



FITZHUGH–NAGUMO REVISITED: TYPES OF BIFURCATIONS, PERIODICAL FORCING AND STABILITY REGIONS BY A LYAPUNOV FUNCTIONAL

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We study several aspects of FitzHugh–Nagumo’s (FH–N) equations without diffusion. Some global stability results as well as the boundedness of solutions are derived by using a suitably defined Lyapunov functional. We show the existence of both supercritical and subcritical Hopf bifurcations. We demonstrate that the number of all bifurcation diagrams is 8 but that the possible sequential occurrences of bifurcation events is much richer. We present a numerical study of an example exhibiting a series of various bifurcations, including subcritical Hopf bifurcations, homoclinic bifurcations and saddle-node bifurcations of equilibria and of periodic solutions. Finally, we study periodically forced FH–N equations. We prove that phase-locking occurs independently of the magnitude of the periodic forcing.

Keywords: FitzHugh–Nagumo; subcritical and supercritical Hopf bifurcation; homoclinic bifurcation; periodic forcing.

1. Introduction

We consider the FitzHugh–Nagumo (FH–N) equations without diffusion,

$$\begin{aligned}\frac{du}{dt} &= \varepsilon g(u) - w + I, \\ \frac{dw}{dt} &= u - aw,\end{aligned}\tag{1}$$

where $g(u) = u(u - \lambda)(1 - u)$, $0 < \lambda < 1$ and

$a, \varepsilon > 0$. We remark that in the existing literature, the term “FitzHugh–Nagumo system” has been used to refer to models both with and without diffusion.

Although Eqs. (1) have been mentioned in practically every mathematical biology book [Brown & Rothery, 1993; Murray, 1989; Strogatz, 1994], as well as some of their aspects have been studied in different contexts [Armbruster, 1997; Dangelmayr

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& Guckenheimer, 1987; Rajasekar & Lakshmanan, 1988a, 1988b; Sato & Doi, 1992] there is no detailed treatment of their dynamics from the point of view of nonlinear dynamics theory.

Our goal in writing the present paper has been to offer a detailed analysis of the FH–N system (1) and to present a theoretical proof of phase-locking of coupled FH–N oscillators.

We demonstrate that the system exhibits many of the known bifurcation types, some of which are executed in a nontypical way.

In various cases the FH–N system possesses unstable periodic solutions, which appear via subcritical Hopf bifurcations. (The instability is probably the reason for which such solutions were not noticed in [Murray, 1989, p. 164].) In other cases, supercritical Hopf bifurcations occur. The Bogdanov–Takens bifurcation [Kuznetsov, 1995] is also characteristic for this system. As noted below, homoclinic bifurcations and saddle-node bifurcations of equilibria and periodic solutions are also exhibited by this system.

It is a common practice to represent a dynamical system by its bifurcation diagram. We show that the possible bifurcation diagrams for the FH–N equation are 8. However, because of the possibilities of occurrence of both supercritical and subcritical Hopf bifurcations, as well as the occurrence of homoclinic orbits of the saddle associated with the appearance/disappearance of periodic orbits, the number of possible sequences of bifurcation events is much larger. Thus a bifurcation diagram is not always sufficiently informative about the system.

As evidence, we present an example which possesses a richness of bifurcation events when the parameter I is varied. The numerical experiments with the example show a sudden disappearance of two (stable and unstable) periodic orbits, which seems to occur simultaneously near a certain value of I . A more careful numerical investigation uncovers that the stable and unstable periodic orbits appear and disappear via different bifurcations associated with the homoclinic orbits of the saddle. The careful study of the mentioned example shows that besides saddle-node bifurcations of equilibria and subcritical Hopf bifurcations, the FitzHugh–Nagumo system exhibits also saddle-node bifurcations of periodic orbits and homoclinic bifurcations which occur in a very narrow interval (of magnitude 10^{-7} values of I). In-between, the structurally unstable homoclinic orbit of the saddle converts into a heteroclinic orbit connecting the saddle and the

unstable equilibrium which further converts back into a homoclinic orbit of the saddle.

In short, from the standpoint of a “bifurcation gems collector”, the well-known, simple-looking system (1) is a treasure box which, we believe, is worthwhile opening once more.

The structure of the paper is as follows.

