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DETERMINISTIC CHAOS SEEN IN TERMS OF FEEDBACK CIRCUITS: ANALYSIS, SYNTHESIS, "LABYRINTH CHAOS"

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This paper aims to show how complex nonlinear dynamic systems can be classified, analyzed and synthesized in terms of feedback circuits. The Rössler equations for deterministic chaos are revisited and generalized in this perspective. It is shown that once a proper set of feedback circuits is present in the Jacobian matrix of the system, the chaotic character of trajectories is remarkably robust versus changes in the nature of the nonlinearities. "Labyrinth chaos", whereby simple differential systems generate large lattices of many unstable steady states embedded in a chaotic attractor, is constructed using this technique. In the limit case of a single three-element circuit without diagonal elements, one finds systems possessing an infinite lattice of unstable steady states between which trajectories percolate in a deterministic chaotic way.

1. Introduction

Complex dynamics, including deterministic chaos, can be generated by surprisingly simple differential equations [Rössler, 1976a, 1976b; Chua *et al.*, 1993; Sprott, 1994]. However, in spite of this simplicity, it is not immediately obvious why a given set of equations should be able to generate complex dynamics, and even less what the role of each term is. We show here that complex dynamics can be advantageously treated in terms of the feedback circuits as present in the Jacobian matrix of the system. Biologists use the term feedback "loops" but we rather adopted the terminology of graph theoreticians ("circuits"), who use "loop" only for one-element circuits. Our feedback circuits, redefined in a more rigourous way below (Sec. 2) are obviously more abstract than those of engineers, but they have the same deep meaning. These circuits describe the *logical structure* underlying dynamical characteristics, not only in the vicinity of steady states, but also at the global level. In this perspective, appropriate circuits or combinations thereof turn out to be necessary conditions for multistationarity, stable periodicity and more complex dynamics including deterministic chaos. We stress that feedback and nonlinearity are qualitatively different concepts. Nonlinearities may not be associated with feedback and, conversely, a feedback may be associated with linear terms only. It is essential to realize that *both* nonlinearity and appropriate feedback circuits are required for such nontrivial behavior as multistationarity, stable periodicity or deterministic chaos.

The notion of feedback has been used for many years by ecologists, economists and biologists. For detailed descriptions, see [Einsenfeld & de Lisi, 1985; Thomas & D'Ari, 1990]. In crude terms, variables x, y and z form a feedback circuit if x influences the rate of change of y, which influences the rate of change of z, which in turn influences the rate of change of x. This is commonly symbolized by a graph of interactions. In the example just mentioned, the interactions are represented by arrows from x to y, from y to z and from z to x. In such a structure, each variable exerts an influence on its *own* future evolution. This influence is indirect (via the other variables of the circuit) except of course in the case of a one-element circuit. Depending on the circuit, either *each* variable exerts a positive influence on its own future, or *each* variable exerts a negative action on its future. Accordingly, one speaks of a positive or a negative feedback circuit. Whether a feedback circuit is positive or negative simply depends on the *parity* of the number of *negative* interactions; positive circuits have an even number of negative interactions, negative circuits, an odd number. In most real cases, one deals with networks in which circuits are more or less densely intertwined. However, even though the operation of a circuit can be hampered by the presence of other circuits in the system, each individual circuit can still be identified and characterized without ambiguity [Snoussi & Thomas, 1993].

The properties of the two types of feedback circuits are strikingly different. Negative circuits function like a thermostat and generate homeostasis (with or without oscillations). In contrast, positive circuits may generate multistationarity; concretely, this means that systems with a positive circuit may have a choice between distinct regimes. As first suggested by Delbrück [1949] and amply documented since, cell differentiation is essentially the biological modality of this more general process of multistationarity, hence the fundamental role of positive circuits in biology. It was conjectured [Thomas, 1981] that (a) a positive circuit is a necessary condition for multistationarity and (b) a negative circuit is a necessary condition for stable periodicity. Both conjectures have now received formal proofs in a wide domain of situations [Plahte *et al.*, 1995; Demongeot, 1998; Snoussi, 1998; Gouzé, 1998]. Furthermore, it was realized that for proper parameter values a circuit can generate one or more steady states, whose nature (stable or unstable node or focus, saddle point, saddle focus, etc.) can be inferred from the structure of the circuit. When only part of the variables are involved in the circuit, however, one may have a "partial" steady state, i.e. a state which is steady only in the subspace of the variables actually invoved in the circuit. When this is the case, a "full steady state" (i.e. a steady state of the full system) can be obtained by the union of disjoint circuits, if required. Partial steady states can play an essential role in the dynamics of a system; for example, we show below (see Sec. 3) that in chaotic systems with a single steady state one or more of the periodicities can be organized around such partial steady states. For an analysis in the case of systems described in terms of step functions, see [Snoussi & Thomas, 1993; Thomas, 1991].

Thus, the presence of appropriate circuits (or unions of disjoint circuits) is not only a way to generate steady states, but a *necessary* (and in particular cases, sufficient) *condition* for their existence. Specifically:

- In any case, the existence of two or more isolated steady states implies the presence of a positive circuit.
- In a two-dimensional space or subspace, periodic motion around a steady state (often a focus) requires the presence of a negative circuit involving the two variables.
- In a three-dimensional space or subspace, a three-element negative circuit can generate a steady state which is attractive in one direction and periodically repulsive along a normal surface, while a three-element positive circuit can generate a saddle-focus which is attractive on a two-dimensional surface and repulsive along a normal direction.

An obvious next step is to ask what logical ingredients are required to generate more complex dynamics, including deterministic chaos. This is the main goal of the present paper.

In Sec. 2, we briefly reformulate the concept of feedback circuit. In Sec. 3, we show how the Rössler equations can be revisited, simplified and generalized in terms of circuits. Using our method, we finally describe in Sec. 4 a new class of dynamical systems which generates a lattice of many steady states, all unstable, between which trajectories percolate in a chaotic way (hence the nickname "labyrinth chaos").

2. Formal Description of Systems in Terms of Feedback Circuits

We first reformulate the concepts of "interaction" and "circuit", introduced above, in a more technical way. This can be done most conveniently by considering the Jacobian matrix of our systems. Let a system be described by the differential equations

$$\dot{x}_i = f_i(x_1, x_2, \ldots, x_n)$$

$$\begin{pmatrix} \cdot & a_{12} & \cdot \\ \cdot & \cdot & a_{23} \\ a_{31} & \cdot & \cdot \end{pmatrix} \qquad \begin{pmatrix} \cdot & \cdot & a_{13} \\ a_{21} & \cdot & \cdot \\ \cdot & a_{32} & \cdot \end{pmatrix}$$

$$\begin{pmatrix} \cdot & \cdot & a_{13} \\ \cdot & \cdot & \cdot \\ a_{31} & \cdot & \cdot \end{pmatrix} \qquad \begin{pmatrix} \cdot & \cdot & \cdot \\ \cdot & a_{22} & \cdot \\ \cdot & \cdot & \cdot \end{pmatrix}$$

Fig. 1. Some of the circuits of a three-element matrix. For example, if terms a_{12}, a_{31} and a_{23} are nonzero, it means that variable 2 acts on variable 1, which acts on variable 3, which in turn acts on variable 2, thus forming a feedback circuit. Note that each nonzero diagonal term defines a one-element circuit (if a_{22} is nonzero, it means that variable 2 exerts a direct influence on its own future, etc...).

We say that variable x_j acts on (or interacts with) variable x_i if term $a_{ij}(= \partial f_i/\partial x_j)$ of the matrix is nonzero. This action is denoted as positive or negative depending on the sign of a_{ij}. Accordingly, in the graph of interactions, each interaction is symbolized by an arrow $x_j \to x_i$ with a + or a − sign, respectively. Once interactions have been defined unambiguously, the feedback circuits of a system can be directly "read" from the Jacobian matrix (see Fig. 1). Formally, they are defined by sequences of elements of the Jacobian matrix whose i (row) and j (column) indices are circular permutations of each other. More generally, as suggested by Cahen, a circuit (or a union of disjoint circuits) can be identified by the existence of *a set of nonzero terms such that the sets of their i (row) and j (column) indices are equal.* A circuit is best characterized by the *product* of its elements; one has a positive or a negative circuit depending on whether this product is itself positive or negative. Note that the matricial and graph descriptions of circuits are *dual* of each other; a nonzero element of the matrix corresponds to an edge, not a vertex of the graph.

In linear systems, the Jacobian matrix is constant throughout phase space, but in nonlinear systems at least one term of the matrix is a function of one or more variables, and consequently the value, and even the sign, of certain terms will depend on the location in phase space. The common practice (see, however [Guckenheimer & Holmes, 1983]) consists of using the Jacobian matrix, as well as its characteristic equation and eigenvalues, only at or very near steady state values of the system. This is because it is only there that they characterize stability properties. In what follows, however, it will be extremely informative to consider fully the Jacobian matrix not only at steady states, but throughout phase space. We call "general Jacobian matrix" a matrix in which each term is represented by its analytical expression and can thus be calculated everywhere. One speaks of a "qualitative Jacobian matrix" when each term is represented by its *sign* only. This concept has been used by Tyson [1975] at the level of the steady states. We use it everywhere in phase space. In this perspective, phase space can be partitioned into domains within which the signs of all terms of the Jacobian matrix are constant. Thus, the sign of a circuit is well-defined within each of these regions, but a circuit can be positive in one region of phase space and negative in another region. *The logical structure of a system will be defined as the network of its feedback circuits, as revealed by the analytic expression of its Jacobian matrix.* In fact, a simple look at the logical structure of a system often tells much about the number and nature of its potential steady states. Conversely, it is tempting to start from a logical structure and build a differential system with desired properties. This latter viewpoint will be at the basis of the developments outlined in the following two sections.

For numerical integrations, we used the programs ROW4A of Gottwald and Wanner [1981], as implemented in De Boer's program GRIND (Figs. 2 and 3), and Mathematica (Figs. 4 and 5).

The Lyapounov exponents were evaluated according to [Wolf *et al.*, 1985], but converted from base 2 to base e.

