs is defined to be a bifurcation point. From a bifurcation point emerge several (two or more) solution branches, either stable or unstable. The representation o f any characteristic property of the solutions as a function of the bifurcation parameter constitutes a bifurcation diagram. (Berge, Pomeau and Vidal, "Order within Chaos" Wiley 1984, p38)

Hopf Bifurcation

Supercritical Hopf bifurcation

$x' = ax - y - x(x^2 + y^2)$
$y' = x + ay - y(x^2 + y^2)$

The use of polar coordinates makes it possible to decouple the equation:
$r' = r(a - r^2)$
$\theta' = 1$

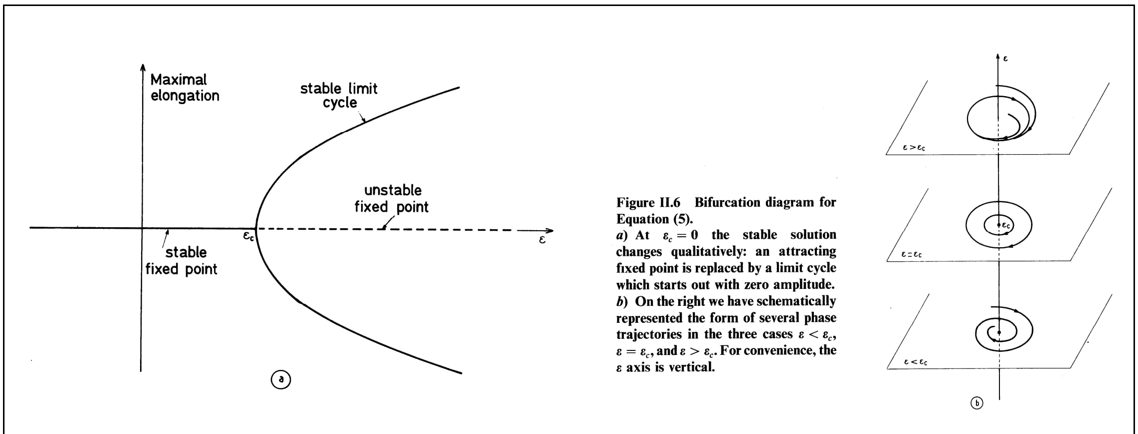


Figure II.6 Bifurcation diagram for Equation (5).
***a*) At $\varepsilon_c = 0$ the stable solution changes qualitatively: an attracting fixed point is replaced by a limit cycle which starts out with zero amplitude.**
***b*) On the right we have schematically represented the form of several phase trajectories in the three cases $\varepsilon < \varepsilon_c$, $\varepsilon = \varepsilon_c$, and $\varepsilon > \varepsilon_c$. For convenience, the ε axis is vertical.**

Berge, Pomeau and Vidal, "Order within Chaos" Wiley 1984, p39

Subcritical Hopf bifurcation

$r' = r(a + 2r^2 - r^4)$

$\theta' = 1$

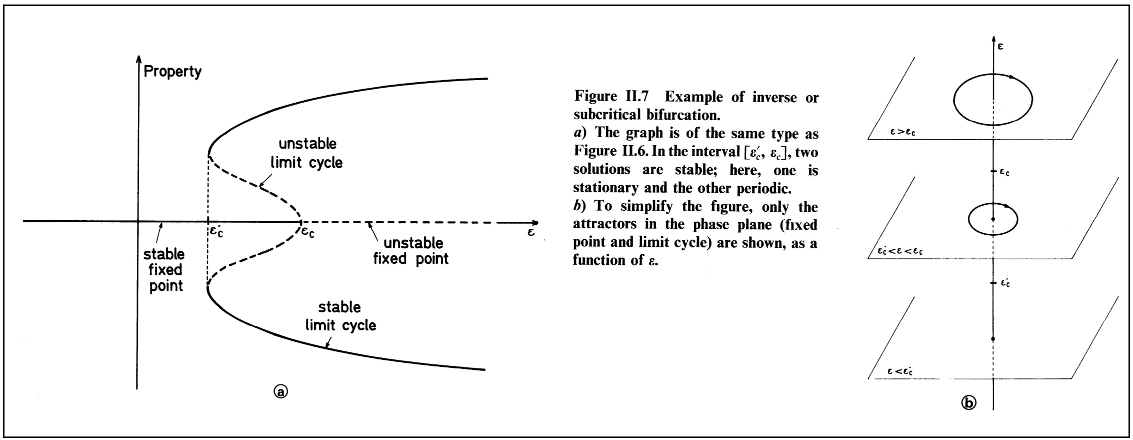


Figure II.7 Example of inverse or subcritical bifurcation.
a) The graph is of the same type as Figure II.6. In the interval $[\varepsilon_c', \varepsilon_c]$, two solutions are stable; here, one is stationary and the other periodic.
b) To simplify the figure, only the attractors in the phase plane (fixed point and limit cycle) are shown, as a function of ε.

