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LETTER TO THE EDITOR

Bifurcations and chaos of the Bonhoeffer–van der Pol model

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Abstract. Periodic and chaotic behaviour of the Bonhoeffer-van der Pol model of a nerve membrane driven by a periodic stimulating current $a_1 \cos \omega t$ is investigated. Results show that there exist ordinary and reversed period-doubling cascades and a mode-locking state. At low driving amplitudes a_1, there are period-doubling and chaotic states, but no impulse solutions. When a_1 is larger than $a_0 = 0.749$, there are chaotic, reversed period-doubling, and mode-locking states and there also exist impulse trains. A mode-locking state with period 4 over a very large range of amplitudes is also found. At $a_1 = 1.7059$ the system goes back to a one-period state.

Theoretical and experimental studies of periodically forced non-linear systems have been of interest from a number of points of view. A prominent example of such a system is the van der Pol oscillator which is one of the most intensively studied in non-linear dynamics and serves as a basic model of self-excited oscillations in physics, electronics, biology, neurology and in many other fields [1-3]. It is believed that many biological rhythmic processes are related to this oscillatory system.

The Bonhoeffer-van der Pol (BVP) model for an excited nerve membrane contains two variables, and describes the propagation of an electrical impulse or voltage pulse along the membrane of a nerve cell [4, 5]. It may be presented as two equations:

$$\dot{x} = x - x^3/3 - y + I(t) \qquad (1)$$

$$\dot{y} = c(x + a - by). \qquad (2)$$

Here x is the membrane potential, y is a variable representing the time constant of recovery of the membrane from stimulation, $I(t)$ is the stimulating current and is considered as a fixed input function in this paper. The terms a, b, and c are membrane radius, the specific resistivity of the fluid inside the membrane and the temperature factor, respectively, and are positive constants which satisfy the inequalities

$$b < 1 \qquad (3)$$

$$3a + 2b \geqslant 3. \qquad (4)$$

In the absence of periodic stimulating current, $I(t) = 0$, equations (1) and (2) have been studied by Kawato and Suzuki [6], Okuda [7] and Treutlein and Schulten [8]. All of these studies were concerned with the stability of in-phase and antiphase

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solutions, threshold and shaping action and the effect of noise, respectively. Recently, a study of (1) and (2) under the action of a periodic stimulating current $I(t) = a_1 \cos \omega t$, $\omega = 1.0$ was made by Rajasekar and Lakshmanan [9], in which period-doubling and chaotic behaviour was found with the amplitude a_1 taking values up to 0.74. However, they did not investigate fully the detailed bifurcation and chaotic behaviour and it is natural to ask what happens when the amplitude is increased. That is, what new characteristic phenomena can be expected in the parameter space? A detailed bifurcation and chaotic behaviour for the increasing amplitude is clearly needed.

In the present letter we want therefore to give examples of bifurcation diagrams of the driven BVP oscillator model which show complete period-doubling cascades. A maximal Lyapunov exponent λ_1 is used to describe the average rate of divergence of nearby trajectories.

For characterising the bifurcating and chaotic behaviour we consider bifurcation diagrams in figure 1 which show the degree of refraction Y_n against the excitation amplitude a_1, i.e. the stroboscopic section of y at a fixed phase $I(t) = 0$ against a_1. All parameters are held constant at $a = 0.7$, $b = 0.8$, $c = 0.1$, which are the typical values used by FitzHugh for the biological meaning [4, 5], $\omega = 1.0$ (here we only give the result for $\omega = 1.0$) and $0 < a_1 < 1.8$. All the numerical calculations are done by using a modified fourth-order Runge–Kutta method. For each value of a_1, we use the final point of the trajectory of the previous a_1 value and discard 200 periods since they might involve a transient. We have also done some calculations with smaller steps and a longer transient, finding that the difference is very small. The Lyapunov exponent is calculated by using the method due to Benettin *et al* [10]. All the values are calculated with double precision.

From figure 1, we can see that periodic oscillations, chaotic and mode-locking oscillations occur. As a_1 increases from zero up to 0.6070, a period-1 state is observed and a simple period-2 bifurcation occurs at $a_1 = 0.6070$. Then period doubling is observed with increasing a_1. At $a_{1c} = 0.7182$ the period-doubling and band-merging