3. The Rössler Equations for Deterministic Chaos Revisited in Terms of Feedback Circuits

Rössler [1976a, 1976b] discovered surprisingly simple sets of differential equations which generate a chaotic dynamics, such as:

$$\begin{aligned} \dot{x} &= -y - z \\ \dot{y} &= x + ay \\ \dot{z} &= bx + xz - cz \end{aligned}$$

in which the only nonlinearity is the term xz. In spite of their admirable simplicity, it is not immediately obvious why these equations should generate a chaotic dynamics, and even less what the role is of each of their terms. For a wide range of parameter values, these equations admit two unstable steady states corresponding to the two complementary types of saddle foci [Gaspard & Nicolis, 1983]. To qualify them more explicitly, we will denote them by the signs of their eigenvalues. Concretely, $-/++$ is taken to mean that there is one real negative root and a pair of complex roots whose real part is positive, $+/--$, the converse. Steady state "I", of structure $-/++$, (which, incidentally, is conveniently located at the origin (0, 0, 0) in this variant of the Rössler systems) is attractive along the z axis and periodically repulsive following the yz plane. Steady state "II", of structure $+/--$, is periodically attractive in a plane and repulsive in a direction transverse to this plane.

We have inquired whether it would be possible to create these two types of steady states *ab initio*, using as ingredients the proper feedback circuits. Let us first deal with steady state (I). In order to have periodicity in the xy plane, one needs a negative feedback circuit in xy in the Jacobian matrix; for this focus to be repulsive, one needs a positive diagonal term in x or y; and in order for the steady state to be attractive along the z axis, one needs a negative diagonal term in z. Matrix (I) below fulfills these requirements. It can be easily checked that even a linear system of this structure will have a steady state of type (I) provided the coefficient a_{22} is not too high.

$$\begin{pmatrix} \cdot & - & \cdot \\ + & + & \cdot \\ \cdot & \cdot & - \end{pmatrix} \tag{I}$$

$$\begin{pmatrix} \cdot & \cdot & - \\ \cdot & + & \cdot \\ + & \cdot & - \end{pmatrix} \tag{II}$$

$$\begin{pmatrix} 0 & - & - \\ + & + & 0 \\ + & 0 & - \end{pmatrix} \tag{III}$$

We now wish to generate a steady state like (II), periodically attractive in, say, the xz plane and repulsive along the y axis. To be periodic in xz, we need a negative circuit in xz; for this periodicity to be attractive, we need a negative diagonal term in x or z, and in order to be repulsive in y, we need a positive diagonal term in y. Matrix (II) fulfills these requirements. Note that matrices (I) and (II) each comprize a union of disjoint circuits which involves all three variables. This is why they can each generate a "full" steady state of the system (steady states "I" and "II", respectively). Matrix (III) is the sum of matrices (I) and (II) [which simply means that the differential equations of system (III) cumulate the terms of the equations of systems (I) and (II)]. If one computes the Jacobian matrix of the Rössler system at the two steady states, it is seen that the corresponding qualitative matrices are identical with each other and also with matrix (III).

This suggests that this matrix might describe the logical structure underlying the Rössler equations. That this is indeed the case can be shown as follows. As mentioned above, the only nonlinearity in the Rössler system is the xz term in the equation for $\dot{z}$. In order to know whether it is there because one imperatively needs a term in xz, or simply because one needs some nonlinearity in the system to avoid runaway to infinity, we delete the xz term and render one of the other terms nonlinear instead, keeping the logical structure as in matrix (III). A system satisfying these conditions is:

$$\begin{aligned} \dot{x} &= -y - z \\ \dot{y} &= x + ay \\ \dot{z} &= f(x) - cz \end{aligned} \tag{1}$$

For $f(x) = x^2$, the system, even (slightly) simpler than Rössler's, has two steady states of the expected type for a wide range of parameter values and generates a chaotic attractor (see Fig. 2 and Table 1).

System (1) has been tested using as $f(x)$ a number of other nonlinearities (monomial functions with integer or not powers, > 1 or < 1, Hill functions with cooperativity exponent ≥ 1, trigonometric, hyperbolic functions). In most cases we could easily find a range of parameter values within which the dynamics is chaotic [Thomas, 1996, 1999]. Some examples are found in Table 1.

A first conclusion is that provided a proper logical structure is preserved the mere ability to generate a chaotic dynamics is rather insensitive to the precise nature of the nonlinearity used.

While the very existence of a choaotic dynamics displays little sensitivity toward the nature of the nonlinearities chosen, it is certainly not a surprise that the shape and other specific characteristics of the chaotic attractor depend at least to some extent on the nature of the nonlinear functions used. For example, in systems (1), when the nonlinearity is

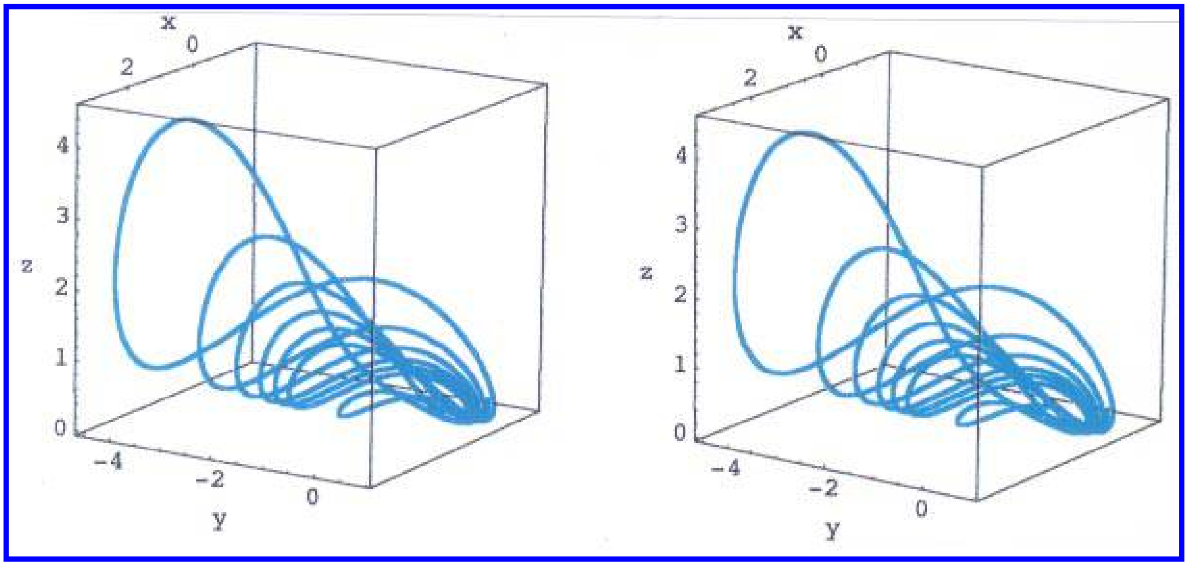


Fig. 2. A trajectory for a Rössler-like system (1) in which the nonlinearity $f(x) = x^2$. Initial state $(0.1, 0.1, 0.1)$, not crucial. Numerical integration following [Gottwald & Wanner, 1981], with initial integration step $h_0 = 0.01$. Trajectory recorded from $t = 50$ to $t = 200$. For more details see Table 1. The two images are tilted by $5°$ around the vertical axis in order to permit a stereoscopic view.

simply a power law, term j_{31} of the Jacobian matrix is zero at steady state (0, 0, 0); consequently, the eigenvalues at this steady state are entirely determined by the circuits described in matrix (I) above, and the structure is $-/++$. In contrast, for nonlinearities like $(\tanh x)$, it is near the other steady state that j_{31} is close to 0. It can be inferred that in such a case it will be this nontrivial steady state which will have the structure $-/++$, and that now it will be steady state (0, 0, 0) which will have the complementary structure $+/--$. That this is indeed the case for $f(x) = b\ \tanh(x)$ is shown in Table 1. Furthermore (Table 1), with odd functions such as x^3 or $\tanh(x)$, one has three steady states, two of which are symmetrical with respect to the origin; in this situation, one has one or two attractors depending on the case, and sometimes simply on parameter values. In the case of these symmetrical systems, we would like to stress that the two outer steady states have exactly the same eigenvalues; their periodic component is generated by the same negative circuit. Thus, a single negative circuit can generate periodicity around more than one steady state. This point will be considered again below.

Functions of similar shape generate similar chaotic attractors, even when the similarity of the functions is only local. For example, the attractors obtained for $f(x) = \sin x$, $f(x) = \tanh x$ and $f(x) = \mathrm{sgn}(x)$ (Table 1) have extremely similar geometries (trajectories not shown). Another striking illustration of this point is shown below (in Sec. 4 because in these cases one does not deal with Rössler-derived systems).

Although changing the sign of an individual term usually results in a complete collapse of the chaotic dynamics, it should be mentioned that whenever a set of two or more terms of the Jacobian matrix belong to the same circuit, one can change signs, provided the circuit itself keeps its sign (for example, $(+-) \to (-+)$ or *vice versa*, which simply changes the sense of rotation; $(+++) \to (+--)$ or $(-+-)$ or $(--+)$, etc...)

Nicolis (personal communication) conjectured that it should be possible to constuct Rössler-like systems with a single steady state. The formulation of the problem in terms of feedback circuits immediately shows that this is indeed the case. Let us permute the coefficients a_{11} and a_{22} in matrix (III) above, and call the new matrix "IV". Just as we had combined matrices (I) and (II), each of which shows the circuits involved in the generation of a given steady state, into matrix (III), we can dissociate matrix (IV) into two submatrices. If one analyzes in this way the shift from matrix (III) to matrix (IV), it can be seen that the circuits which generated steady state (I) are not altered by the change (and as a matter of fact the

Table 1. Five systems of the Rössler type [structure (1)] and two derived systems with a single steady state.