In Sec. 2 we introduce a Lyapunov functional for the system, which is of help in establishing various useful results. We use it to state global stability results for certain sets of parameter values and to prove the boundedness of the solutions of the system. In Sec. 3, we carry out the phase plane and bifurcation analysis of the system. In Sec. 4 we study the case when I is not a constant. Since a system of the type (1) represents an oscillator (as in many cases it possesses a limit cycle), an interesting problem is to study periodically forced FH–N equations. Results from [Farkas, 1994] are used to prove the existence of periodic solutions with the same period as the forcing term. We note that our result predicts the occurrence of phase-locking, regardless of the amplitude of the forcing term.

2. Stability and Boundedness via a Lyapunov Functional

2.1. Existence and linear stability of equilibrium points

Depending on the parameters, system (1) can have one, two or three equilibrium points. At least one equilibrium always exists and the number of equilibria cannot be more than three.

Let $b_1 = g'(u_e)$. It is trivial to establish (noticing that b_1 is a function of a):

Proposition 2.1. *Let (u_e, w_e) be an equilibrium point. Let $\varepsilon ab_1 < 1$, then (u_e, w_e) is locally asymptotically stable if $\varepsilon b_1 < a$ and is a repeller if $\varepsilon b_1 > a$. If $\varepsilon ab_1 > 1$, then (u_e, w_e) is a saddle point. If $\varepsilon ab_1 = 1$, then (u_e, w_e) is unstable if $\varepsilon b_1 > a$.*

2.2. A Lyapunov functional for FitzHugh–Nagumo’s Equations

We introduce the values

$$T = (1 - \varepsilon b_1 a) - \frac{2\varepsilon ab_2^2}{9}$$

and

$$S = \frac{b_2^2}{3} + b_1 - \frac{a}{\varepsilon}$$

where $b_1 = g'(u_e)$ and $b_2 = g''(u_e)/2$.

Proposition 2.2. Let (u_e, w_e) be an equilibrium of (1). Let

$$V(u, w) = \frac{1}{2}[u - u_e - a(w - w_e)]^2 + G(w - w_e), \quad (2)$$

where $G(x) = (1/4)\varepsilon ax^2[a^2x^2 - (4/3)ab_2x - 2(b_1 - (1/a\varepsilon))]$.

Let the line L be defined by $L = \{(u, w) | u = u_e + a(w - w_e)\}$. Then,

- (a) $V(u, w) > 0$ for all $(u, w) \neq (u_e, w_e)$ if and only if $T > 0$. If $T \leq 0$, then $V \leq 0$ in a bounded set S , which is symmetric about the line L .
- (b) On L the derivative $\dot{V} \equiv (\partial V/\partial u)\dot{u} + (\partial V/\partial w)\dot{w} = 0$. Additionally, $\dot{V} < 0$ iff $S < 0$ and $(u, v) \notin L$. If $S \geq 0$, there exists an ellipse $\partial\mathcal{E}$, surrounding a region \mathcal{E} such that: (i) $\dot{V} < 0$ if (u, w) belongs to the complement of $\partial\mathcal{E}^0 \cup \mathcal{E}^0 \cup L$; (ii) $\dot{V} > 0$ if $(u, w) \in \mathcal{E} \setminus (L \cap \mathcal{E})$.
- (c) If $\varepsilon b_1 a < 1$ and $\varepsilon b_1 > a$, there exists a neighborhood of the equilibrium (u_e, w_e) which no solution enters. If $\varepsilon b_1 a < 1$ and $b_1 \varepsilon < a$, there is a neighborhood of the equilibrium which no solution leaves. These neighborhoods can be found explicitly by using level curves of V .
- (d) Suppose $T > 0$ and $S < 0$. If (u_e, w_e) is unique, it is globally asymptotically stable. If (u_e, w_e) is not unique, it is the only stable equilibrium.

Proof

- (a) After the transformations $v = u - u_e$, $s = w - w_e$, and $v - as = y$, $s = x$ the system can be rewritten as

$$\dot{x}(t) = y \quad \dot{y}(t) = -yf(x, y) - g_1(x),$$

where

$$\begin{aligned} f(x, y) &= \varepsilon(y^2 + (3ax - b_2)y \\ &\quad + (3a^2x^2 - 2b_2ax - b_1)) + a, \\ g_1(x) &= -\varepsilon(b_1ax + b_2a^2x^2 - a^3x^3) + x. \end{aligned}$$

The line L is the one with equation $y = 0$.