Berge, Pomeau and Vidal, "Order within Chaos" Wiley 1984, p41

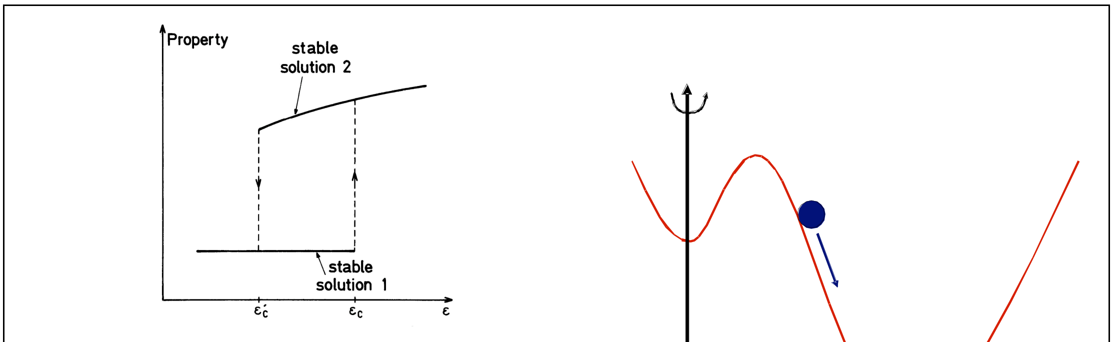


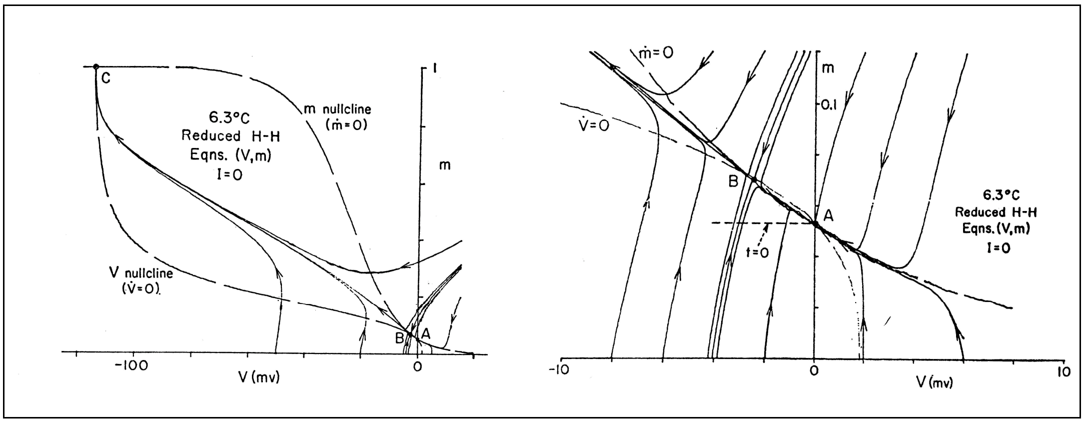
Figure II.8 Hysteresis phenomenon associated with a subcritical bifurcation. Because two stable solutions coexist on a finite interval of the bifurcation parameter, the transitions between them — when the parameter crosses the boundaries of this interval — take place at different values, depending on the direction of crossing: ε_c as ε is increased, ε_c' as ε is decreased (see arrows).

Berge, Pomeau and Vidal, "Order within Chaos" Wiley 1984, p42 (left)

Let us imagine varying the parameter successively in one direction and then the other. We will observe the hysteresis phenomenon shown schematically in the above figure. Hysteresis is the property of a subcritical Hopf bifurcation that is qualitatively different from that of a supercritical Hopf bifurcation.

Phase space methods

The aim is to expose to view part of the inner working mechanism of the Hodgkin-Huxley (H-H) equations. A knowledge of their mathematical properties can provide a guide for making future modifications of the model to match improved experimental data. A general conclusion of this analysis is that many of the physiologically important properties of the Hodgkin-Huxley model arise from certain qualitative mathematical properties of their equations.

