

Chaos: principles and implications in biology

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Abstract

In this paper we review some of the basic principles of the theory of dynamical systems. We introduce the reader to the definition of chaos and strange attractors and we discuss their implications in biology.

Over the last decade physicists, astronomers, biologists and scientists from many other disciplines have developed a new way of looking at complexity in nature. This new way has been termed 'chaos'. Chaos, which is defined as randomness generated by simple dynamical systems, allows us to see order in processes that were thought to be completely random. It is the purpose of this paper to introduce the reader to the concept and implication of chaos in biology.

In the preceding paragraph the term 'dynamical systems' was used. What is a dynamical system? In simple terms it is a system whose evolution from some initial state (which we know) can be described by some rule(s). These rules are conveniently expressed as mathematical equations. The evolution of such a system is best described by the so-called state space. Let us first give an example of a simple dynamical system and its state space.

A pendulum is allowed to swing back and forth from some initial state as described in Figure 1a. This initial state can be completely described by the speed and position of the pendulum. The position of the pendulum at any time can be given by the angle x . Under such an arrangement, Newtonian Physics provide the equations (rules) which describe the evolution of that initial state in time.

Let us assume that to begin with the pendulum is held at position 1. Then its initial state will be $x = x_1$, and velocity $v = 0$. The pendulum is then let free. As the pendulum moves towards point 0, its speed increases due to gravity acceleration. Therefore, after a while (position 2) the pendulum will be closer to point 0 and will have a higher speed. Once the pendulum crosses point 0 its speed decreases because now gravity acts in a direction opposite to its motion. Therefore at some point (position 3) the pendulum's speed will become zero again. Immediately after that the pendulum will begin to swing back, and after it crosses point 0 it will once again attain, at

some point, a zero speed (position 4). Because there is always some friction, however, the points at which the speed becomes zero (to the right and left of point 0) are not fixed but are found closer and closer to point 0. Finally the pendulum will come to rest at point 0.

Apparently, the evolution of the above dynamical system can be completely described by two variables, namely velocity and angle x . These two variables define the coordinates of the so-called state space. If one plots the velocity (v) as a function of the angle (x) of the pendulum one will get Figure 1b. The

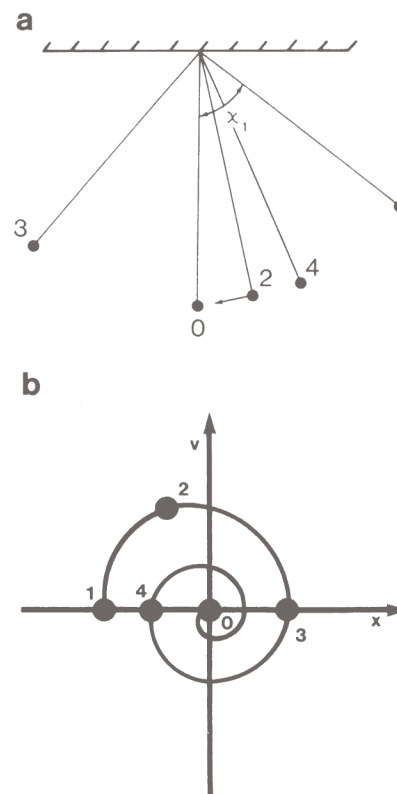


Fig. 1. (a) A dynamic system is a system whose evolution from initial state can be determined by some rules. In the above figure the motion of the pendulum can be completely described by the laws of physics if its initial position and velocity are known. (b) A useful concept in studying the evolution of dynamical system is the state space. The coordinates of the state space are necessary variables that are needed to completely describe the evolution of the dynamical system in question. In our example these coordinates are the velocity and the angle x of the pendulum. As the pendulum swings back and forth it follows a trajectory in the state phase which converges to a fixed point. This point is called an attractor of the dynamical system.

