2008 Lecture No.3

Mathematics of Excitability and Oscillation

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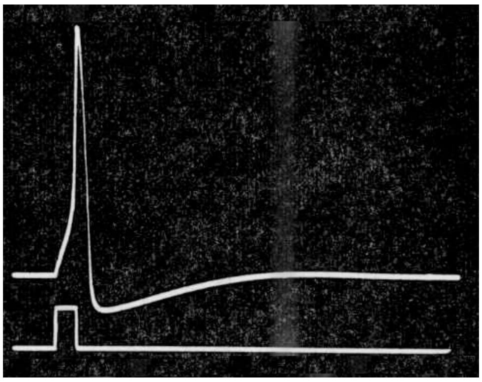
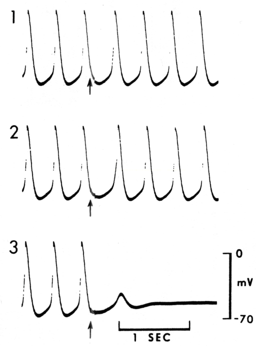
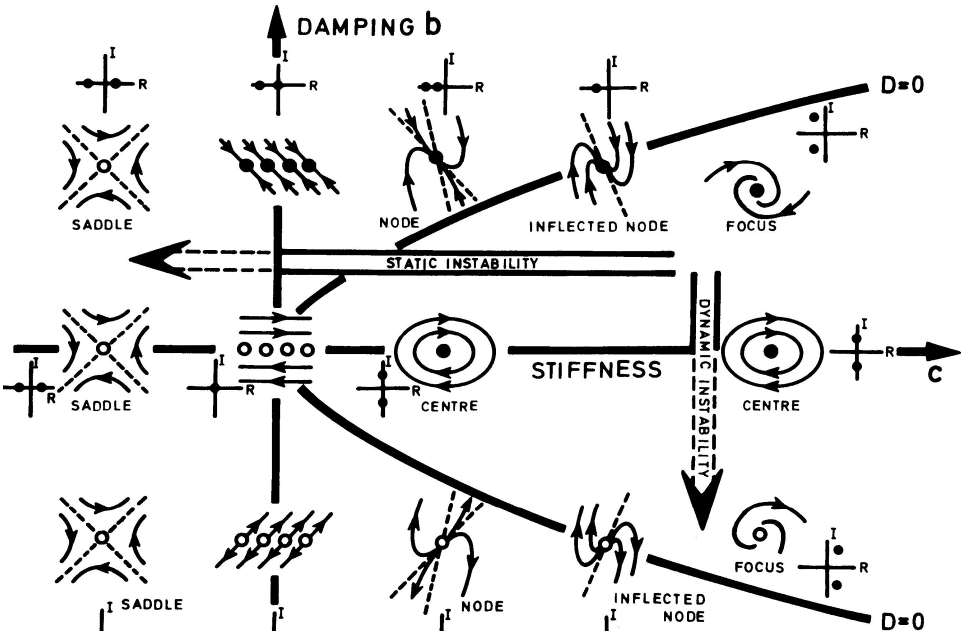


松本　元 「神経興奮の現象と実態」(丸善、1981)上、p106



Phase resetting (1 and 2) and cessation of spontaneous activity (3) of sinoatrial (SA) nodal pacemakers from kittens by brief subthreshold , deploarizing pulses. The spontaneous activity is only annihilated if the stimulus occurs over a narrow range of stimulus amplitude and phase.

From Jalife and Antzelevitch Science 206, 695 -697 (1979)



The phase portraits and root structure of a liner oscillator
From J.M.T. Thompson & H. B. Stewart
“Nonlinear Dynamics and Chaos ” Wiley 1986

This system can be described by the *van der Pol* equation[1] (see e.g. Schmidt and Tondl, 1986):

$$\frac{d^2x}{dt^2} - \varepsilon(1 - x^2)\frac{dx}{dt} + x = 0 \tag{1.4}$$

where the damping parameter $\varepsilon(1 - x^2)$ changes sign at $x = \pm 1$. (If $x < 1$, then the system switches on to increase x, and vice versa.) Here, ε plays an important role in determining oscillatory behaviour (Fig. 1.3). The *characteristic* function of equation (1.4) is given by