Equations	Parameters	Steady States	Eigenvalues at Steady States	Lyapunov Exponents
$\dot{x} = -y - z$		0, 0, 0	$-2.00,\ +0.19 \pm 0.98i$	$+0.049$
$\dot{y} = x + ay$	$a = 0.385$			$\lvert < 10^{-4} \rvert$
$\dot{z} = \mathbf{x^2} - cz$	$c = 2$	5.19, −13.5, +13.5	$+0.18,\ -0.89 \pm 3.18i$	-1.66
	see Fig. 2			
$\dot{x} = -y - z$		0, 0, 0	$-1.00,\ +0.40 \pm 0.91i$	$+0.146$
$\dot{y} = x + ay$	$a = 0.8$	+1.11, −1.39, +1.39	$+0.46,\ -0.33 \pm 2.03i$	$\lvert < 10^{-4} \rvert$
$\dot{z} = \mathbf{x^3} - cz$	$c = 1$	−1.11, +1.39, −1.39	$+0.46,\ -0.33 \pm 2.03i$	-0.346
$\dot{x} = -y - z$	$a = 0.7$	0, 0, 0	$+0.31,\ -0.30 \pm 1.84i$	
$\dot{y} = x + ay$	$b = 3$	+2.02, −2.89, +2.89	$-0.86,\ +0.28 \pm 0.95i$	
$\dot{z} = b\,\mathbf{tanh}(\mathbf{x}) - cz$	$c = 1$	−2.02, +2.89, −2.89	$-0.86,\ +0.28 \pm 0.95i$	
$\dot{x} = -y - z$	$a = 0.7$	0, 0, 0	$+0.188,\ -0.244 \pm 1.55i$	$+0.090$
$\dot{y} = x + ay$	$b = 2.1$	1.46, −2.087, +2.087	$-0.84,\ +0.27 \pm 0.95i$	$\lvert < 10^{-4} \rvert$
$\dot{z} = b\,\mathbf{sin}(x) - cz$	$c = 1$	−1.46, +2.087, −2.087	$-0.84,\ +0.27 \pm 0.95i$	-0.390
$\dot{x} = -y - z$				
$\dot{y} = x + ay$	$a = 0.4$	0, 0, 0	$+0.386,\ -0.493 \pm 1.0i$	
$\dot{z} = \mathbf{sgn}(x) - cz$	$c = 1$	+0.4, −1, +1	$-1.0,\ +0.2 \pm 9.8i$	
		−0.4, +1, −1		
$\dot{x} = ax - y - z$	$a = 0.25$			$+0.088$
$\dot{y} = x$	$c = 2$	0, 0, 0	$-2.0,\ +0.125 \pm 0.99i$	$\lvert < 2.10^{-4} \rvert$
$\dot{z} = \mathbf{x^2} - cz$	see Fig. 3(a)			-1.84
$\dot{x} = -y$	$a = 3.3$			$+0.069$
$\dot{y} = x + ay - z$	$c = 4$	0, 0, 0	$+2.96,\ +0.33,\ -4.0$	$\lvert < 10^{-4} \rvert$
$\dot{z} = \mathbf{y^3} - cz$	see Fig. 3(b)		(a saddle point)	-0.769

eigenvalues at steady state (I) remain exactly the same for equal values of the parameters). In contrast, the circuits which generated steady state (II) in system (1) are not able any more to generate a full steady state, because now they involve only two of the three variables. Rather, they generate a "partial steady state" (see Sec. 1), that is, a steady state in the subspace of only part of the variables (here, x and z). Figure 3 and Table 1 describe the attractor generated by this new system [Fig. 3(a)], as well as another Rössler-like system [Fig. 3(b)] which has also a single full steady state. This last system was derived in a different way but following the same general principle. In this case, the nonlinearity is y^3. The full steady state is a saddle point of structure $(-++)$, topologically equivalent to a

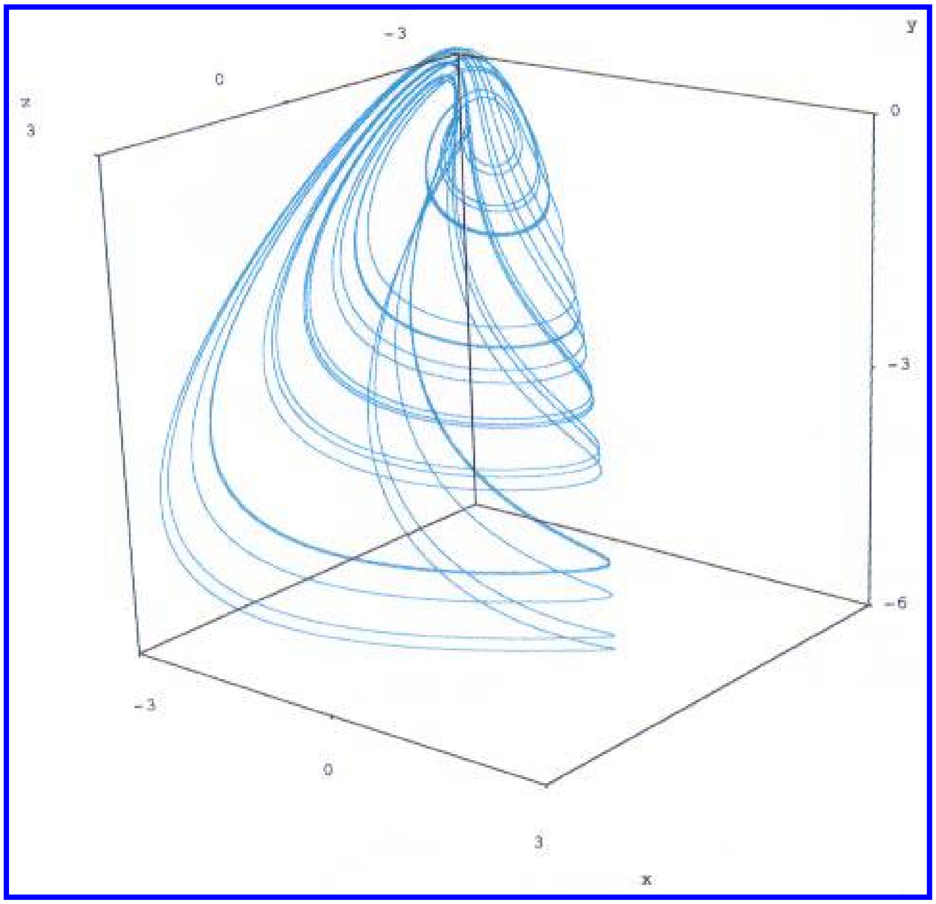
Fig. 3. (*following page*) (a and b) Trajectories for two Rössler-like systems modified in order to have a single steady state.

(a) $\dot{x} = ax - y - z$, $\dot{y} = x$, $\dot{z} = x^2 - cz$; $a = 0.25$, $c = 2$

(b) $\dot{x} = -y$, $\dot{y} = x + ay - z$, $\dot{z} = y^3 - cz$; $a = 3.3$, $c = 4$

In both cases the unique full steady state is located at (0, 0, 0). For system (a), the steady state is a saddle focus of type $-/++$, for system (b), it is a saddle point of type $-++$ (topologically equivalent). Initial state (0.1, 0.1, 0.1), not crucial. Other aspects, see the legend for Fig. 2.

(a)



(b)

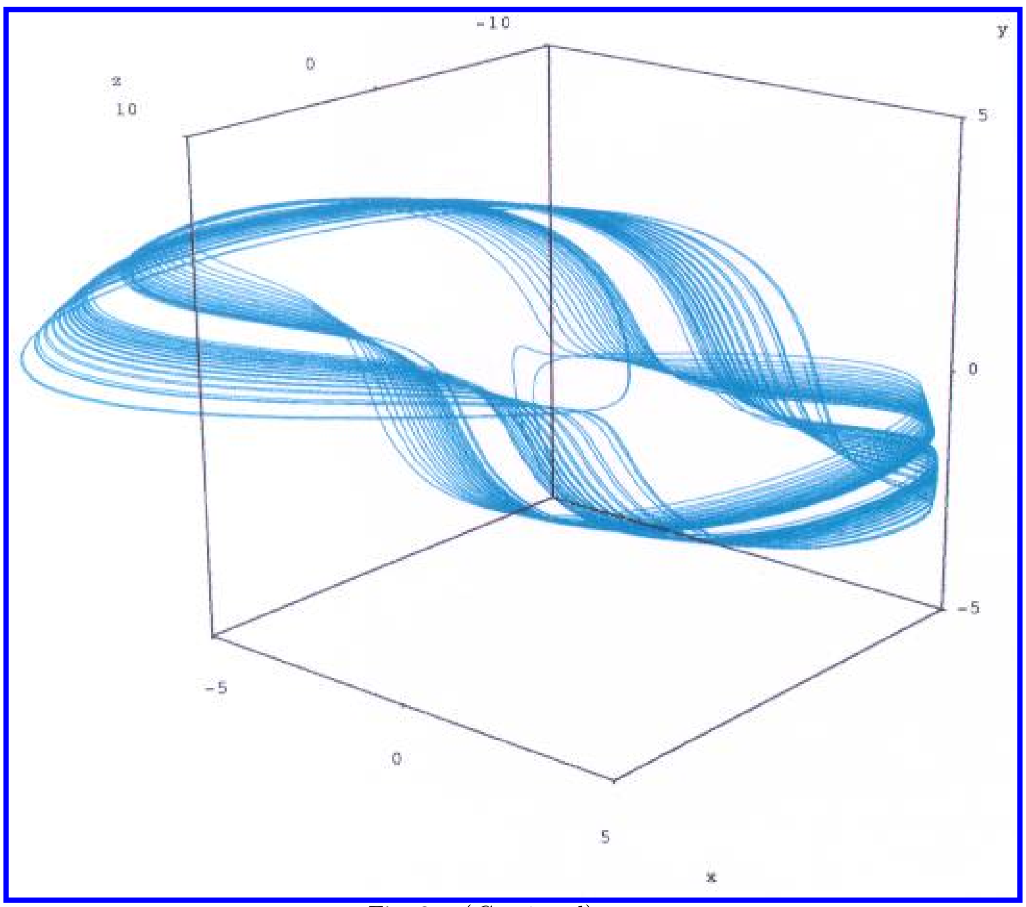


Fig. 3. (*Continued*)

saddle focus of type $(-/++)$, and there are two symmetrical partial steady states, around each of which a periodicitiy is organized.

As a matter of fact, using the ideas above one is in the position to synthesize whole classes of three- and four-dimensional dynamical systems showing chaotic behavior, tailored to satisfy various requirements [Thomas, 1996, 1999]. Other systems, including those of Lorenz [1963], Chua [Madan, 1993] (and continuous equivalents of it), and the remarkably simple systems recently developed by Sprott [1994] can be analyzed along similar lines. The main impression emerging from this analysis is that an essential requirement to generate a chaotic motion is to have at least two oscillatory motions which are *distinct* (in the sense that they take place in the vicinity of distinct steady states (full or "partial"), and *yet coupled* at the level of the overall system. However, as mentioned above, two periodicities can be generated by the same negative circuit. This is the case when a system comprises a single negative circuit which generates oscillations in the vicinity of two or more distinct steady states. In order to have a chaotic dynamics, one would thus need at least one negative circuit (with at least two elements) to generate the oscillations, and (at least if there is only one functional negative circuit) one positive circuit to ensure complete or "partial" multistationarity.

4. Chaotic Behavior Generated by a Single Feedback Circuit: Labyrinth Chaos

In this section, we show that chaotic dynamics can be generated by a *single* feedback circuit, provided this circuit is positive or negative depending on its location in phase space.

