

4.4 Dynamics on Networks

So far, we simply identified the topology of connections between the nodes of a network. In many cases the connectivity is merely the prelude to describing the different states of the network that may arise from the coordinated evolution of its elements. Let us assign a variable $x_i(t)$ to each node, whose time evolution is governed by

$$\frac{dx_i}{dt} = F_i(\text{values of } x_j \text{ on sites connected to } i). \quad (4.19)$$

We have assumed that the dynamics is governed by coupled *first order* differential equations in time. This is a good approximation in many biological problems. For example, a network of chemical reactions, or proteins and mRNA, could be described (in the mean-field limit) by a set of rate equations for the concentrations $C_i(t)$, such that

$$\begin{aligned} \frac{dC_i}{dt} = & + \text{ Flux from chemical reactions creating } i \\ & - \text{ Flux from chemical reactions destroying } i. \end{aligned}$$

For example, in the simple reaction $A+B \xrightleftharpoons[k_+]{k_-} C$, the concentration of A varies as

$$\frac{d[A]}{dt} = -k_+[A][B] + k_-[C]. \quad (4.20)$$

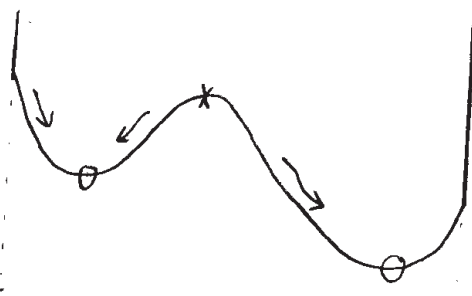
What dynamic behaviors can be encoded in such systems of equations? We shall discuss stationary fixed points and cycles as important examples.

4.4.1 Attractive fixed points

With only one variable, the generic outcome is for it to approach an attractive fixed point. This is because the one dimensional equation can be regarded as describing descent in a potential $V(x)$, as

$$\frac{dx}{dt} = F(x) = -\frac{\partial V}{\partial x}, \quad \text{where} \quad V(x) = -\int^x dx' F(x'). \quad (4.21)$$

The coordinate x will descend in this potential, settling down to possible fixed points that are solutions to $F(x^*) = 0$. Note that a general function $F(x)$ does not necessarily have a zero. However, in most physically relevant situations the variable x is constrained to a finite interval; for example, the concentration of a chemical has to be positive and less than some maximal value. In such cases $V(x)$ is effectively infinite outside the allowed interval, and the potential will have a minimum, possibly at the limits of the interval. The function $V(x)$ is also relevant to the stochastic counterpart of Eq. (4.21): The addition of uncorrelated noise $\eta(t)$ to this equation (with $\langle \eta(t) \rangle = 0$ and $\langle \eta(t)\eta(t') \rangle = 2D\delta(t-t')$) results in a Langevin equation with steady state probability density $p^*(x) \propto [-V(x)/D]$.



The above conclusions hold for coupled equations with many variables, *only if* they correspond to gradient descent in a multi-variable potential $V(x_1, x_2, \dots, x_N)$, i.e. for

$$\frac{dx_i}{dt} = -\frac{\partial \mathcal{V}(x_1, x_2, \dots, x_N)}{\partial x_i} \equiv F_i. \quad (4.22)$$

The equality of second derivatives then immediately implies that

$$\frac{\partial F_i}{\partial x_j} = \frac{\partial F_j}{\partial x_i}. \quad (4.23)$$

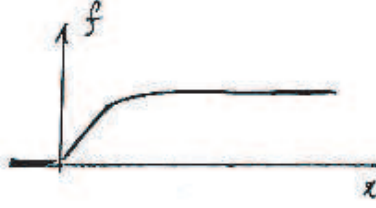
This condition is too constraining, for example in a linear system with $F_i = \sum_j W_{ij}x_j$ it requires symmetric interactions with $W_{ij} = W_{ji}$.