$$\lambda^2 - \varepsilon\lambda + 1 = 0. \tag{1.5}$$

The roots of this equation are

$$\lambda = \frac{\varepsilon \pm \sqrt{D}}{2} \tag{1.6}$$

where

$$D = \varepsilon^2 - 4. \tag{1.7}$$

If ε is small (e.g. $\varepsilon = 0.1$ or 1 in Fig. 1.3), the *discriminant*, D, is negative and thus we have two complex conjugate roots. In the $(x, dx/dt)$ phase plane, the singular point at the origin becomes an unstable *focus*. The oscillatory pattern is quite simply similar to that of a harmonic oscillator. It is useful to consider the motion of a ball in a potential field in this system. Using polar coordinates (see Haken, 1977, Thompson and Stewart, 1986), the following decoupled first-order equations are obtained

$$\frac{dr}{dt} = -\frac{dU}{dr} \tag{1.8a}$$

$$\frac{d\theta}{dt} = \text{constant} \tag{1.8b}$$

where r is the amplitude, θ is the phase, and U is the potential-energy function which has a vertical axis of rotation (Fig. 1.4). Then we can imagine a ball moving along the wall with the angular velocity $d\theta/dt$.

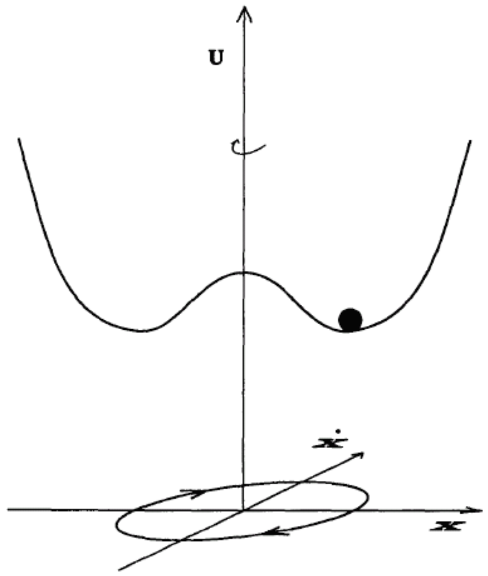


Figure 1.4 The limit-cycle oscillation illustrated by a circle on the (x, dx/dt) plane (below) and the movement of a ball on the rotational potential function (above) for small ε values. The temporal oscillations are quasi-sinusoidal because of the small ε values. The singular point (0, 0) becomes an unstable focus.

From Maatoshi Murase "The Dynamics of Cellular Motility" Wiley (1992) p7

When ε becomes large, highly nonlinear oscillation called *relaxation oscillation* results. In this case, the singular point $(x_0, dx_0/dt) = (0, 0)$ becomes an unstable *node*. By using *Liénard's transformation* (see Minorsky, 1947), the following differential equations are obtained:

$$\frac{dx}{dt} = \varepsilon(y - x^3 + x) \qquad (1.9a)$$

$$\frac{dy}{dt} = -\frac{1}{\varepsilon}x. \qquad (1.9b)$$

Since y is a more slowly changing variable than x (except for near the *horizontal isocline* or the *y-nullcline* or $dy/dt = 0$), the potential function is defined over the (x, y) phase plane (Fig. 1.5). According to the motion of a ball acted on by the potential function, we can recognize two processes: the slow change of the energy-accumulating process and the fast change of the energy-supplying process. The relaxation oscillations are characterized by these two distinct processes.

It is interesting to notice the close link between oscillations and excitability. The most famous example of excitability is provided by the nervous system as modelled by Hodgkin and Huxley (1952).[2] FitzHugh (1961, 1969) and Nagumo *et al.* (1962) developed a simple model, which is described by the following set of differential equations:

$$\frac{dx}{dt} = \varepsilon(y - x^3 + x) + Z \tag{1.10a}$$

$$\frac{dy}{dt} = -\frac{1}{\varepsilon}(x - a + by) \tag{1.10b}$$

where a and b are fixed parameters and Z is stimulus intensity. Since this model resembled the phase-plane model used by Bonhoeffer to explain the behaviour of passivated iron wires, FitzHugh called it the Bonhoeffer–van der Pol model (BVP for short). When $a = b = Z = 0$, the BVP model described by equations (1.10) can be reduced to the model for the relaxation oscillation described by equations (1.9).

Figure 1.6 shows the typical x- and y-nullclines of the BVP model. When $Z = 0$, the x-nullcline (solid curve) intersects with the y-nullcline (solid line) at the stable point (denoted by s). All trajectories approach this stable point. There is excitability in that movement of the phase point depends on the initial displacement of the phase point from the stable point. Of course, this system exhibits the oscillations under negative constant values of Z. This occurs because the x-nullcline is raised by the negative Z values as shown by the broken curve and the intersection (denoted by u) becomes unstable which leads to limit-cycle oscillation.