Let us first consider systems comprising negative linear diagonal terms in addition to the three-element circuit as in Chua's "standard CNN" equation [Chua, 1997]. Note that these one-element negative circuits cannot generate any periodicity by themselves.

$$\begin{aligned}\dot{x} &= -bx + f(y)\\ \dot{y} &= -by + f(z)\\ \dot{z} &= -bz + f(x)\end{aligned} \tag{2}$$

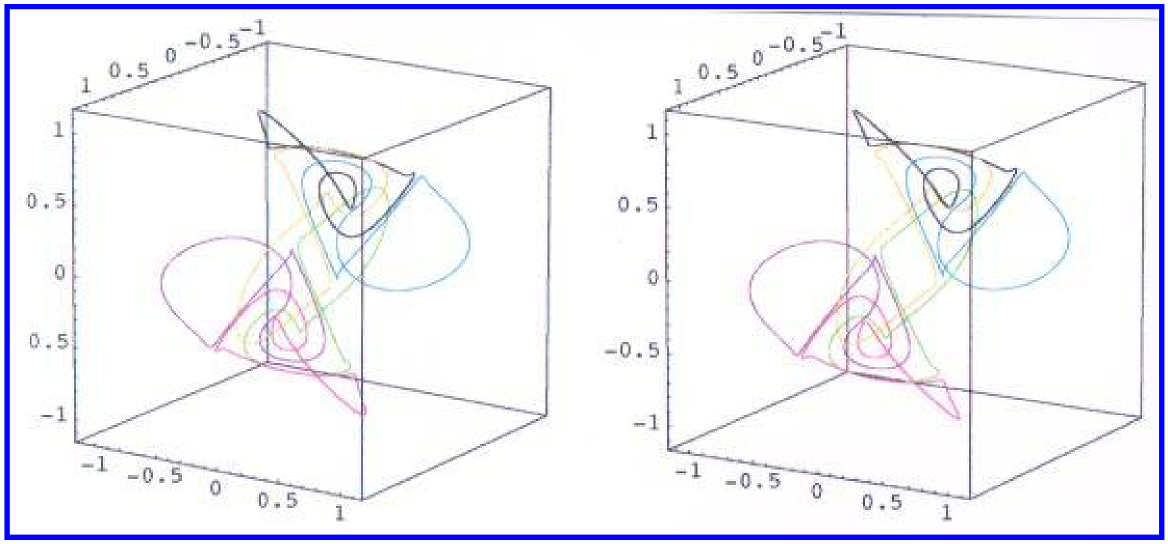
For $f(u) = au - u^3$, the Jacobian matrix is:

$$\begin{pmatrix} -b & a-3y^2 & 0 \\ 0 & -b & a-3z^2 \\ a-3x^2 & 0 & -b \end{pmatrix}$$

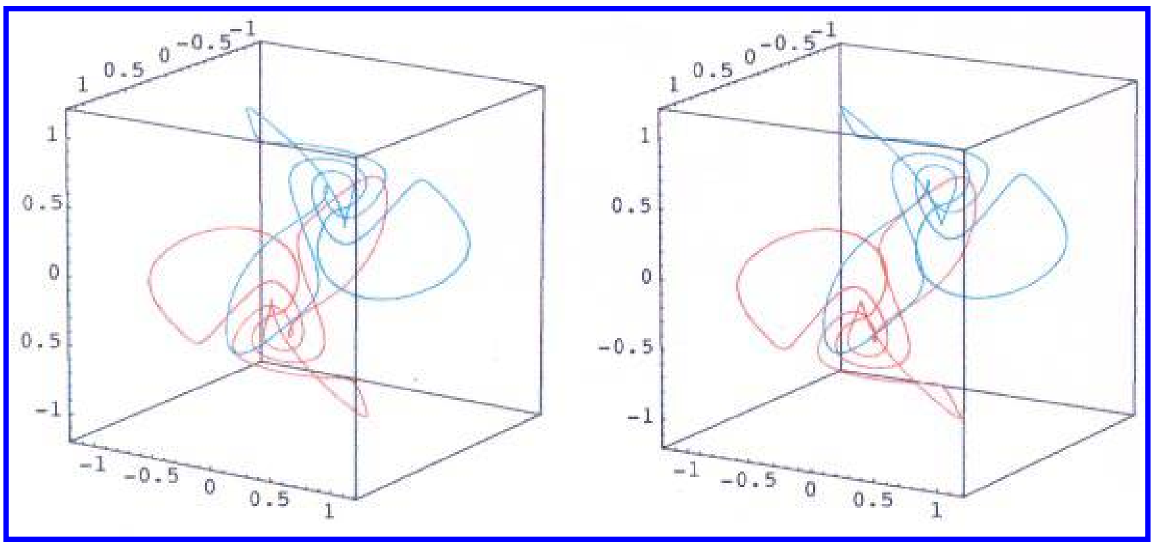
and each of the three matrix elements of the type $(a - 3u^2)$ is positive for small values of $|u|$, negative for $|u| > (\sqrt{a/3})$. Thus, the three-element circuit is positive or negative according to a three-dimensional quincunx structure comprising 27 (3^3) domains. As anticipated, for a wide range of parameter values this system has 27 steady states, one per box, *all unstable*. In agreement with the previous comments about the relationship between feedback circuits and steady states, these steady states are saddle foci, of two types ($+/--$ or $-/++$) according to whether they are located in a region in which the circuit is positive or negative. Trajectories percolate between these many unstable steady states. For proper parameter values, the dynamics is chaotic [see Figs. 4(c), 4(d) and 4(f)]. The pathway followed towards and from chaos for $b = 0.3$ and increasing values of a (or as well for $a = 1.2$ and decreasing values of b) may be of some interest. For $a = 1.0$, there are six stable limit cycles [Fig. 4(a)]. For $a = 1.03$, these have fused three by three to generate two limit cycles of a quite complex shape [Fig. 4(b)]. For $a = 1.09$, following the classical cascade of doublings, we have two chaotic attractors [Fig. 4(c)]. For $a = 1.10$, these have fused into a single chaotic attractor [Fig. 4(d)], and near

Fig. 4. (*following pages*) Trajectories of system (2), with $f(u) = au - u^3$. Parameter $b = 0.3$. (a) $a = 1.00$ — Six limit cycles, (b) $a = 1.03$ — Two complex limit cycles, (c) $a = 1.09$ — Two distinct chaotic attractors, (d) $a = 1.10$ — A single chaotic attractor, (e) $a = 1.208$ — Three limit cycles, (f) $a = 1.27$ — A chaotic attractor again. **Initial states:** When there is a single attractor : $(0.01, 0, 0)$, not crucial, two attractors: (0.01, 0, 0) and (−0.01, 0, 0), three attractors: (0.01, 0, 0), (0, 0.01, 0) and (0, 0, 0, 01), six attractors: (±0.01, 0, 0), (0, ±0.01, 0), (0, 0, ±0.01). **Time:** From 100 to 1000 time units for chaotic trajectories, from 100 to 200 time units for limit cycles (in order to eliminate transitories). **Stereoscopic view:** Look at the couple of images vertically from 50 cm or so, with ample lighting, squeeze slightly in order to see a third image, between the two "real" images. Once you have succeeded in focusing on the third image, you see it clearly in three dimensions.

(a)



(b)



(c)

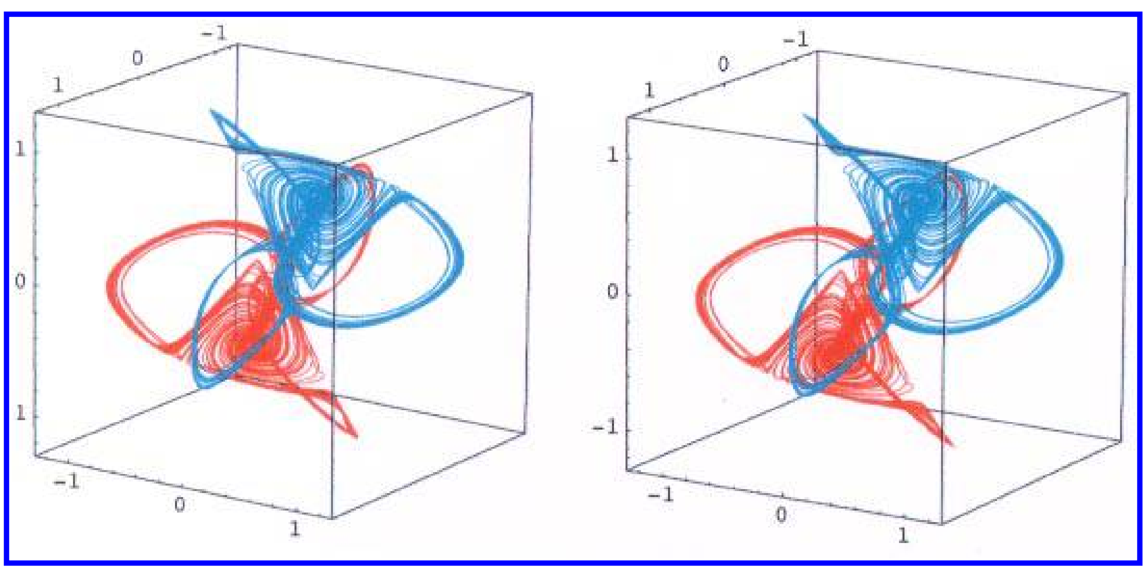


Fig. 4. (*Continued*)