An interesting variant of gradient descent that avoids the constraint of symmetric interactions is provided by Hopfield's model of a neural network with graded response. In this model the activity of each neuron is indicated by a variable x_i (related to the spiking rate of the neuron), and evolves in time according to

$$\frac{dx_i}{dt} = -\frac{x_i}{\tau} + f\left(\sum_j W_{ij}x_j + b_i\right). \quad (4.24)$$

In Eq. (4.24), τ is a natural time constant for decay of activity in the absence of stimuli, and for simplicity we set it to unity; b_i represents external input to the network, say from sensory cells; and W_{ij} is a matrix encoding the strength of synaptic connections from neuron j to neuron i . (The matrix does not have to be symmetric and in general $W_{ij} \neq W_{ji}$.) The function f captures the input/output characteristics of the neuron's response; it is assumed to be a monotonic function of its argument, typically a sigmoidal form that switches between a low and a high value at a threshold input (which can be folded into the parameter b_i). A simplified version of the neural network assigns discrete binary values (say -1 and +1) to each neuron, and a randomly selected neuron i asynchronously switches depending on the sign of $\sum_j W_{ij}x_j + b_i$. Hopfield in fact introduced the model with continuous variables $\{x_i(t)\}$ to address criticism that the binary model was too removed from biological neurons.¹

¹J.J. Hopfield, Proc. Nat. Acad. Sci. **81**, 3088 (1984).



For asymmetric connections,

$$\frac{\partial F_i}{\partial x_j} = -\delta_{ij} + f' \left(\sum_k W_{ik} x_k + b_i \right) W_{ij} \neq \frac{\partial F_j}{\partial x_i} = -\delta_{ij} + f' \left(\sum_k W_{jk} x_k + b_j \right) W_{ji},$$

and the Hopfield model does not correspond to gradient descent in a potential. Nonetheless, we can still demonstrate the existence of fixed points by introducing a *Lyapunov function*,

$$\mathcal{L}(x_1, x_2, \dots, x_N) = \sum_{i=1}^N [G(x_i) - b_i x_i] - \frac{1}{2} \sum_{i,j} W_{ij} x_i x_j, \quad (4.25)$$

where the function G shall be defined shortly. The time derivative of \mathcal{L} is given by

$$\begin{aligned} \frac{d\mathcal{L}}{dt} &= \sum_i \frac{\partial \mathcal{L}}{\partial x_i} \cdot \frac{dx_i}{dt} \\ &= \sum_i \left[G'(x_i) - b_i - \sum_j W_{ij} x_j \right] \cdot \left[-x_i + f \left(b_i + \sum_j W_{ij} x_j \right) \right]. \end{aligned}$$

With appropriately chosen G , we can show that \mathcal{L} is always either decreasing or stationary. To achieve this goal, let us set

$$G'(x) \equiv f^{-1}(x), \quad (4.26)$$

where $f^{-1}(x)$ is the inverse function such that $f^{-1}[f(x)] = x$. This definition implies that

$$\frac{d\mathcal{L}}{dt} = \sum_i [\alpha_i - \beta_i] \cdot [-f(\alpha_i) + f(\beta_i)], \quad (4.27)$$

where we have made the auxiliary definitions

$$\alpha_i \equiv G'(x_i) = f^{-1}(x_i), \quad \text{and} \quad \beta_i \equiv b_i + \sum_j W_{ij} x_j. \quad (4.28)$$

Note that since $f(x)$ is monotonically increasing, the two factors in Eq. (4.27) always have opposite signs, unless they happen to be zero, and thus

$$\frac{d\mathcal{L}}{dt} \leq 0. \quad (4.29)$$

The proof of Eq. (4.29) is similar in spirit to that for the Boltzmann’s H -theorem in Statistical Physics. A similar proof exists for the discrete (binary) version of the network.