Many excitable–oscillatory phenomena (e.g. Belouzov–Zhabotinsky reactions, glycolitic systems) can be accounted for by this mechanism (see e.g. Krinsky, 1984 and Zykov, 1987). Here, we can see an interesting analogy between these oscillations and the machine sketched in Figure 1.2. That is, a constant flow causes oscillations.

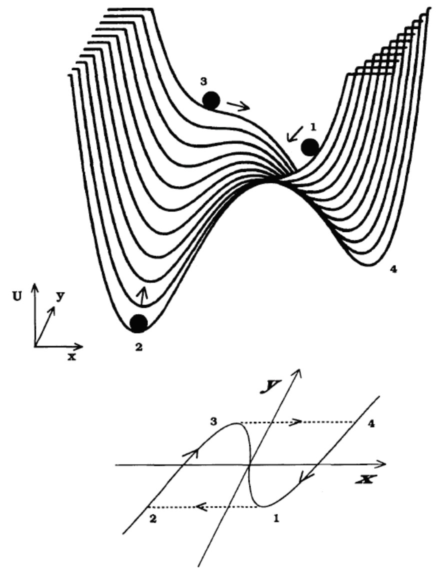


Figure 1.5 The relaxation oscillation illustrated by a bi-phasic path on the (x, y) phase plane (below) and the movement of a ball on the potential function (above) for large ε values. There are two distinct time-scales corresponding to the *fast* equation (1.9a) and the *slow* equation (1.9b). The movement of the ball summarizes the trajectory on the phase plane. The numbered balls correspond to the phase points numbered on the trajectory.

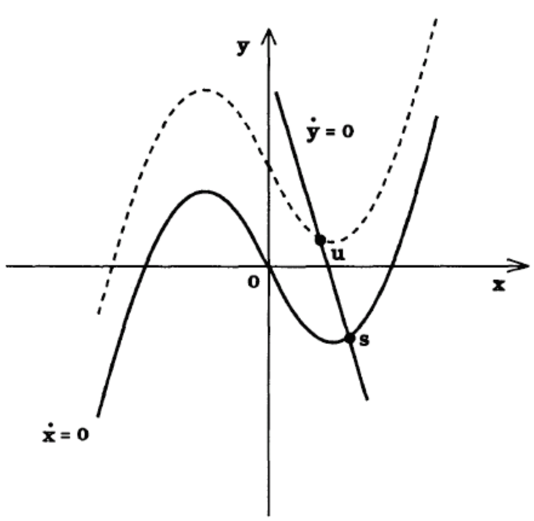
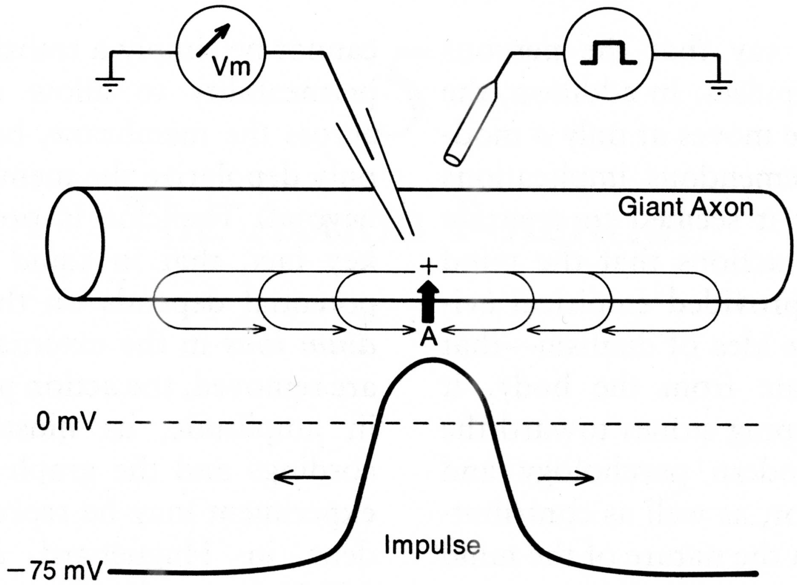
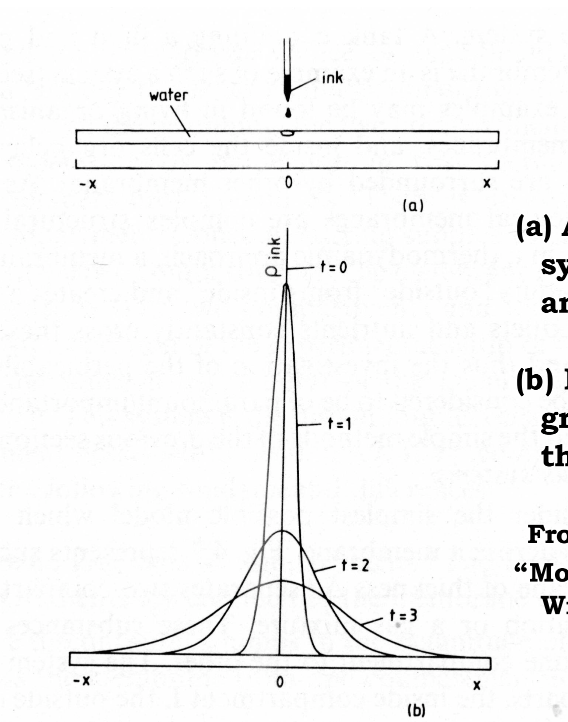