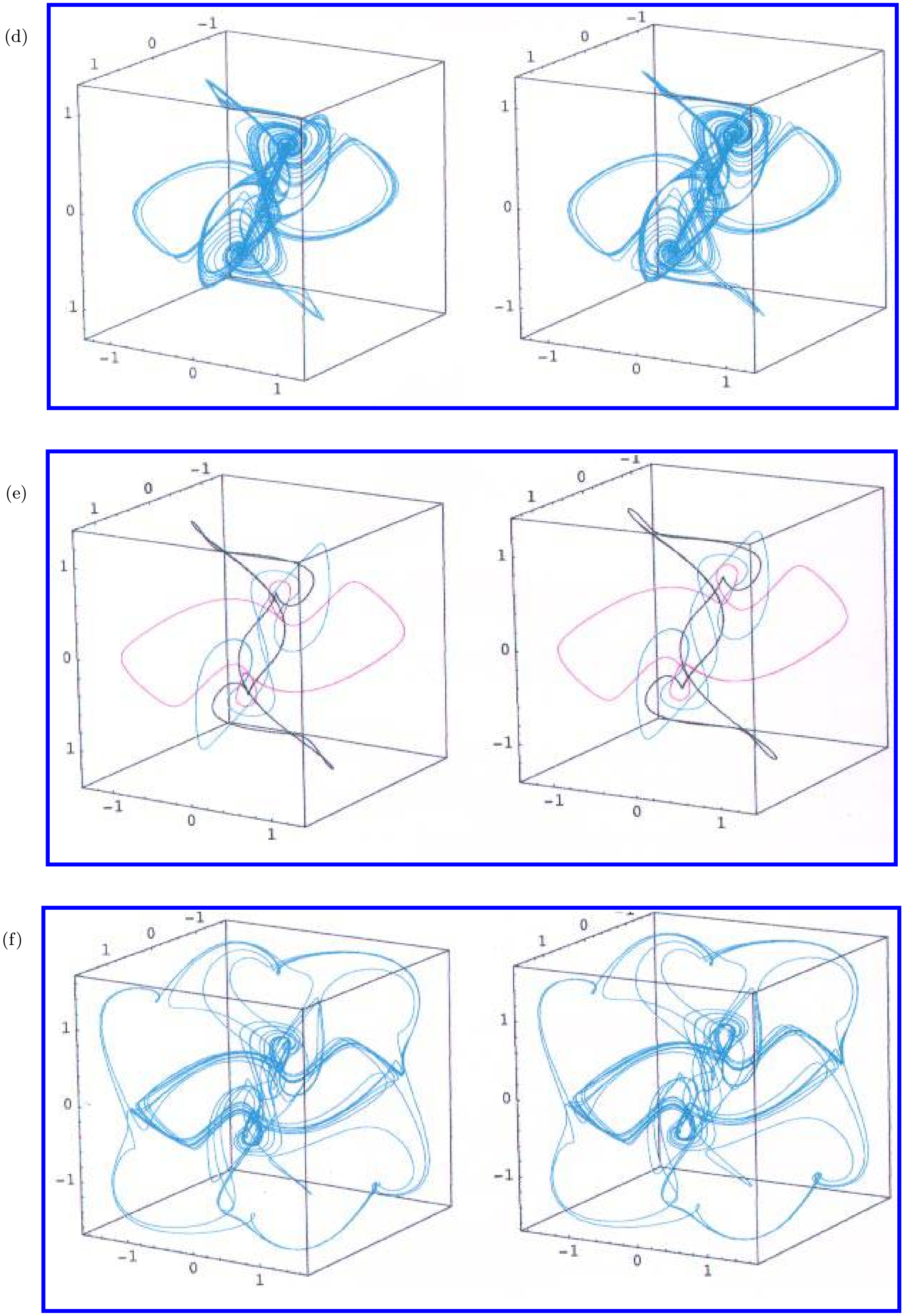


Fig. 4. (*Continued*)

Table 2. The systems $\dot{x} = -bx + f(y)$, $\dot{y} = -by + f(z)$, and $\dot{z} = -bz + f(x)$ with (a) $f(u) = au - u^3$, (b) $f(u) = \sin u$, and (c) a piecewise-linear caricature of (a):

$$
\begin{array}{ll}
\text{for } u \leq -1 & f(u) = -(c+a) - cu \\
\text{for } -1 < u \leq 1, & f(u) = au \\
\text{for } 1 < u & f(u) = +(c+a) - cu
\end{array}
$$

Equations	Parameters	Steady State Values	Eigenvalues	Lyapunov Exponents
(a)	$a = 1.0$	27 steady states*	all of types	
	$b = 0.3$	**No chaos:**	$+/--$ or $-/++$*	$\vert < 2.10^{-5}\vert$
	see Fig. 4(a)	**six limit**		-0.103
		cycles		-0.796
$\dot{x} = -bx + ay - y^3$	$a = 1.1$	27 steady states*	"	$+0.092$
$\dot{y} = -by + az - z^3$	$b = 0.3$			$\vert < 5.10^{-4}\vert$
$\dot{z} = -bz + ax - x^3$	see Fig. 4(d)	**Chaos**		-0.992
	$a = 1.200$	27 steady states*	"	$+0.053$
	$b = 0.3$			$\vert < 2.10^{-4}\vert$
		Chaos		-0.953
	$a = 1.208$	27 steady states*	"	$\vert < 10^{-3}\vert$
	$b = 0.3$	**No chaos:**		-0.023
	see Fig. 4(e)	**Three complex**		-0.877
		limit cycles		
(b)	$b = 0.18$	27 steady states*	all of types	0.034
			$+/--$ or $-/++$*	$\vert < 10^{-4}\vert$
$\dot{x} = -bx + \sin y$	see Fig. 5(c)	**Chaos**		-0.574
$\dot{y} = -by + \sin z$				
$\dot{z} = -bz + \sin x$				
	$b = 0$	An infinite number		
		of steady states		
		$x = k\Pi$	If s** even	$+0.095$
	see Fig. 5(h)	$y = 1\Pi$	1.0, $-0.5 \pm 0.866i$	$\vert < 5.10^{-4}\vert$
		$z = m\Pi$	If s** odd,	
		Chaos	-1.0, $+0.5 \pm 0.866i$	-0.095
(c)				
$f(u)$ is a piecewise-	$a = 1$	27 steady states*	all of types	Not
linear caricature of	$b = 0.3$		$+/--$ or $-/++$*	determined
$au - u^3$	$c = 1.8$			
(see legend)	see Fig. 4(c)			

*All steady states and the corresponding eigenvalues were determined but not listed here.
**In system (b), k, l, m are integers, positive or negative, which give the position of steady states; $s = k \bmod 2 + 1 \bmod 2 + m \bmod 2$. This sum gives the number of odd terms in the unique circuit of the Jacobian matrix; depending on whether s is even or odd, the circuit is positive or negative.

$a = 1.208$, the chaotic attractor abruptly dissociates into three limit cycles [Fig. 4(e)]. The dynamic becomes chaotic again for still higher values of a [see Fig. 4(f), for $a = 1.27$]. Note that much of this complex pattern can be understood, and in fact, could have been predicted, in terms of the geometry of the steady states and the positive versus negative character of the circuit at each level. Additional data are found in Table 2(a). Compare the Lyapouvov exponents for two close values of a ($a = 1.2$, which gives a chaos; $a = 1.208$, which gives three complex limit cycles).

As briefly mentioned above, systems with a proper logical structure are extremely robust toward changes in the precise nature of the nonlinearities. A nonlinearity can often be replaced by a gross caricature without altering the general shape of the attractor. In particular, $(ax - x^3)$ can be replaced by $\sin x$, and a further idealization consists of a three-element piecewise-linear caricature [Table 2(a)–2(c)]. Almost indistinguishable attractors can indeed be obtained using these various functions (not shown for the piecewise-linear function; for $ax - x^3$ and $\sin x$, compare Figs. 4 and 5).

Let us now consider again system (2), this time with $f(u) = \sin u$. For the (unique) parameter $b \geq 1$, there is a single steady state. As b decreases, the number of steady states can be predicted to (and indeed does) jump to higher and

(a)

(b)