The activities of neurons in the Hopfield network thus proceed to attractive fixed points which are solutions to $x_i^* = f(b_i + \sum_j W_{ij} x_j^*)$. The fixed points of the Hopfield model can be interpreted as associative, or content addressable memories. The idea is to first imprint a memory in the network by appropriate choice of the couplings W_{ij} . For a particular “memory” represented by $\{x_i^*\}$, the network is trained according to $\Delta W_{ij} = \eta x_i^* x_j^*$. The new network will be described by a Lyapunov function, $\mathcal{L} + \Delta\mathcal{L}$, with a deeper minimum at the encoded memory as

$$\Delta\mathcal{L}(\{x_i^*\}) = -\frac{1}{2} \sum_{i,j} \Delta W_{ij} x_i^* x_j^* = -\frac{\eta}{2} \sum_{i,j} (x_i^* x_j^*)^2 < 0. \quad (4.30)$$

The imprinting procedure is a computational implementation of the so called *Hebbian rule* according to which “neurons that fire together wire together.” If the thus trained network is presented with a partial or corrupted version of the stored memory, it is likely to be in the basin of the Lyapunov function that is attracted to the original memory. In principle one can store many different memories in the network, each with its own separate basin of attraction. Of course at some point the memories interfere, and the network has a finite capacity dependent on the number of its nodes.

4.4.2 Stability, Bifurcation, and Cycles

Let us consider a bounded set of variables $\{x_i\}$ evolving in time as $\dot{x}_i = F_i(\{x_j\})$. Fixed points are possible solutions to $F_i(\{x_j^*\}) = 0$, but they will correspond to potential outcomes (attractors) of the dynamics, only if all eigenvalues of the matrix

$$M_{ij} = \left. \frac{\partial F_i}{\partial x_j} \right|_*, \quad (4.31)$$

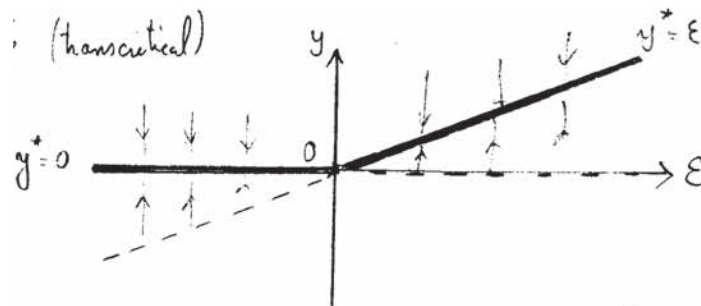
have negative real parts. (This is the condition for *linear stability*. For zero eigenvalues stability is determined by examining higher derivatives.) We are interested in physical problems where the functions F_i , and hence all elements of the matrix M_{ij} , are real. The eigenvalues $\{\lambda_i\}$ of a real-valued matrix are either real, or come in complex conjugate pairs $u \pm iv$.

In the biological context, the functions F_i may determine the evolution of protein concentrations, and could then include parameters that depend on external stimuli. As such parameters are changed, a fixed point (protein concentrations) may become unstable, causing the system to switch to another state. The initial fixed point becomes unstable at the point where the real part of an eigenvalue changes sign from negative to positive. If this happens for a real eigenvalue, we can focus on the dynamics along the corresponding eigendirection— a one dimensional parametrization is then sufficient to capture the change in behavior near such an instability. If the real part of a complex eigenvalue pair changes sign, we need to analyze the behavior in the corresponding two dimensional surface spanned by the eigenvectors.

Let us first consider a single eigenvalue $\lambda(\epsilon)$ that changes sign as a control parameter ϵ goes through zero. Indicating deviations along the corresponding eigendirection by y , at linear level we have $\dot{y} = \epsilon y$. The fixed point at $y^* = 0$ is stable for $\epsilon < 0$, and unstable for $\epsilon > 0$. Higher order terms in the expansion in y are then necessary to determine the fate of the fixed point. The simplest addition is a quadratic term, leading to

$$\dot{y} = \epsilon y - y^2. \quad (4.32)$$

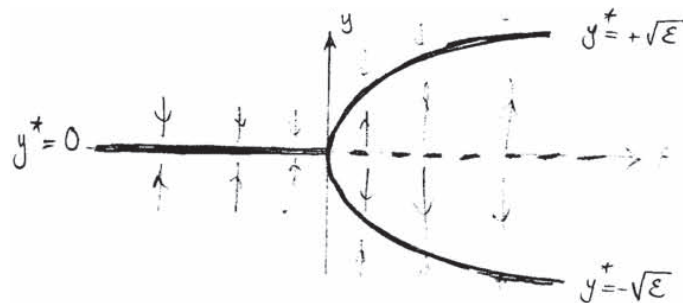
(The coefficient of the quadratic term can be set to 1 with proper scaling of y .) This model then admits a stable fixed point at $y^* = \epsilon$ for $\epsilon > 0$. In this (*transcritical*) scenario, a stable and an unstable fixed point collide and exchange stability.