Figure 1.6 x- and y-nullclines of the BVP model described by equations (1.10). When $Z = 0$, the cubic x-nullcline intersects with the straight y-nullcline at the stable point. As Z is decreased from 0, the x-nullcline is raised without any change in the y-nullcline. For certain values of Z, the two nullclines intersect in the region where the x-nullcline has a negative slope. This means that the intersection, or the steady state, becomes unstable, which leads to oscillations.

From Maatoshi Murase "The Dynamics of Cellular Motility" Wiley (1992), p9 (left) and p10 (right).



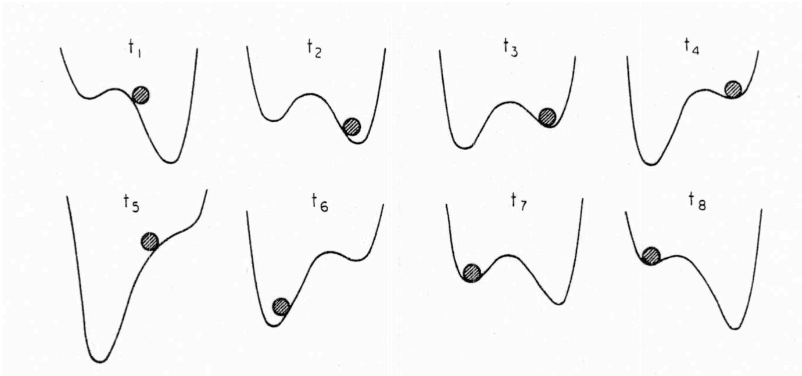
The impulse has been triggered by a brief depolarization at A.
From G. M. Shepherd
"Neurobiology" Oxford University Press 1994



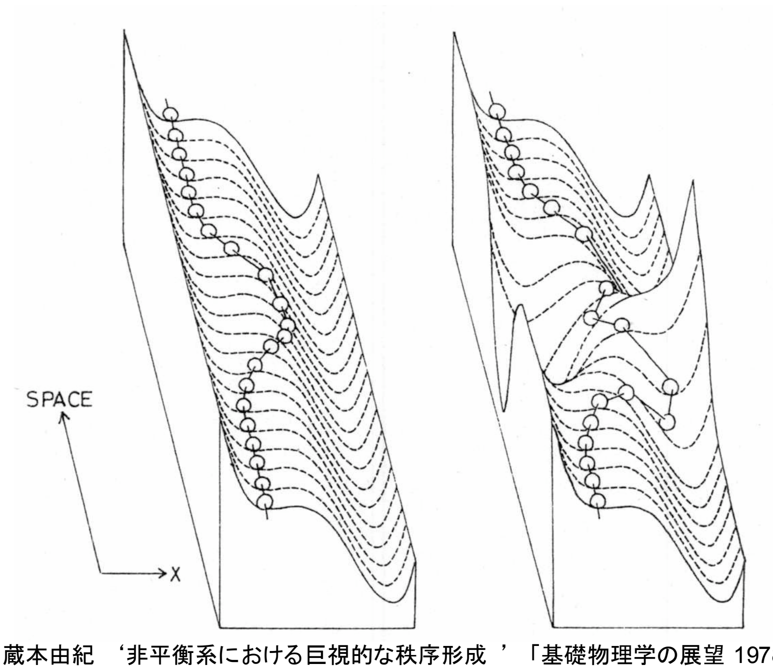
(a) An inhomogeneous system: a drop of ink and water.

(b) Diffusion process gradually homogenizes the system.

From A. Babloyantz
"Molecules, Dynamics & Life" Wiley 1986



蔵本由紀 ‘非平衡系における巨視的な秩序形成 ’「基礎物理学の展望 1978」」
京都大学基礎物理学研究所刊行より



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