Then

$$V(x, y) = y^2/2 + G(x),$$

and

$$G(x) = \int_0^x g_1(\xi) d\xi. \quad (3)$$

A simple computation yields that $G(x) > 0, \forall x \neq 0$ (and therefore $V(x, y) > 0, \forall (x, y) \neq (0, 0)$) if and only if $T > 0$. The level curves $V(x, y) = c, c > 0$ are closely nested ovals encircling the origin.

If $T < 0$, the set $V(x, y) = 0$ consists of $(0, 0)$ and a closed curve, defined by

$$y^2 = \frac{1}{2}\varepsilon ax^2 \left[-a^2x^2 + \frac{4}{3}ab_2x + 2 \left(b_1 - \frac{1}{\varepsilon a} \right) \right]. \quad (4)$$

If $T = 0$, the set $V(x, y) = 0$ consists of $(0, 0)$ and another point on the $y = 0$ axis.

It is symmetric about the axis $y = 0$ and surrounds a bounded set S such that $V(x, y) \leq 0$ if $(x, y) \in S$.

- (b) $\dot{V}(x, y) = -y^2f(x, y)$ and obviously $\dot{V} = 0$ on L and $\dot{V} < 0$ iff $f(x, y) > 0$ and $y \neq 0$. The last is true for all (x, y) iff $S < 0$ which is calculated by transforming $f(x, y)$ into a quadratic form and analyzing it.

Alternatively, the curve $f(x, y) = 0$ is an ellipse \mathcal{E} in the (x, y) -plane if and only if $S > 0$. $\dot{V} > 0$ only in the interior of the ellipse excluding its intersection with L .

- (c) That the mentioned neighborhoods exist follows from Proposition 2.1. Next we clarify the construction of the level curves.

If $\varepsilon ab_1 < 1$ then there exists a neighborhood of $(0, 0)$ such that $V(x, y) > 0$ for all $(x, y) \neq (0, 0)$ in this neighborhood. That is, if S exists, it does not contain the origin. If also $\varepsilon b_1 > a$, then $S > 0$. Therefore $\dot{V} > 0$ inside \mathcal{E} (which exists according to (b)) except on $L \cap \mathcal{E}$. \mathcal{E} surrounds the origin because $f(0, 0) = -\varepsilon b_1 + a$, i.e. $\dot{V} > 0$ in the vicinity of the origin (except on the line $y = 0$). It is then enough to find a level curve $V = c$ which is outside of S (if it exists) and inside \mathcal{E} to ensure that the trajectories of all solutions starting on the curve do not enter the region surrounded by it.

Alternatively, if $\varepsilon b_1 < a$, the ellipse \mathcal{E} either does not exist or does (provided $S > 0$) but the origin lies outside it. Then the level curve we are looking for is one that does not cross both S and \mathcal{E} .

- (d) If $T > 0$ and $S < 0$, then $V > 0$ and $\dot{V} \leq 0$ (with $\dot{V} = 0$ only on $y = 0$). Since V is monotone decreasing along the trajectory of any nonequilibrium solution and bounded below,

the solution must converge to a point $(x^*, 0)$ and the only such point is the equilibrium. ■

If (u_e, w_e) is not unique, let (u_*, w_*) be any other equilibrium. Take the region surrounded by the level curve $V(x, y) = V(u_* - u_e, w_* - w_e) - \delta$ for arbitrarily small $\delta > 0$. All solutions starting in this region converge to an equilibrium contained in the region, which is either (u_e, w_e) or at most another one (the third) equilibrium. Because δ is arbitrarily small, (u_*, w_*) cannot be stable.

Finally, to obtain the statements of the proposition, we return back to coordinates u, w .

2.3. Boundedness of the solutions

The Lyapunov functional allows to prove the boundedness of solutions of (1) in an elegant way.

Proposition 2.3. *There exists a family of nested bounded forward invariant sets of (1) covering the whole (u, w) -plane. Thus, every solution of (1) is bounded for $t > 0$.*

Proof. Consider the functional V defined by (2). Let \mathcal{S} and \mathcal{E} be the regions from the previous section, if they exist.