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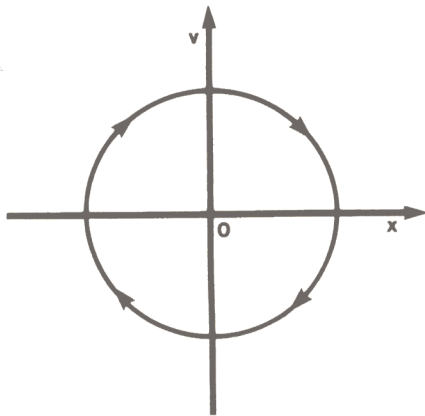


Fig. 2. Another form of an attractor is the limit cycle. In this case all trajectories are attracted by the limit cycle which represents a period evolution. The grandfather clock is a system which possesses a limit cycle as an attractor. Another familiar system with a limit cycle as its attractor is the heart.

solid line is called a trajectory in the state space and apparently describes the evolution of our dynamical system. As it can be seen, the trajectory converges to point 0. As a matter of fact, any other trajectory which will correspond to an evolution of the above dynamical system from a different initial state (velocity and angle) will converge to point 0 (i.e. no matter what the initial state, the pendulum will always come to rest at point 0). The point 0 in the state space is called an attractor. It 'attracts' all the trajectories in the state space. Apparently, the behavior of the dynamical system in question can be completely understood. Long-term predictability is guaranteed. The evolution of that system can be accurately predicted. The pendulum will always rest at point 0. Point attractors, therefore, correspond to systems that reach steady state of no motion.

So far we have discussed only one form of attractor (i.e. a point). The next simplest form of attractor is the limit cycle (Figure 2). A limit cycle in the state space indicates a periodic motion. An example of a system whose attractor is a limit cycle is the grandfather clock where loss of kinetic energy due to friction is compensated mechanically via a mainspring. No matter how the pendulum clock is set swinging a perpetual periodic motion will be achieved. This periodic motion manifests itself in the state space as a limit cycle. Again, in the cases of systems which have a limit cycle as an attractor, long-term predictability is guaranteed.

Another form of an attractor is a torus. The torus looks like the surface of a donut (Figure 3). In this case all the trajectories in the state space are attracted to and remain on that surface. Systems that possess a torus as an attractor are quasi-periodic. In a quasi-periodic evolution a periodic motion is modulated by a second motion, itself periodic, but with another frequency. The combination of frequencies will produce a time series whose regularity is not clear. The power spectrum, however, should consist of sharp peaks at each of the basic frequencies with all its other prominent features being com-

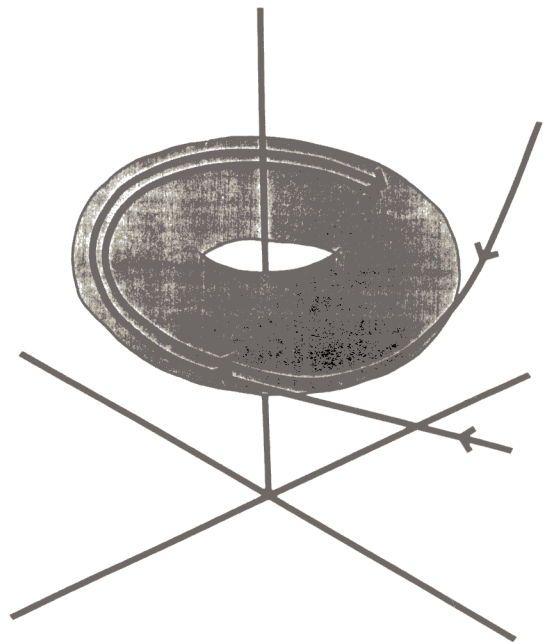


Fig. 3. Another form for an attractor is the torus. In this case the evolution of the corresponding dynamical system from any initial condition will follow a trajectory in the state space which will eventually be attracted and remain forever on the torus. The most important characteristic of a system which exhibits such an attractor is that if the two involved frequencies have no common divisor two initially nearby trajectories on the attractor remain nearby forever.

binations of the basic frequencies. Geometrically a quasi-periodic trajectory fills the surface of a torus in the appropriate state space. An important characteristic of such an attractor is that when the two frequencies have no common divisor any two trajectories which represent the evolution of the system from different initial conditions and which are close to each other when they approach the attracting surface will remain close to each other forever (see Figure 3). This characteristic can be translated as follows. The two points in the state space where the trajectories enter the attractor can be two measurements (initial states) which differ by some amount. Since these trajectories remain close to each other it means that the states of the system at a later time are going to differ by the same amount that they differed initially. Thus, if we know the evolution of such a system from an initial condition we can predict the evolution of the system from some other initial condition accurately. Again in this case long-term predictability is guaranteed.

The above-mentioned forms of attractors are 'well behaved' attractors and usually correspond to a system whose evolution is predictable. Often they are called non-chaotic attractors. In mathematical terms the above-mentioned attractors are topological submanifolds of the available state space.