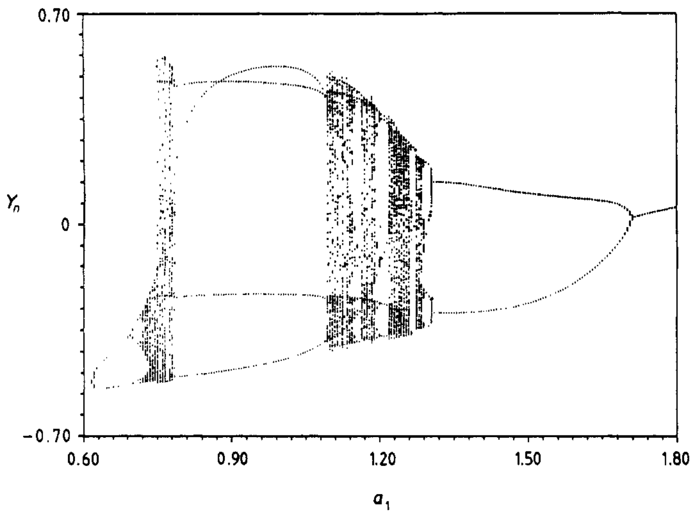

Figure 1. Bifurcation diagrams of the BVP model equation showing projections of the attractors in the stroboscopic section onto the Y_n against the excitation amplitude a_1. The step of a_1 is 0.005. For each step 350 points are plotted after eliminating 200 transient periods.

points accumulate and, in the chaotic region above a_{1c}, we find small windows of higher-period cascades with periods $q \times 2^n$, where q is an integer, and n denotes the degree of the period doubling of a fundamental periodic orbit of period q. There results cannot be found in [9], and the period-doubling accumulation is not at $a_1 = 0.74$, but at a smaller value $a_1 = 0.7182$†. Two sections of figure 1 showing details of a parameter interval between $a_1 = 0.7$ and $a_1 = 0.8$, and of an interval between $a_1 = 1.09$ and $a_1 = 1.29$ are given in figures 2 and 3, respectively.

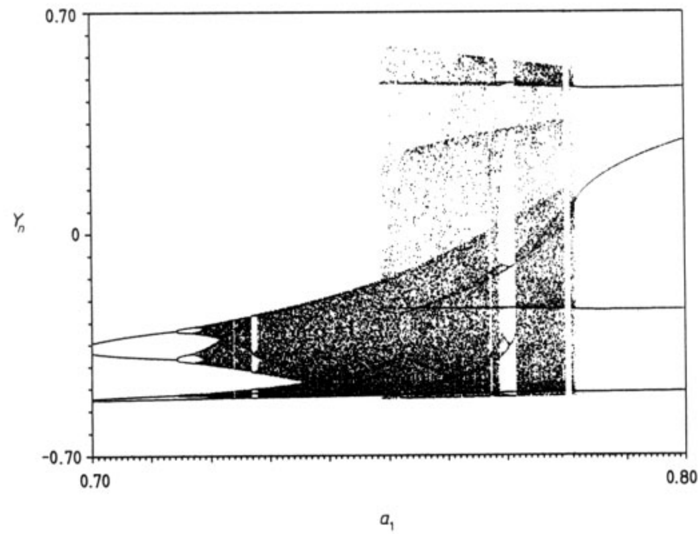

Figure 2. A section of figure 1 showing detailed bifurcation and chaotic behaviour of the parameter interval between $a_1 = 0.7$ and $a_1 = 0.8$. The step of a_1 is 0.0002. For each step 350 points are used after eliminating 200 transient periods.

From figures 1–3 we see that there are ordinary and reversed bifurcation and chaotic regions, as well as periodic windows. Over a very long range $a_1 \in [0.7815, 1.092]$, a mode-locking state with period 4 is also observed. Finally, for $a_1 > 1.302$ one can see that there exist reversed period-doubling bifurcations, and at $a_1 = 1.7059$ the system goes back to a period-1 state (see figure 1).

In figures 4, 5 and 6, we show the largest Lyapunov exponent against the amplitude a_1 in the region corresponding to figure 1. It is obvious that we have positive Lyapunov exponents for the chaotic state, and negative ones for the periodic state even for the small periodic windows. For the periodic state all trajectories lie on a limit cycle within the three-dimensional phase space.

As mentioned above, the bifurcation and chaotic behaviour of the BVP model system is very complicated. From biology, we know that a basic property of the nerve membrane is the existence of a threshold to stimulation. A stimulus above a certain value, a_0 (the threshold), produces a nerve impulse. The electrical component of the impulse (which is a complex electrochemical process) is a pulse-shaped action potential lasting about a millisecond. Stimuli below threshold, subthreshold, produce no impulse.

† Notice that in [9], the accumulation point was claimed to be at $a_1 = 0.74$, and most of the structure to be described below was missed.