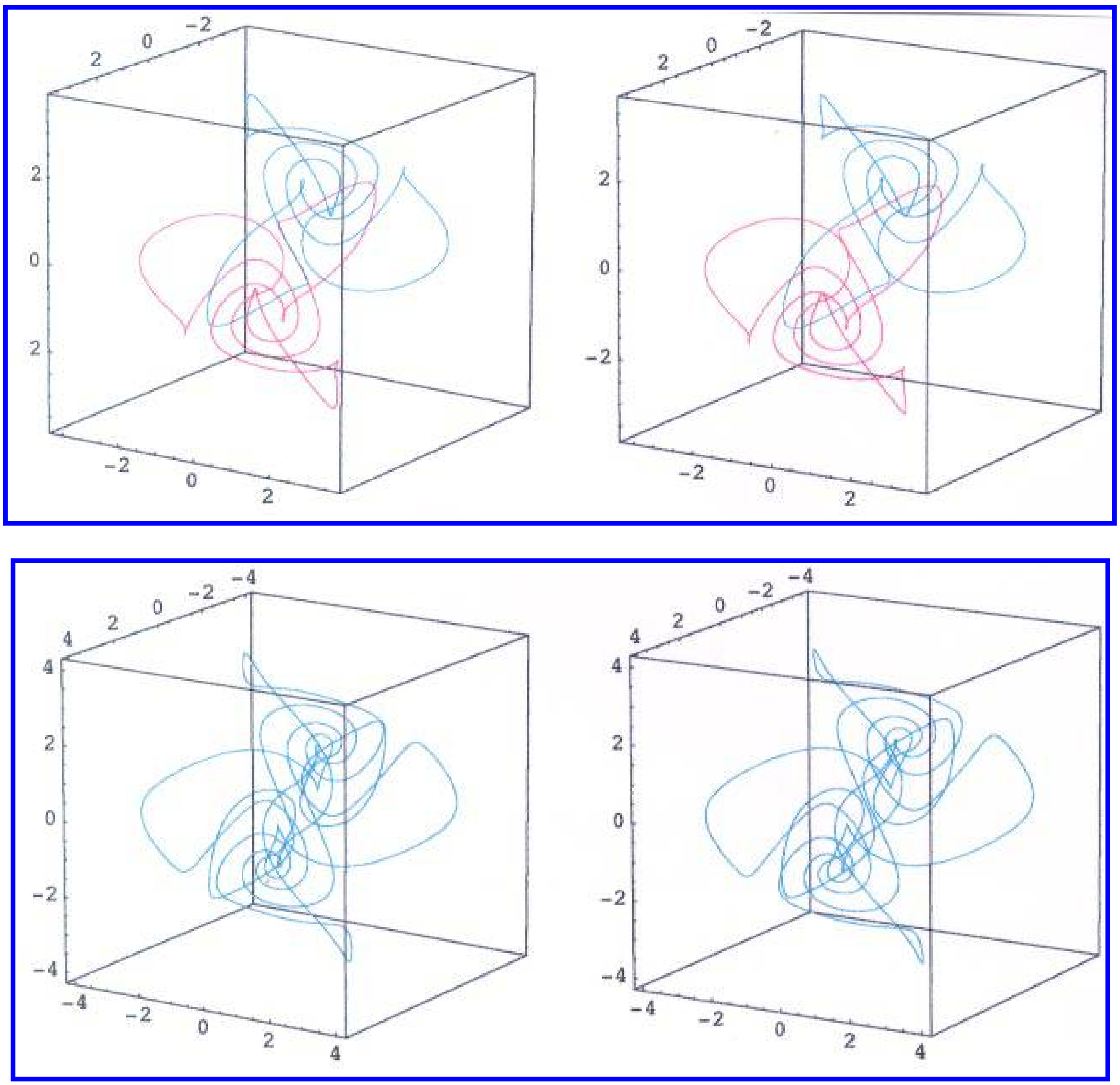
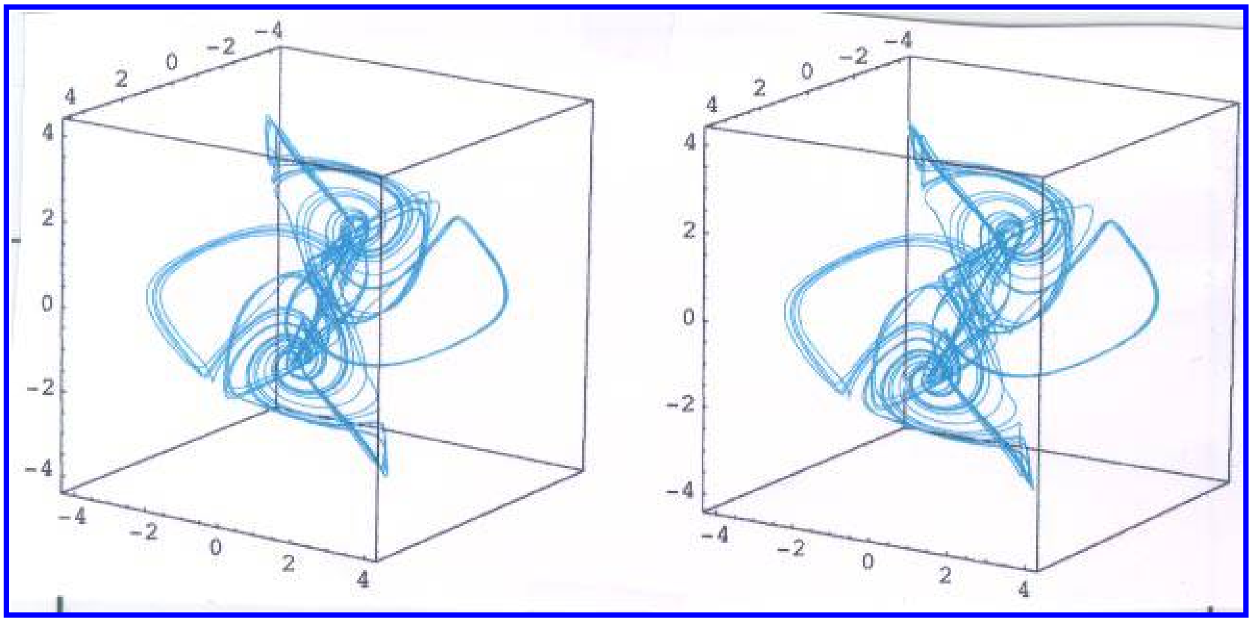
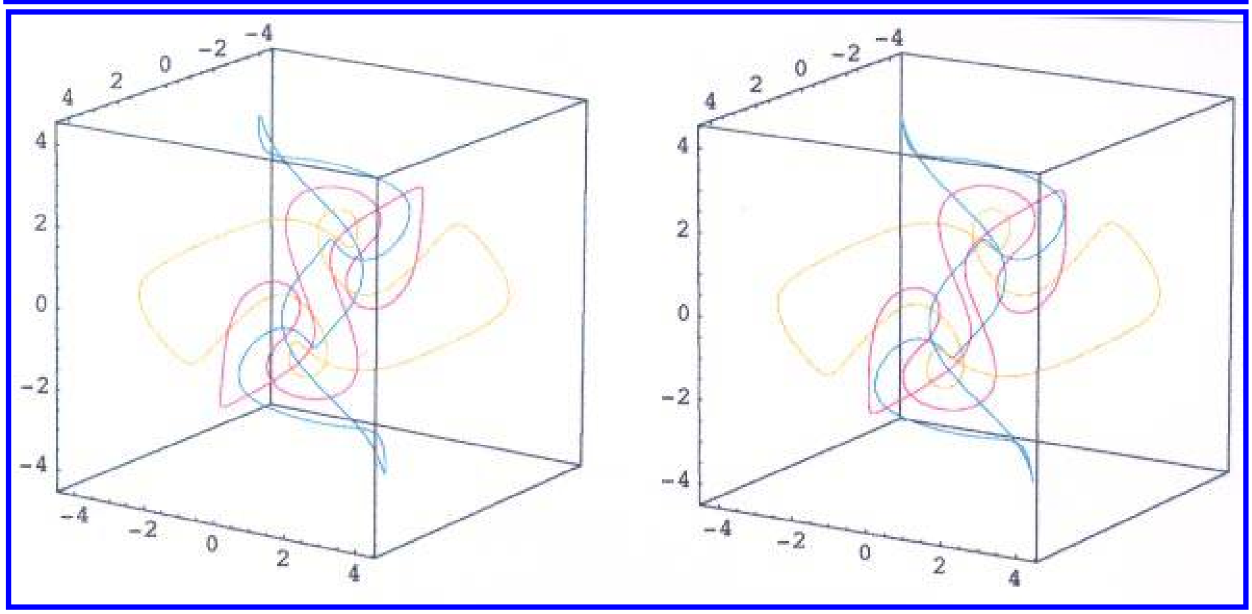


Fig. 5. Trajectories for system (2) with $f(u) = \sin(u)$. (a) $b = 0.22$ — Two limit cycles, (b) $b = 0.19$ — A single, complex, limit cycle, (c) $b = 0.18$ — A chaotic attractor, (d) $b = 0.17$ — Three limit cycles, (e) $b = 0.13$ — Three limit cycles, (f) $b = 0.10$ — Chaos, (g) $b = 0.01$ — Chaos, and (h) $b = 0.0$ — Chaos. For other aspects, see the legend of Fig. 4.

(c)



(d)



(e)

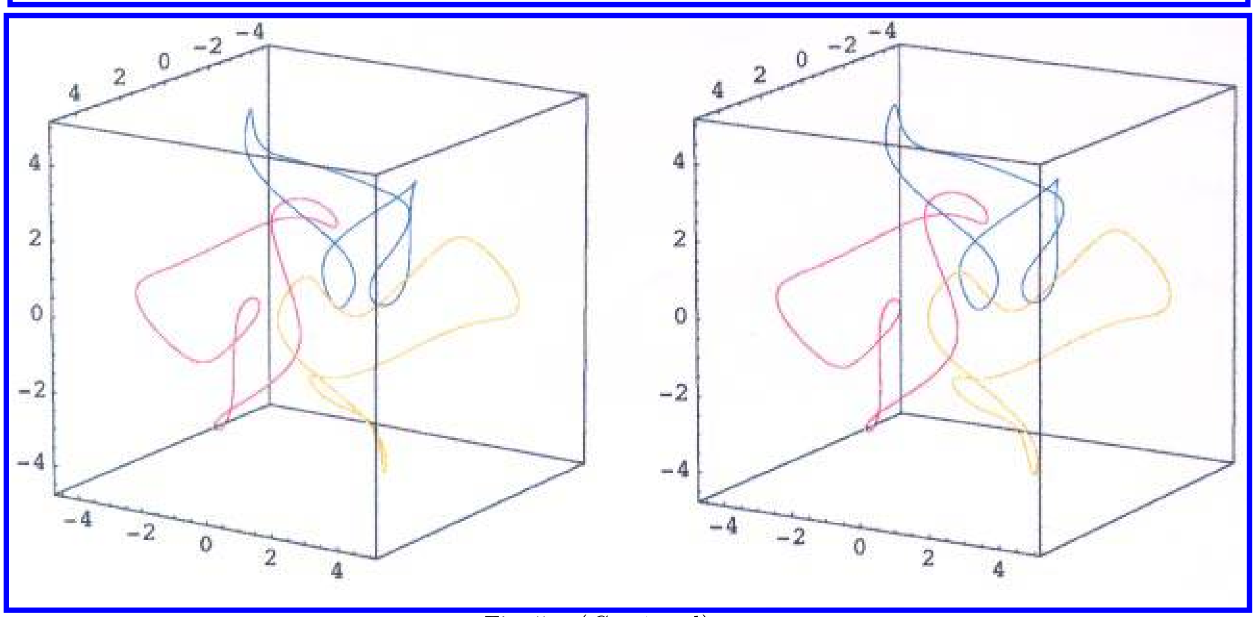
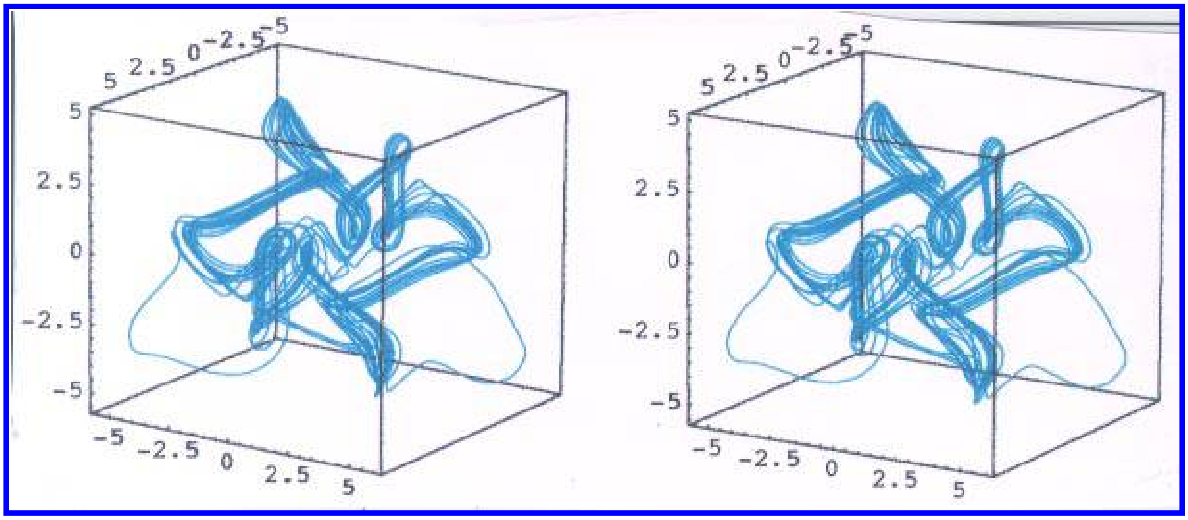
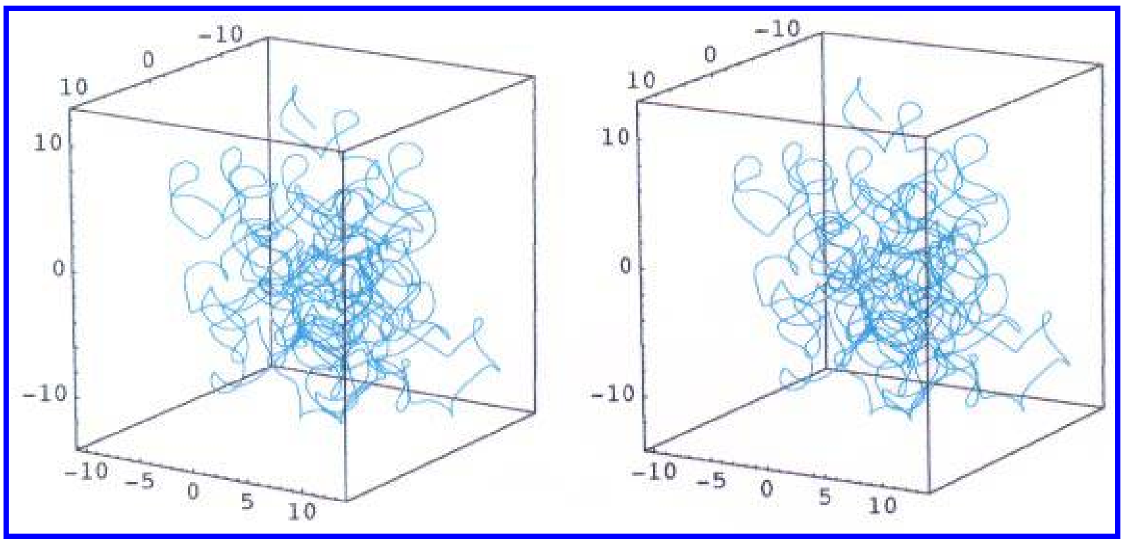