In 1963, Lorenz, in a paper which started everything, discovered a system which under certain circumstances possessed an attractor that did not look like anything described

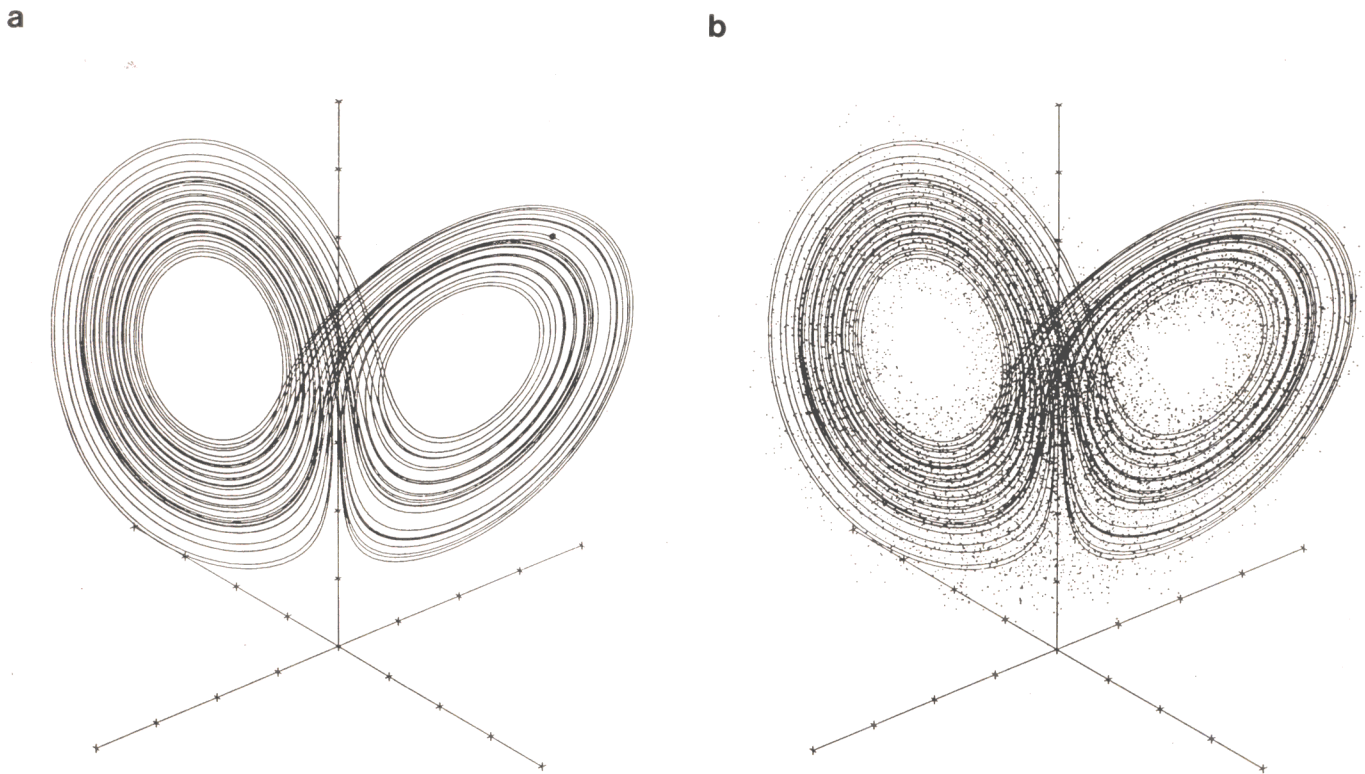


Fig. 4. (a) An example of a strange attractor. This structure in the state space represents the attractor of a fluid flow which travels over a heated surface. All trajectories (which will represent the evolution of that system for different initial conditions) will eventually converge and remain on that structure. However, any two initially nearby trajectories in the attractor do not remain nearby but they diverge. (Figure courtesy of Dr James Crutchfield.) (b) The effect of the divergence of initially nearby trajectories in the attractor. The dot in (a) represents 10 000 measurements (initial conditions) which are so very close to each other that they are practically indistinguishable. If we allow each one of these states to evolve according to the rules, because their trajectories diverge irregularly, after a while their states can be practically anywhere. (Figure courtesy of Dr James Crutchfield.)