The quadratic term in Eq. (4.34) is generically present, unless forbidden by a symmetry. In particular, the symmetry $y \rightarrow -y$ is consistent only with odd powers of y in the equation for \dot{y} , in which case Eq. (4.34) has to be replaced with

$$\dot{y} = \epsilon y - y^3. \quad (4.33)$$

In such a *pitchfork bifurcation* a pair of stable fixed points appears at $\pm\sqrt{\epsilon}$ for $\epsilon > 0$, and the choice of one or the other is by *spontaneous symmetry breaking*.

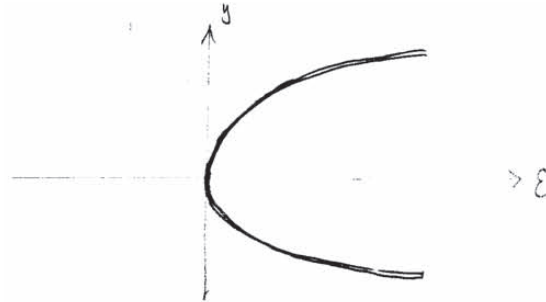


The above changes in dynamic behavior as a parameter is varied are examples of bifurcations. If we do not insist upon starting with a stable fixed point as we have done so far,

other forms of bifurcation is possible. For example, if the sign of the cubic term in Eq. (4.34) is changed to positive, there is no longer a stable fixed point for $\epsilon < 0$. The stable fixed points now all appear for $\epsilon > 0$, colliding at $\epsilon = 0$, with a single unstable fixed point for $\epsilon > 0$. Yet another scenario by which a pair of stable fixed points disappear is provided by

$$\dot{y} = \epsilon - y^2, \quad (4.34)$$

where a pair of fixed points (one stable and one unstable) for $\epsilon > 0$ collide and disappear for $\epsilon < 0$.



If the real part of a complex eigenvalue pair, $\lambda_{\pm} = u(\epsilon) \pm iv$, changes sign, we can focus on the two dimensional plane spanned by the corresponding eigenvectors. The trajectories on this plane now transition from inward spirals to outward spirals.



Of course bounded variables cannot spiral out forever, and the by *Poincaré-Bendixon* theorem states that the bounded spiral must approach a closed curve around which it cycles. As an example, let us consider the pair of equations

$$\begin{aligned} \dot{x} &= \epsilon x - \omega y - (x^2 + y^2)x \\ \dot{y} &= \omega x + \epsilon y - (x^2 + y^2)y. \end{aligned} \quad (4.35)$$

These equations were in fact constructed to have a simple form in polar coordinates (r, θ) in terms of which $x = r \cos \theta$ and $y = r \sin \theta$. It is then easily verified that Eqs. (4.35) are equivalent to

$$\begin{aligned}\dot{\theta} &= \omega \\ \dot{r} &= \epsilon r - r^3.\end{aligned}\tag{4.36}$$

The trajectory now rotates at a uniform angular velocity ω , converging to the center for $\epsilon \leq 0$, and to a circle of radius $r^* = \sqrt{\epsilon}$ for $\epsilon > 0$.



Note that a symmetric matrix $M_{ij} = M_{ji}$ only has real eigenvalues. Complex eigenvalues, and hence periodic cycles can only occur for antisymmetric matrices. In the above example, the asymmetry is parametrized by ω which sets the angular velocity, but does not enter in the equation for r . Indeed, it is easy to check that for a two by two matrix, complex eigenvalues can only be obtained if the off-diagonal elements have opposite signs (as is the case in Eq. (4.35)). Indeed, in the biological context, a simple scheme for generating oscillations is to use an excitatory element (with positive interactions) in concert with an inhibitory component. (with negative couplings). Other schemes, with three elements each inhibiting the next in a cycle, as in the repressilator², also lead to oscillations by this mechanism.

²M. B. Elowitz and S. Leibler; Nature. **403**, 335 (2000).

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