Fig. 5. (*Continued*)

(f)



(g)



(h)

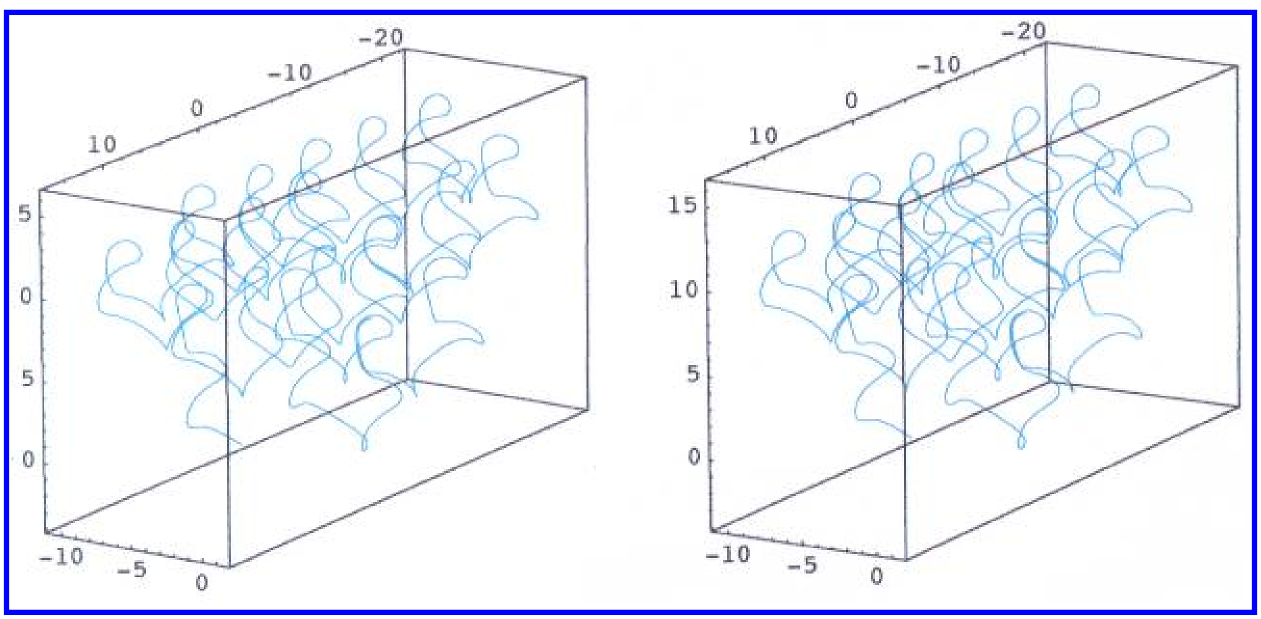


Fig. 5. (*Continued*)

higher values. The evolution of the system (Fig. 5) first strikingly resembles the preceeding one (with $f(x) = ax - x^3$). In particular, the dynamics is chaotic for $b = 0.18$ [Fig. 5(c) and Table 2]. For lower values of b, there are three complex periodic attractors [Figs. 5(d) and 5(e)] and for $b \leq 0.10$ the trajectory again becomes chaotic [Figs. 5(f)–5(h)]. The size and complexity of the strange attractor, as well as the number of steady states (all unstable) steadily increase (this time unlike system $(ax - x^3)$ and its piecewise-linear caricature, in which the number of steady states is of course limited to 3^3).

Consider now the limiting case of a system without diagonal terms (and thus conservative):

$$\begin{aligned} \dot{x} &= \sin\, y \\ \dot{y} &= \sin\, z \\ \dot{z} &= \sin\, x \end{aligned} \tag{3}$$

The Jacobian matrix is:

$$\begin{pmatrix} 0 & \cos\, y & 0 \\ 0 & 0 & \cos\, z \\ \cos\, x & 0 & 0 \end{pmatrix}$$

There is now a single, three-element circuit. Each term of this circuit periodically changes from positive to negative at intervals of Π as a function of the relevant variable. Thus, phase space is entirely filled by an infinite three-dimensional checkerboard, in whose boxes the unique feedback circuit is alternatively positive and negative. As expected, each box contains an unstable steady state at which the eigenvalues of the matrix are $(+1.0$ and $-0.5 \pm (\sqrt{3}/2)i)$ or $(-1.0$ and $+0.5 \pm (\sqrt{3}/2)i)$ for positive and negative boxes, respectively. The trajectory, which percolates within the lattice of unstable steady states of the system [Fig. 5(h)], is chaotic, as shown by the Lyapunov exponents [Table 2(b)].

5. Discussion and Perspectives

In this work, we showed how the concept of feedback circuit can be used to decifer the logical structures underlying complex dynamical systems. The basic idea is that the Jacobian matrix can be used not only in the close vicinity of steady states (where it provides us with the ingredients for linear stability analysis) but also elsewhere in phase space, thus providing essential qualitative information on global aspects of the dynamics. Considering the analytical expression of the Jacobian matrix anywhere in phase space indeed permits one to partition phase space into well-defined regions within which the signs of the terms of the matrix are constant and, consequently, within which each circuit has a constant sign.

We also used throughout this work (not described in detail here) a partitioning of phase space according to the signs of the eigenvalues or their real parts.

That feedback circuits, as defined above, indeed play a crucial role in dynamics, becomes obvious once it has been recognized that, among the nonzero elements of a Jacobian matrix, only those which belong to a circuit are present in the characteristic equation and, thus, contribute directly to the eigenvalues of the matrix. This results directly from the structure of the characteristic determinant. In the development of a determinant of size $(n \times n)$, each term is a product of factors which represent either a circuit or a union of disjoint circuits. The elements of the Jacobian matrix which do not belong to a circuit are combined with zero terms, and thus form vanishing products (see [Thomas, 1994]). As a matter of fact, the expanded determinant of the Jacobian matrix is nothing else than the list of those circuits and unions of disjoint circuits which involve all the variables of the system.

One of the most rewarding aspects of this work is the remarkable robustness of chaotic dynamics versus the exact nature of nonlinearities. Two functions with, even locally, similar shapes, often produce extremely similar strange attractors, and in many cases, provided the logical structure is preserved, one can obtain chaotic attractors with almost any type of nonlinearity.

There is obviously a problem about how to characterize system "$\dot{x} = -bx + \sin\, y$" etc… in the limiting case $b = 0$, in which the diagonal terms have vanished. In this case, the lattice of unstable steady states and the envelope of the trajectories fill phase space entirely. Is it still legitimate to use the term "attractor" for this unbounded object? At any rate, the trajectories are still chaotic even in this limiting case, as shown by the values of the Lyapunov exponents. Note that, as anticipated, using $(-\sin)$ or $(\cos)$ instead of $(\sin)$ provides trajectories of a different shape but similar nature. Also, "labyrinth" structures using a single feedback circuit can be extended without any difficulty to 5, 7... dimensions. The "labyrinth" system is a striking example of how different the structural complexity of a chaotic system can be at the analytic level (complexity of the equations), at the logical level (feedback circuits) and at the level of the organization of phase space. Here, the logical structure is exceedingly simple (a single feedback circuit), the differential equations are very simple (even though they involve transcendental functions), but phase space itself has become very complex, partitioned as it is into a high number of domains each containing an unstable steady state.

We emphasized (see also [Thomas, 1991, 1994]) the conceptual distinction between feedback circuits (= "logical structure") and nonlinearities, both absolutely essential for "nontrivial behavior". We find in particular that when a nonlinearity and a circuit have to cooperate to generate complex dynamics, the nonlinearity does not have to be located on the circuit (e.g. in part of the Rössler-like systems studied here, the only positive circuit — term j_{22} — is linear). We are still far from a full understanding of the functional interactions between circuits and nonlinearities. However, a firm theoretical foundation including a treatment of topological equivalence, can be found in [Wu & Chua, 1996]. Finally, further developments should be expected from systems of the type considered in Sec. 4, whose analytical and logical structures are extremely simple. Strikingly, the mere decrease of a parameter (responsible for the dissipative character of the dynamics) can result in unlimited inflation and complexification of the chaotic attractor, which progressively invades more and more of phase space.

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References

Chua, L. O. [1997] "CNN: A vision of complexity," *Int. J. Bifurcation and Chaos* **7**(10), 2219–2425.

Chua, L. O., Wu, C.-W., Huang, A. & Zhong, G.-Q. [1993] "A universal circuit for studying and generating chaos," *IEEE Trans. Circuits Syst.* **40**(10), 745–761.

Delbruck, M. [1949] "Discussion" in *Unités Biologiques douées de continuité génétique*, (Editions du Centre National de la Recherche Scientifique, Paris), pp. 33–35.

Demongeot, J. [1998] "Multistationarity and cell differentiation," *J. Biol. Syst.* **6**(1), 1–2.