above. Lorenz was experimenting with a very simple model of three differential equations that describe the motion of a fluid flow which travels over a heated surface. The warmer fluid formed at the bottom is lighter and it tends to rise, creating convection. The attractor of this dynamical system is shown in Figure 4a. Since the state of the system is described by three equations the state space has three coordinates. Not only does this attractor not look like anything described above, but also it has two very important properties: (i) the evolution described by a trajectory is deterministic but strictly nonperiodic (never repeats itself); and (ii) as with all attractors all trajectories converge on the attractor but two nearby trajectories do not stay close to each other but they very soon diverge and follow totally different paths in the attractor. That means that the evolution of the system from two slightly different initial conditions will be completely different. The above is very effectively demonstrated in Figure 4a and b. The dot in Figure 4a represents 10 000 initial conditions that are so close to each other in the attractor that they are indistinguishable. They may be viewed as 10 000 initial situations that differ only slightly from each other. If we allow these initial conditions to evolve according to the rules (equations) that describe the system we see (Figure

4b) that after some time the 10 000 dots can be anywhere in the attractor. In other words, the state of our system after some time can be anything despite the fact that the initial conditions were very close to each other. Apparently, the evolution of the system is very sensitive to initial conditions. In this case we say that our system has generated randomness. We then see that there exist systems which even though described by simple deterministic rules can generate randomness. Randomness generated this way has been termed chaos. These systems are called chaotic dynamical systems and their attractors are called strange or chaotic attractors. These attractors are not topological submanifolds of the total available space, but they are fractals (Mandelbrot, 1983; Tsonis and Tsonis, 1987; Tsonis and Elsner, 1988).

We now proceed in presenting an example of a biological system with a variety of periodic and chaotic solutions. The system is described by the following 'logistic' difference equation which is used to model population dynamics (May, 1976):