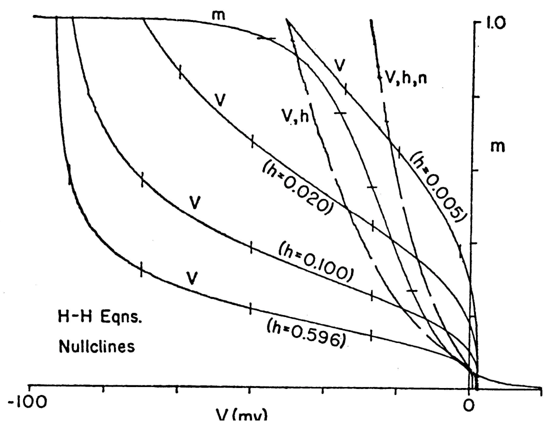


Left: Phase plane of V, m reduced Hodgkin-Huxley system, with h and n fixed at their resting values and I = 0. Right: Enlarged detail of the left panel to show two singular points.

FitzHugh, R. J. Gen. Physiology 43, p874, 875 (1960).

Even without solving a non-linear differential equation, one can often discover by these methods much useful information about the overall qualitative behavior of the solutions, such as the presence of stable and unstable states, threthold phenomena, and oscillations. Since the four-dimensional phase space of the Hodgkin-Huxley equations with coordinates V, m, h, n cannot be visualized, it is best to study first the properties of lower dimensional phase spaces obtained by omitting one or two coordinates.

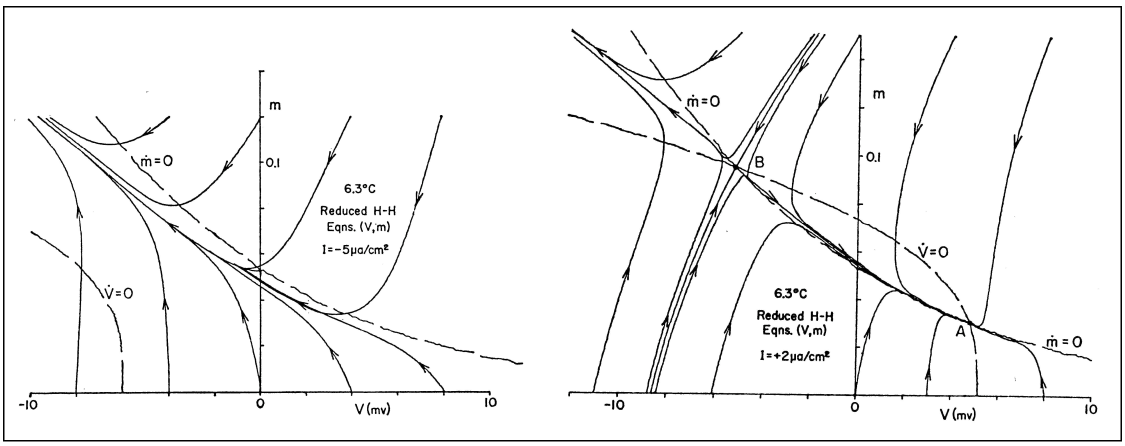
It is helpful to build up the system of equations conceptually step by step from its component parts. The variables are divided into two pairs according to the orders of magnitudes of their time constants. For brief periods of time, during which h and n change very little, V and m vary markedly. The behavior of V and m can therefore be studied, to a first approximation, by arbitrarily setting h and n constant and equal to their resting values, and solving the resulting V, m reduced system.



Solid lines are V and m nullclines. With decreasing h, the V nullcline rises and two fo its intersections with the m nullcline vanish, leaving only the resting singular point. Also shown as broken lines are the V, h nullcline (V' = h' = 0 in the V, m, h reduced system), which has three intersections with the m nullcline, and the V, h, n nullcline (complete system), which has only one. FitzHugh, R. J. Gen. Physiology 43, p876 (1960).

Next, the effect on the behavior of this reduced system produced by changing h and n to other constant values, or by changing I, can be investigated. Then h and n are reintroduced as variables to give the V, m, h and V, m, n reduced systems and finally the complete V, m, h, n system.

This synthetic process leads to a better understanding of the complete system than can be obtained by considering all the variables at once, and suggests how modifications in the separate equations will affect the behavior of the complete system.



When I is negative, V nullcline is lowered, singular points A and B have vanished, and excitation occurs (lfet). When I is positive, V nullcline is raised and singular points A and B have moved farther apart. FitzHugh, R. J. Gen. Physiol. 43, p877 (left) 878 (right) (1960).