Since \mathcal{E}, \mathcal{S} are bounded sets, we choose $\bar{c} = \min\{c \geq 0 | V(u, w) = c \supset \mathcal{E} \cup \mathcal{S} \cup (u_e, w_e)\}$. Then for any sequence

$$\{c_i\}, c_i > c_{i-1} > \dots > \bar{c}, c_i \rightarrow \infty, i \rightarrow \infty,$$

the curves $V(u, w) = c_i$ enclose nested bounded sets D_i such that any point (u, w) belongs to such a set for a sufficiently large c_i . Each of the sets D_i is a forward invariant set. Thus, each solution of (1) is bounded and confined in a forward invariant set containing its initial condition. ■

3. Phase Plane and Bifurcation Analysis

The possible phase plane portraits of the system (1) were revealed in [Armbruster, 1997]. Here we are interested in *how* such portraits can appear, the types of bifurcations, the values of the parameters when changes arise.

Proposition 3.1. *As the eigenvalues μ_1, μ_2 of any equilibrium (u_e, w_e) are of the form*

$$\mu_{1,2} = \frac{1}{2}R(\varepsilon, a, b_1) \pm \frac{1}{2}\sqrt{R^2 + 4Q}, \quad (5)$$

where $Q(\varepsilon, a, b_1) \equiv \varepsilon ab_1 - 1$ and $R \equiv \varepsilon b_1 - a$, Hopf bifurcation occurs in cases when $R = 0$ and $Q < 0$.

3.1. The case with $I = 0$

We consider this case separately because the equilibria can be found explicitly.

In this case $(u_e, w_e) = (0, 0)$ is always an equilibrium point. Then $b_1 \equiv g'(u_e) = -\lambda < 0$, and according to Proposition 2.1, it is always locally stable.

3.1.1. Single equilibrium point

First, $(0, 0)$ is the only equilibrium point if and only if

$$1 - \frac{4}{\varepsilon a(1 - \lambda)^2} < 0. \quad (6)$$

Proposition 3.2. *Let $I = 0$, suppose $(0, 0)$ is a unique equilibrium point. Suppose*

$$a > \frac{1}{4}\varepsilon \quad \text{and}$$

$$\frac{1}{2} - \sqrt{3\left(\frac{a}{\varepsilon} - \frac{1}{4}\right)} < (1 - \lambda) < \frac{1}{2} + \sqrt{3\left(\frac{a}{\varepsilon} - \frac{1}{4}\right)} \quad (7)$$

holds, then the equilibrium point $(0, 0)$ is globally asymptotically stable.

The proof uses the Lyapunov functional and is in Appendix A.

For the case when (7) does not hold, one can only state

Proposition 3.3. *Let $(0, 0)$ be a unique equilibrium point. If (7) does not hold, $(0, 0)$ is either globally asymptotically stable, or there exists a stable periodic orbit.*

The proof follows from Poincaré–Bendixon’s theorem. However, we have not been able to observe an instance when such an orbit exists for the case of unique equilibrium.

As $(0, 0)$ is always stable, Hopf bifurcations do not occur in this case.

3.1.2. More than one equilibrium: Subcritical Hopf and Bogdanov–Takens bifurcation

On the two-dimensional parameter surface $\varepsilon a(1 - \lambda)^2 = 4$ a saddle-node bifurcation of equilibria occurs. Bogdanov–Takens (B–T) bifurcations

[Kuznetsov, 1995] occur when $a = 1$ and $\epsilon a(1 - \lambda)^2 = 4$. Small limit cycles exist in the vicinity of the curve $a = 1$, $\epsilon = 4/(1 - \lambda)^2$ at least for $a < 1$. Here we describe in some detail how the B-T bifurcation is accomplished.

If $\epsilon a(1 - \lambda)^2 > 4$, there are two equilibrium points in the first quadrant, $E_1 = (u_1, w_1)$ and $E_2 = (u_2, w_2)$, where

$$u_1 = p - r\sqrt{q}, \quad u_2 = p + r\sqrt{q}, \quad w_i = \frac{u_i}{a} \quad \text{and} \quad (8)$$

$$q = 1 - \frac{4}{\epsilon a(1 - \lambda)^2}, \quad p = \frac{1 + \lambda}{2}, \quad r = \frac{1 - \lambda}{2}.$$

At E_1 , $\epsilon a b_1 > 1$, which, according to Proposition 2.1 implies that E_1 is always a saddle point.