$$X_{t+1} = aX_t(1 - X_t), \quad 0 < X < 1, \quad 1 < a < 4$$

This equation relates the population of a given generation X_t

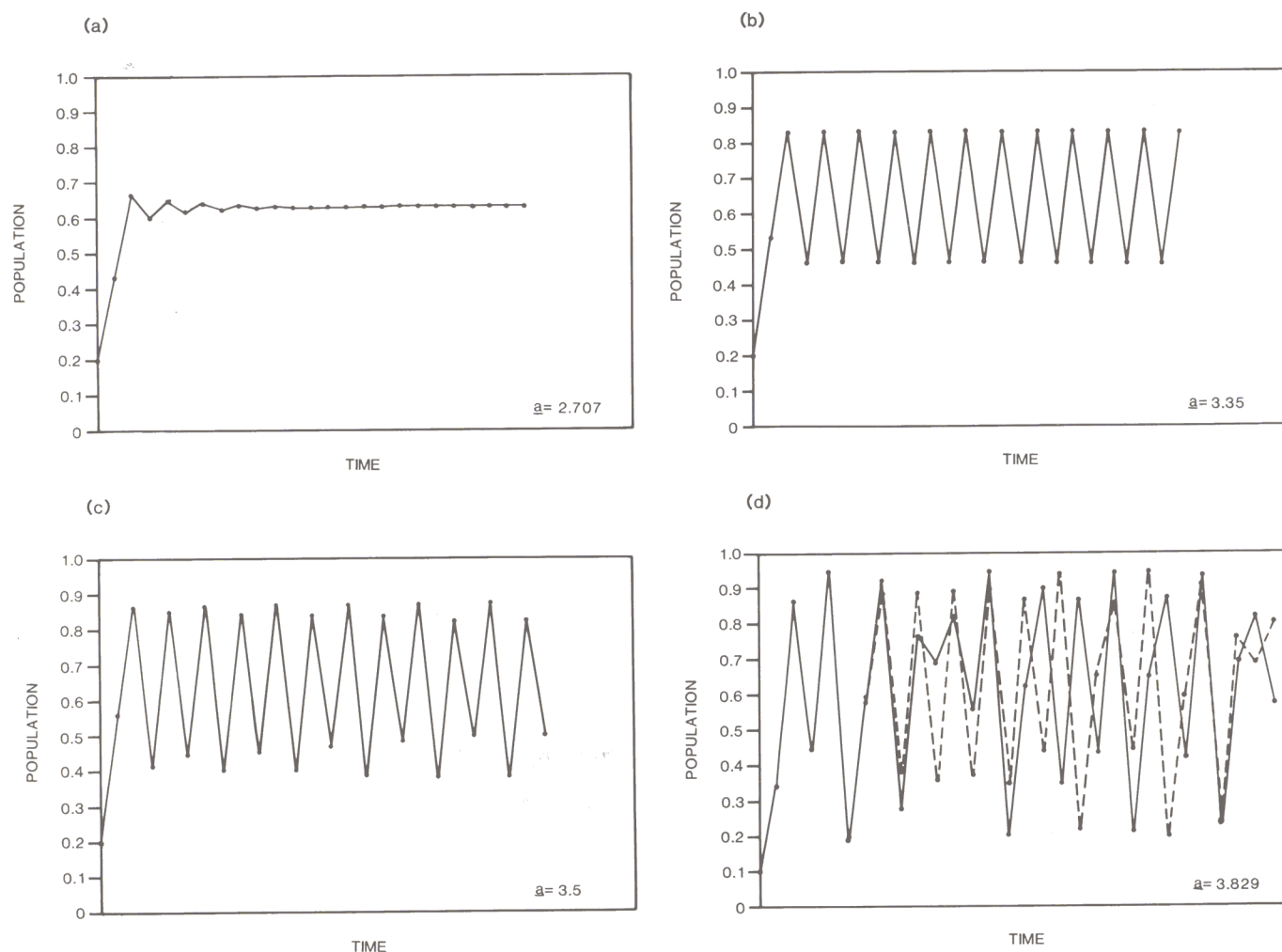


Fig. 5. Based on the equation $X_{t+1} = aX_t(1 - X_t)$ this figure shows the population evolution from some initial condition X_0 and for different choices of the parameter a : (a) for $X_0 = 0.2$ and $a = 2.707$ the population finally reaches a steady state of no change; (b) for $X_0 = 0.2$ and $a = 3.35$ the population becomes periodic of period two (i.e. it repeats every two generations); (c) for $X_0 = 0.2$ and $a = 3.5$ the population becomes periodic of period four; (d) for $a = 3.829$ the evolution becomes chaotic with no distinct periodicity. The solid line shows the evolution from an initial value of $X_0 = 0.1$ and the broken line from an initial value of $X_0 = 0.101$. After some time the two evolutions are completely different. This demonstrates the very important characteristic of chaotic dynamics referred to as the divergence of initially nearby trajectories. Due to the underlying chaotic dynamics the initially close trajectories diverge irregularly. Such divergence cannot be observed for the periodic cases which are not sensitive to fluctuations in the initial conditions. The above results can be obtained by pressing a button in a programmable calculator. Type in $f(x) = ax(1 - x)$ choose your a and enter your first value (initial condition). Press the button. The number X_1 will then appear on the display. Press the button again. The number X_2 will appear and so on.

to the population of the next generation X_{t+1} . The parameter a is called the nonlinearity parameter and it represents a growth rate which may be related to the food supply, to fertility, etc. The philosophy behind this equation is that it represents a function which increases when the population is small, reduces growth at intermediate values and decreases as the population becomes large. By iterating (repeating) the above equation one can obtain the population's evolution from some initial value for a given choice of the parameter a . The dynamics of the logistic equation have been studied extensively by May (1976) who discovered an amazing variety of possible evolutions as the parameter a was varied. For a value of $a < 3.0$ the population settles into a steady state (no change). As the

parameter a is varied slightly > 3.0 something surprising happens. The population now settles into a period-two (repeating every other generation) oscillation. A further increase of a and the evolution becomes a period-four oscillation (repeating every four generations). The 'magic' continues as the nonlinearity parameter increases by giving rise to periods increasing in powers of 2 ($2^3, 2^4, 2^5, \dots$). And then this period doubling comes to an end when for a value of $a > 3.5700$ the evolution becomes chaotic (or strictly speaking periodic with a period 2^∞).

This means that the evolution even though deterministic is for all practical purposes nonperiodic. The system is said in this case to oscillate with no recognisable frequency (chaotic