Eisenfeld, J. & de Lisi, C. [1985] "On conditions for qualitative instability of regulatory circuits with applications to immunological control loops," *Mathematics and Computers in Biomedical Applications*, eds. Eisenfeld, J. & de Lisi, C. (Elsevier), pp. 39–53.

Gaspard, P. & Nicolis, G. [1983] "What can we learn from homoclinic orbits in chaotic dynamics?" *J. Stat. Phys.* **31**, 499–518.

Gottwald, B. A. & Wanner, B. [1981] "A reliable Rosenbrock integrator for stiff differential equations," *Computing* **26**, 355–360.

Gouzé, J.-L. [1998] "Positive and negative circuits in dynamical systems," *J. Biol. Syst.* **6**(1), 11–15.

Guckenheimer, J. & Holmes, P. [1983] "Nonlinear oscillations, dynamical systems and bifurcations of vector fields," *Appl. Math. Sci.* **42**, 1–459.

Lorenz, E. N. [1963] "Deterministic non-periodic flows," *J. Atmos. Sci.* **20**, 130–141.

Madan, R. N. [1993] *Chua's Circuit: A Paradigm for Chaos* (World Scientific, Singapore).

Pikva, L., Wu, C.-W. & Huang, A. [1996] "Lorenz equation and Chua's equation," *Int. J. Bifurcation and Chaos* **6**(12B), 2443–2489.

Plahte, E., Mestl, T. & Omholt, S. [1995] "Feedback loops, stability and multistationarity in dynamical systems," *J. Biol. Syst.* **3**, 409–413.

Rössler, O. E. [1976a] "An equation for continuous chaos," *Phys. Lett.* **A57**, 397–398.

Rössler, O. E. [1976b] "Different types of chaos in two simple differential equations," *Z. Naturforsch.* **31a**, 1664–1670.

Snoussi, E. H. [1998] "Necessary conditions for multistationarity and stable periodicity," *J. Biol. Syst.* **6**, 3–9.

Snoussi, E. H. & Thomas, R. [1993] "Logical identification of all steady states: The concept of feedback loop characteristic states," *Bull. Math. Biol.* **55**, 973–991.

Sprott, J. C. [1994] "Some simple chaotic flows," *Phys. Rev.* **E50**, 647–650.

Thomas, R. [1981] "On the relation between the logical structure of systems and their ability to generate multiple steady states or sustained oscillations," *Springer Series in Synergetics* **9**, 180–193.

Thomas, R. [1991] "Regulatory networks seen as asynchronous automata: A logical description," *J. Theoret. Biol.* **153**, 1–23.

Thomas, R. [1994] "The role of feedback circuits: Positive feedback circuits are a necessary condition for positive real eigenvalues of the Jacobian matrix," *Ber. Bunzenges. Phys. Chem.* **98**, 1148–1151.

Thomas, R. [1996] "Analyse et synthèse de systèmes à dynamique chaotique en termes de circuits de rétroaction (feedback circuits)," *Bull. Cl. Sci. Acad. Roy. Belg.* **7**, 101–124.

Thomas, R. [1999] "The Rössler equations revisited in terms of feedback circuits," *J. Biol. Syst.* **7**(2), 225–237.

Thomas, R. & D'Ari, R. [1990] *Biological Feedback* (C.R.C., Boca Raton, FL), 316 pp.

Tyson, J. [1975] "Classification of instabilities in chemical reaction systems," *J. Chem. Phys.* **62**, 101–1015.

Wolf, A., Swift, J. B., Swinney, H. L. & Vastano, J. A. [1985] "Determining Lyapunov exponents from a time series," *Physica* **D16**, 285–317.

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5. J.M. González-Miranda. 2012. Stability, attractors, and bifurcations of the A2 symmetric flow. *Chaos, Solitons & Fractals* **45**:3, 341-350. [CrossRef]
6. Hong-Bo Lei, Ji-Feng Zhang, Luonan Chen. 2011. Multi-equilibrium property of metabolic networks: Exclusion of multi-stability for SSN metabolic modules. *International Journal of Robust and Nonlinear Control* **21**:15, 1791-1806. [CrossRef]
7. R Gilmore, Jean-Marc Ginoux, Timothy Jones, C Letellier, U S Freitas. 2010. Connecting curves for dynamical systems. *Journal of Physics A: Mathematical and Theoretical* **43**:25, 255101. [CrossRef]
8. J.M. González-Miranda. 2010. Linear stability analysis of a boundary crisis in a minimal chaotic flow. *Physica D: Nonlinear Phenomena* **239**:6, 322-326. [CrossRef]
9. Daniel J. Cross, R. Gilmore. 2010. Equivariant differential embeddings. *Journal of Mathematical Physics* **51**:9, 092706. [CrossRef]
10. B-G. Xin, J-H. Ma, T. Chen, Y-Q. Liu. 2010. A Fractional Model of Labyrinth Chaos and Numerical Analysis. *International Journal of Nonlinear Sciences and Numerical Simulation* **11**:10. . [CrossRef]
11. R. THOMAS, P. NARDONE. 2009. A FURTHER UNDERSTANDING OF PHASE SPACE PARTITION DIAGRAMS. *International Journal of Bifurcation and Chaos* **19**:03, 785-804. [Abstract] [References] [PDF] [PDF Plus]
12. Mieczyslaw Jessa. 2009. On some properties of even-symmetric and odd-symmetric dynamical systems. *Kybernetes* **38**:7/8, 1171-1181. [CrossRef]
13. G. Rowlands, J. C. Sprott. 2008. A simple diffusion model showing anomalous scaling. *Physics of Plasmas* **15**:8, 082308. [CrossRef]
14. QIGUI YANG, GUANRONG CHEN, KUIFEI HUANG. 2007. CHAOTIC ATTRACTORS OF THE CONJUGATE LORENZ-TYPE SYSTEM. *International Journal of Bifurcation and Chaos* **17**:11, 3929-3949. [Abstract] [References] [PDF] [PDF Plus]
15. M. Kaufman, C. Soulé, R. Thomas. 2007. A new necessary condition on interaction graphs for multistationarity. *Journal of Theoretical Biology* **248**:4, 675-685. [CrossRef]
16. Christophe Letellier, Robert Gilmore. 2007. Symmetry groups for 3D dynamical systems. *Journal of Physics A: Mathematical and Theoretical* **40**:21, 5597-5620. [CrossRef]
17. Christophe Letellier, Gleison F. V. Amaral, Luis A. Aguirre. 2007. Insights into the algebraic structure of Lorenz-like systems using feedback circuit analysis and piecewise affine models. *Chaos: An Interdisciplinary Journal of Nonlinear Science* **17**:2, 023104. [CrossRef]
18. Konstantinos E. Chlouverakis, J. C. Sprott. 2007. Hyperlabyrinth chaos: From chaotic walks to spatiotemporal chaos. *Chaos: An Interdisciplinary Journal of Nonlinear Science* **17**:2, 023110. [CrossRef]
19. Chaohong Cai, Guanrong Chen. 2006. Synchronization of complex dynamical networks by the incremental ISS approach. *Physica A: Statistical Mechanics and its Applications* **371**:2, 754-766. [CrossRef]
20. J. RicardCHAPTER 10 Gene networks **40**, 227-253. [CrossRef]
21. Christophe Letellier, Luis Aguirre. 2005. Graphical interpretation of observability in terms of feedback circuits. *Physical Review E* **72**:5. . [CrossRef]
22. ZHISHENG DUAN, JIN-ZHI WANG, LIN HUANG. 2005. FREQUENCY DOMAIN METHOD FOR THE DICHOTOMY OF MODIFIED CHUA'S EQUATIONS. *International Journal of Bifurcation and Chaos* **15**:08, 2485-2505. [Abstract] [References] [PDF] [PDF Plus]
23. Zhisheng Duan, Jin-Zhi Wang, Lin Huang. 2005. Attraction/repulsion functions in a new class of chaotic systems. *Physics Letters A* **335**:2-3, 139-149. [CrossRef]

24. FEDERICO I. ROBBIO, DIEGO M. ALONSO, JORGE L. MOIOLA. 2004. DETECTION OF LIMIT CYCLE BIFURCATIONS USING HARMONIC BALANCE METHODS. *International Journal of Bifurcation and Chaos* **14**:10, 3647-3654. [Abstract] [References] [PDF] [PDF Plus]

25. Detlef Pingel, Peter Schmelcher, Fotis K. Diakonos. 2004. Stability transformation: a tool to solve nonlinear problems. *Physics Reports* **400**:2, 67-148. [CrossRef]

26. FEDERICO I. ROBBIO, DIEGO M. ALONSO, JORGE L. MOIOLA. 2004. ON SEMI-ANALYTICAL PROCEDURE FOR DETECTING LIMIT CYCLE BIFURCATIONS. *International Journal of Bifurcation and Chaos* **14**:03, 951-970. [Abstract] [References] [PDF] [PDF Plus]

27. René Thomas, Vasileios Basios, Markus Eiswirth, Thomas Kruel, Otto E. Rössler. 2004. Hyperchaos of arbitrary order generated by a single feedback circuit, and the emergence of chaotic walks. *Chaos: An Interdisciplinary Journal of Nonlinear Science* **14**:3, 669. [CrossRef]

28. Christophe Letellier, Olivier Vallée. 2003. Analytical results and feedback circuit analysis for simple chaotic flows. *Journal of Physics A: Mathematical and General* **36**:44, 11229-11245. [CrossRef]

29. Marcelle Kaufman, René Thomas. 2003. Emergence of complex behaviour from simple circuit structures. *Comptes Rendus Biologies* **326**:2, 205-214. [CrossRef]

30. Christophe Letellier, Jean-Marc Malasoma. 2001. Unimodal order in the image of the simplest equivariant chaotic system. *Physical Review E* **64**:6. . [CrossRef]

31. René Thomas, Richard d'Ari. 2001. An algorithm for targeted convergence of Euler or Newton iterations. *Comptes Rendus de l'Académie des Sciences - Series III - Sciences de la Vie* **324**:4, 285-296. [CrossRef]

32. R. Thomas, M. Kaufman. 2001. Multistationarity, the basis of cell differentiation and memory. I. Structural conditions of multistationarity and other nontrivial behavior. *Chaos: An Interdisciplinary Journal of Nonlinear Science* **11**:1, 170. [CrossRef]

33. Jacques Demongeot, Marcelle Kaufman, René Thomas. 2000. Positive feedback circuits and memory. *Comptes Rendus de l'Académie des Sciences - Series III - Sciences de la Vie* **323**:1, 69-79. [CrossRef]