It is easy to check that for E_2 , $b_1 = (1/a\epsilon) - (1 - \lambda)\sqrt{q}u_2$. Then $Q < 0$ and it follows that E_2 is stable if $R < 0$, a repeller if $R > 0$ and undergoes Hopf bifurcation when $R = 0$. The type of Hopf bifurcation (super or subcritical) cannot be determined in general, but in particular, for each given set of values of the parameters calculations to determine it can be carried out, as done in Appendix B.

More precisely, if $\epsilon a(1 - \lambda)^2 > 4$, the equilibrium E_2 is unstable if

$$aR \equiv 1 - a^2 - \epsilon a(1 - \lambda)\sqrt{q} \left[\frac{1 + \lambda}{2} + \frac{1 - \lambda}{2}\sqrt{q} \right] > 0. \quad (9)$$

We see from (9) that if $a \geq 1$, E_2 is stable independently of the values of ϵ , λ , because then $R < 0$ and $Q < 0$. Some trajectories are attracted by E_0 , others, by E_2 . Figure 1 shows a typical phase portrait in that case. The basins of attraction of both

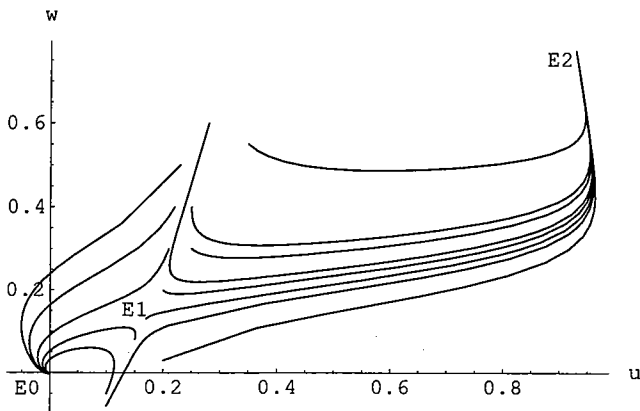


Fig. 1. Phase plane trajectories in the (u, w) -plane, when both E_0, E_2 are stable. $I = 0$, $a = 1.2$, $\lambda = 0.1$, $\epsilon = 14$. $E_0 = (0, 0)$ and $E_2 = (0.928, 0.77)$.

equilibria are separated by the stable manifold of the saddle E_1 .

If $a < 1$, E_2 is a repeller for sufficiently small values of q , i.e. near the surface $\epsilon a(1 - \lambda)^2 = 4$, immediately after the saddle-node bifurcation that causes the appearance of E_1 and E_2 .

For example, if $\epsilon = 14$, $a = 0.37$ and $\lambda = 0.1$, there are two positive equilibria besides the origin, and E_2 is a repeller, because (9) holds as is verified by direct calculation. All orbits, with the exception of the stable manifold of E_1 , are attracted to the origin.

Stated otherwise, if we fix $\epsilon > 4$ and consider the curve $a = 4/(1 - \lambda)^2$, for each $a < 1$ there is a value of λ (in fact an interval of values of λ) such that E_2 is a repeller. Starting from such values of a , ϵ , λ , while keeping $\epsilon > 4$ fixed and increasing a , since R is a decreasing function of a , R will eventually become negative and therefore E_2 will become stable. The exchange of stability is realized via Hopf bifurcation, because $Q < 0$. In the example above, by increasing a from 0.37, R becomes equal to 0 for $a \approx 0.379785$, which is the value of a for which Hopf bifurcation occurs. Numerical simulations show that the bifurcation is subcritical. An unstable periodic orbit exists for values of a larger than 0.379785, i.e. when E_2 is stable, as shown in Fig. 2. Solutions, starting inside the unstable periodic orbit, approach E_2 , while solutions, starting outside of the unstable periodic orbit (with the exception of E_1 and its stable manifold), approach the other stable equilibrium $(0, 0)$ (Fig. 2).