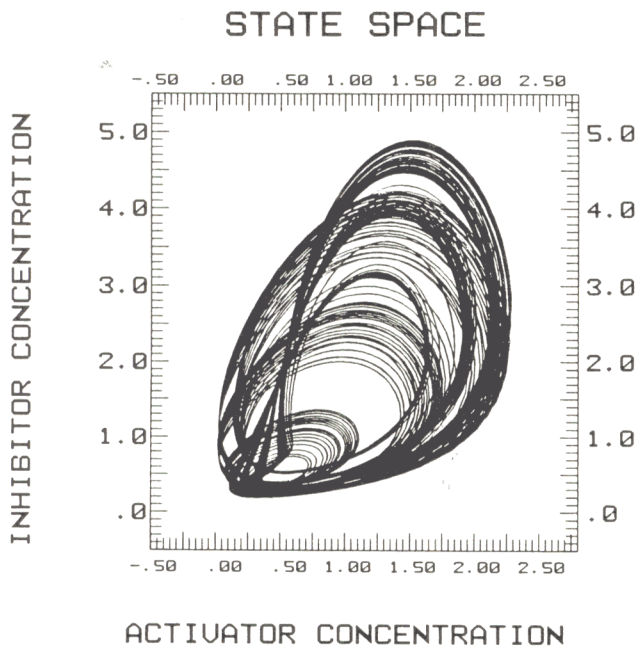


Fig. 6. This figure shows results from a diffusion–reaction model for biological pattern formation used by Tsonis *et al.* (1989). The model begins with adjacent cells which are allowed to evolve from some initial steady state which is slightly perturbed. Then by numerical integration the evolution of each cell is obtained. The figure shows the evolution of one of the cells. As it can be seen the trajectory is irregular and ‘wanders’ on a well-defined area of the state space which looks ‘strange’. This is an indication of a chaotic evolution. For more details see Tsonis *et al.* (1989).

evolution). As was the case with the Lorenz system, in this case as well, small uncertainties in the initial conditions can drive the system to completely different evolution (see Figure 5 for an illustration of the above).

Soon after that chaos invaded biology Glass *et al.* (1987) showed that clinically observed irregular cardiac rhythms may be associated with determinism in mathematical models of the intact human heart. Similarly Glass and Mackey (1979) demonstrated that respiratory and hematological arrhythmias are associated with chaos. Martiel and Goldbeter (1985) found that aperiodic oscillations (chaos) in cAMP synthesis can significantly affect the morphogenesis of *Dictyostelium discoideum*.

King *et al.* (1984) reported on the behavior of a mathematical model which described the dynamics of the central dopaminergic neuronal system. They found that for certain values of a parameter which monitors the efficacy of dopamine at the postsynaptic receptor chaotic solutions appear. They also found that predicted transitions to chaotic regimes correlate well with the observed increased variability in behavior among schizophrenics, and the lability of mood in some patients with an affective disorder. Hess and Markus (1987) reported on chaos in glycolysis, observed under certain conditions, in yeast extracts subjected to a sinusoidal input flux of glucose. Nicolis (1988) showed that one-dimensional spatially asymmetric and

information-rich sequences, like the ones observed in biopolymers carrying biological information, may be generated from a time-irreversible dynamics possessing a chaotic attractor. Ohno (1988) found that chaos is applicable to coding sequences of the genetic material. Tsonis *et al.* (1989) demonstrated that when biological pattern formation is modelled according to a forced reaction–diffusion process chaotic solutions are possible. Their model predicts the evolution of a row of adjacent cells from some slightly perturbed steady state. Their results suggest that, depending on the choice of some controlling parameters, periodic, quasi-periodic and chaotic patterns may emerge naturally from the interplay of a simple reaction–diffusion process and an external forcing. An example of their results is given in Figure 6 which shows the evolution of a randomly selected cell. The trajectory follows an irregular path on a strange attractor and thus the evolution is chaotic. In such a case an ‘irregular’ pattern will emerge.

The implications of chaos are profound. If one knows exactly the initial conditions, one can follow the trajectory that corresponds to the evolution of the system from those initial conditions and basically predict the evolution forever. The problem, however, is that, because of the always present microscopic random fluctuations, any initial condition is only approximately known. In such a case, even if we completely know the physical laws that govern our system, due to the action of the underlying attractor, the state of the system at a later time can be totally different than it would have been if we knew exactly the initial condition. Simply, due to the nature of the system, initial microscopic errors are amplified to a macroscopic scale. In this case we say that the prediction power of the system is very limited. Therefore, we see that the existence of a strange or chaotic attractor, coupled with the fact that we can only know approximately an initial situation, naturally imposes prediction limits to the system. However, the macroscopic randomness is confined in a very well-defined region of the total available state (the attractor) and, thus, in chaos there is some underlying order. This, together with the fact that a chaotic trajectory is quite deterministic, suggests that processes that look completely random may be in fact chaotic and thus more predictable and describable than they were thought to be.

Chaos has opened new horizons in science and it is already considered by many the third most important discovery in the twentieth century, after relativity and quantum mechanics. Philosophically speaking, chaos has brought some pessimism since it imposes limits on prediction. At the same time, however, it has offered a new forum for the understanding and description of irregularity, complexity and unpredictability in Nature.

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