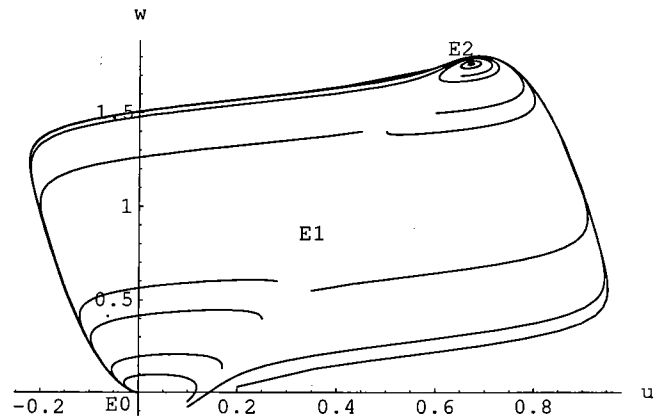


Fig. 2. Phase plane trajectories in the (u, w) -plane, when both E_0, E_2 are stable, but an unstable periodic solution surrounds E_2 . All solutions starting near the orbit on its outer side approach E_0 . Solutions starting inside approach E_2 . $I = 0$, $a = 0.38$, $\lambda = 0.1$, $\epsilon = 14$.

That the Hopf bifurcation is subcritical can also be shown by direct calculation of the value G_4 (see Appendix B). The constant G_4 determining the type of bifurcation is positive (22.5165), i.e. the bifurcation is subcritical.

The analyzed case illustrates a Bogdanov–Takens bifurcation, as when a passes through 1 at the intersection with the curve $a = 4/(1 - \lambda)^2$ for each fixed $\varepsilon > 4$, both eigenvalues of the newly emerged equilibrium are 0. The Hopf bifurcation curve in the (a, λ) space passes through this intersection point.

We note that, when compared to the case delineated in [Kuznetsov, 1995, p. 281], our example is different in the order of events. In the case described in [Kuznetsov, 1995] the newly emerged equilibrium is stable and destabilizes while a stable periodic orbit appears. In our case, it is unstable near the bifurcation curve and stabilizes later with the appearance of an unstable periodic solution. Although this observation does not describe some completely new phenomenon, it is worthwhile mentioning from an educational point of view.

3.2. The case with $I \neq 0$

3.2.1. Existence of equilibria

The equilibria in this case satisfy the equations

$$\begin{aligned} \varepsilon g(u) - \frac{u}{a} + I &= 0, \quad I > 0, \\ w &= \frac{u}{a}. \end{aligned} \tag{10}$$

Here again, there might be one, two or three equilibria. Let $\Phi(u) \equiv \varepsilon g(u) - (u/a)$. An equilibrium (u_e, w_e) should satisfy the equation $\Phi(u_e) = -I$. There are three distinct cases.

(a) If

$$s = (1 - \lambda)^2 + \lambda - \frac{3}{a\varepsilon} < 0, \tag{11}$$

$\Phi(u)$ is decreasing, thus there exists a unique equilibrium for all values of I .

(b) When $s = 0$, Φ has an inflection point at $u = (1 + \lambda)/3$. The three-dimensional set $s = 0$, $-I = \Phi[(1 + \lambda)/3]$ consists of saddle-node bifurcation points. $\Phi(u)$ is decreasing, and there exists a unique equilibrium for all values of I .

(c) If $s > 0$, $\Phi(u)$ has a maximum $I_M = \Phi[(1 + \lambda + \sqrt{s})/3]$ and a minimum $I_m = \Phi[(1 + \lambda - \sqrt{s})/3]$. Depending on the relation between I_M , I_m and I there can be 1, 2 or 3 equilibria. If $I_M < -I$

or if $I_m > -I$ there is only one equilibrium, if $I_m < -I < I_M$, there are three equilibria, while $I = -I_M$ and $I = -I_m$ are saddle-node bifurcation values of the parameter I .

3.2.2. Single equilibrium point: Stable, unstable and supercritical Hopf bifurcation

If only one equilibrium, $E_0 = (u_0, w_0)$ exists, unlike $(0, 0)$ for the $I = 0$ case, it can be either stable or unstable. The considerations in the previous section show that if (u_0, w_0) is a unique equilibrium and if $s \neq 0$, then $\Phi'(u_0) = \varepsilon g'(u_0) - (1/a) < 0$. If $s = 0$, then $\Phi'(u_0) \leq 0$.

Further, Proposition 2.1 tells us that if $\varepsilon g'(u_0) - (1/a) < 0$, then E_0 is asymptotically stable if

$$\varepsilon g'(u_0) < a. \tag{12}$$

Thus, if E_0 is unique, it is asymptotically stable if (12) holds with the exception of the case when $s = 0$ and $I = -\Phi[(1 + \lambda)/3]$. It is unstable if $\varepsilon g'(u_0) > a$. In this case a stable limit cycle exists, which follows from Poincaré–Bendixon’s theorem. Because the exchange of stability is achieved via Hopf bifurcation (see Proposition 3.1) the stable cycle appears as a result of a supercritical one when $\varepsilon g'(u_0) = a$.

We can combine these observations and the results from the previous section to obtain the following

Proposition 3.4. *If $s < 0$ or if $s \geq 0$ and either $I < -\Phi[(1 + \lambda + \sqrt{s})/3]$ or $I > -\Phi[(1 + \lambda - \sqrt{s})/3]$ hold, then the unique equilibrium $E_0 = (u_0, w_0)$ is asymptotically stable if either $a > 1$ or $\varepsilon g'(u_0) < a \leq 1$ and unstable if $a < \varepsilon g'(u_0) \leq 1$. In the last case, a stable periodic orbit exists around E_0 .*

When E_0 is unique and stable, there are cases in which we can prove that it is globally stable by using the Lyapunov functional from Sec. 2.

Let us examine a numerical example with $a = 0.06$, $\varepsilon = 14$, $\lambda = 0.5$ and vary I from 4 to 13 (Fig. 3). There is a unique equilibrium for all these parameter values and two Hopf bifurcations take place. For $I < 4.2$ the unique equilibrium is stable and loses stability near this value. A supercritical Hopf bifurcation leads to the appearance of a limit cycle, whose amplitude increases initially with increase in I and later decreases again until a second Hopf bifurcation takes place at approximately $I = 12.43$, and the equilibrium becomes

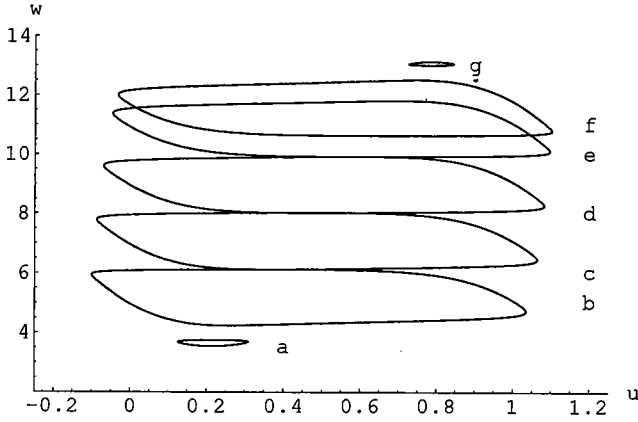


Fig. 3. A limit cycle appears through Hopf bifurcation, moves upward and disappears through another Hopf bifurcation. $a = 0.06$, $\lambda = 0.5$, $\epsilon = 14$. (a) $I = 4.26$, (b) $I = 5$, (c) $I = 7$, (d) $I = 9$, (e) $I = 11$, (f) $I = 11.75$, (g) $I = 12.42$.

stable again. The supercriticality of the Hopf bifurcations is also supported by calculating the value of G_4 (see Appendix B) which is the same negative value in both cases, $G_4 = -6.11724$.

3.2.3. More than one equilibrium: Subcritical Hopf bifurcations

Keeping a , λ , ϵ fixed, the values $I = I_M$ and $I = I_m$ are equilibrium saddle-node bifurcation points, as noted in Sec. 3.2.1. These bifurcations occur when the slopes of the nullclines are the same, i.e. when $\epsilon g'(u_e) = 1/a$. Similarly to the case when $I = 0$, these points are B-T bifurcation points if $a = 1$.

Suppose that (10) has three positive solutions: $E_0 = (u_0, w_0)$, $E_1 = (u_1, w_1)$, $E_2 = (u_2, w_2)$, where $u_0 < u_1 < u_2$. E_1 is always a saddle point, since $\epsilon g'(u_1) > (1/a)$. For E_0 and E_2 it is easily seen that $\Phi'(u_i) = \epsilon g'(u_i) - (1/a) < 0$, $i = 0, 2$. The equilibrium points E_0 and E_2 will be locally stable or repellers, depending on whether $\epsilon g'(u_i)$ is less or greater than a .

- (A) Obviously, if $a \geq 1$, the condition $\Phi'(u_i) < 0$, $i = 0$ or 2 implies stability of E_i .
- (B) Let $a < 1$. Let us denote $\Psi(u) = \epsilon g(u) - au$. Then E_i , $i = 0, 2$ is asymptotically stable if $\Psi'(u_i) < 0$ and unstable if $\Psi'(u_i) > 0$. Let $\alpha_M > \alpha_m$ be the roots of Φ' and $\gamma_M > \gamma_m$ be the roots of Ψ' . An easy calculation shows that $\alpha_M < \gamma_M$ and $\alpha_m > \gamma_m$. Since $\Phi'(u_i) < 0$, then $u_i < \alpha_m$ or $u_i > \alpha_M$. Therefore E_i is stable if $u_i < \gamma_m$ or $u_i > \gamma_M$ (see Fig. 4). Thus the

stability of E_0 and E_2 depends on the relative location of the roots of $\Phi(u) + I$ with respect to the roots of Ψ' when I varies.

Starting from a value of $I < -I_M$ and increasing I until $I > -I_m$, first only E_0 exists and it is stable if I is small enough (as in (a) in Fig. 4). When I is increased:

- (α) E_0 becomes unstable;
 (β) E_1 and E_2 appear via a saddle-node bifurcation, E_2 being unstable [as in Fig. 4(b)];
 (γ) E_2 becomes stable.

These three phenomena always occur but not always in this order.

- (δ) E_1 and E_0 disappear [as in Fig. 4(c)].

Eight different scenarios are possible which can be described in the following way. Let us denote by E_i^q , $i = 0, 2$, $q = s, u$ the equilibria E_i , $i = 0, 2$ in the cases when they are stable ($q = s$) or unstable ($q = u$). Then the eight scenarios can be described as

- (i) $E_0^s \rightarrow \{E_0^s, E_2^u\} \rightarrow \{E_0^u, E_2^u\} \rightarrow \{E_0^u, E_2^s\} \rightarrow E_2^s$;
 (ii) $E_0^s \rightarrow E_0^u \rightarrow \{E_0^u, E_2^u\} \rightarrow E_2^u \rightarrow E_2^s$;
 (iii) $E_0^s \rightarrow \{E_0^s, E_2^u\} \rightarrow \{E_0^s, E_2^s\} \rightarrow \{E_0^u, E_2^s\} \rightarrow E_2^s$;
 (iv) $E_0^s \rightarrow \{E_0^s, E_2^u\} \rightarrow \{E_0^u, E_2^s\} \rightarrow E_2^s$;
 (v) $E_0^s \rightarrow \{E_0^u, E_2^u\} \rightarrow \{E_0^u, E_2^s\} \rightarrow E_2^s$;
 (vi) $E_0^s \rightarrow E_0^u \rightarrow \{E_0^u, E_2^u\} \rightarrow \{E_0^u, E_2^s\} \rightarrow E_2^s$;
 (vii) $E_0^s \rightarrow \{E_0^s, E_2^u\} \rightarrow \{E_0^u, E_2^u\} \rightarrow E_2^u \rightarrow E_2^s$;
 (viii) $E_0^s \rightarrow \{E_0^s, E_2^u\} \rightarrow \{E_0^u, E_2^u\} \rightarrow E_2^s$.

(13)

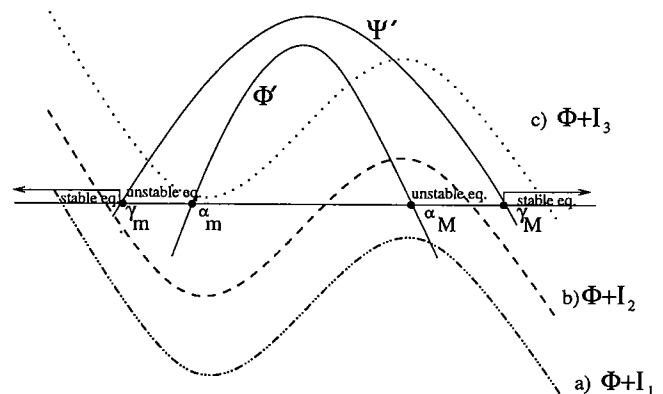


Fig. 4. E_i , $i = 0, 2$ is stable if u_i is located to the left of γ_m or to the right of γ_M and unstable if located between γ_m , α_m or α_M , γ_M . See text for more detail.