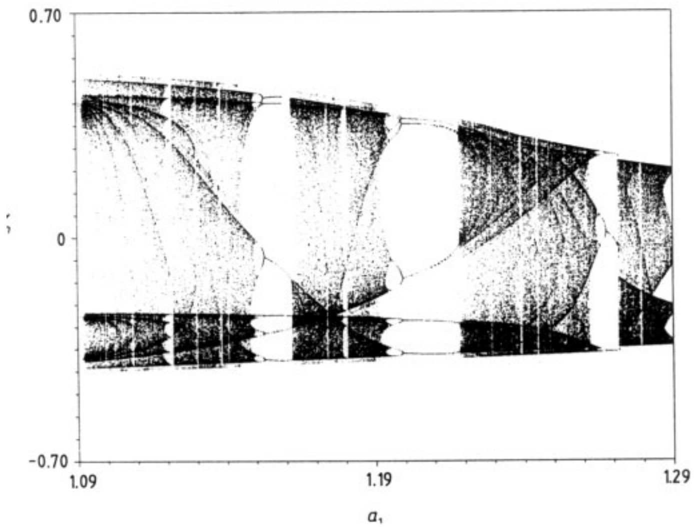

Figure 3. A section of figure 1 showing detailed bifurcation and chaotic behaviour of the parameter interval between $a_1 = 1.09$ and $a_1 = 1.29$. The step of a_1 is 0.0002. For each step 350 points are used after eliminating 200 transient periods.

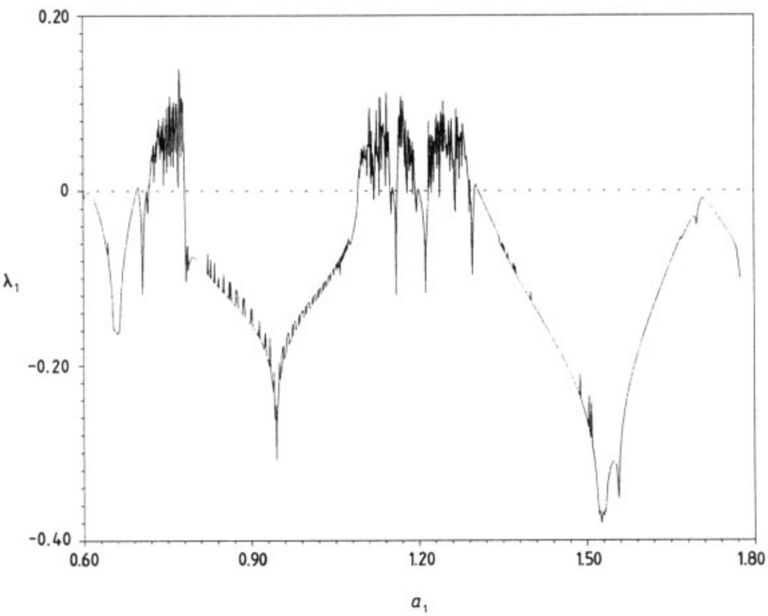

Figure 4. The largest Lyapunov exponent against the excitation amplitude a_1 corresponding to figure 1.

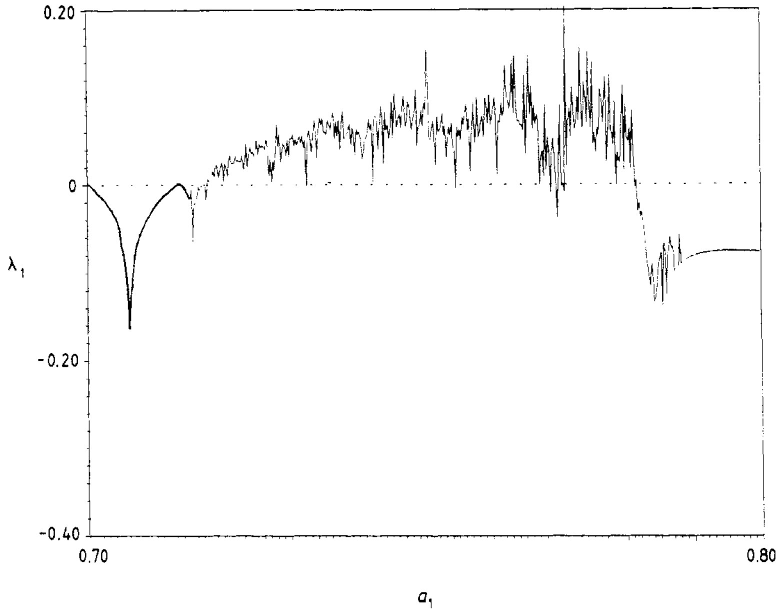

Figure 5. The largest Lyapunov exponent against the excitation amplitude a_1 corresponding to figure 2.

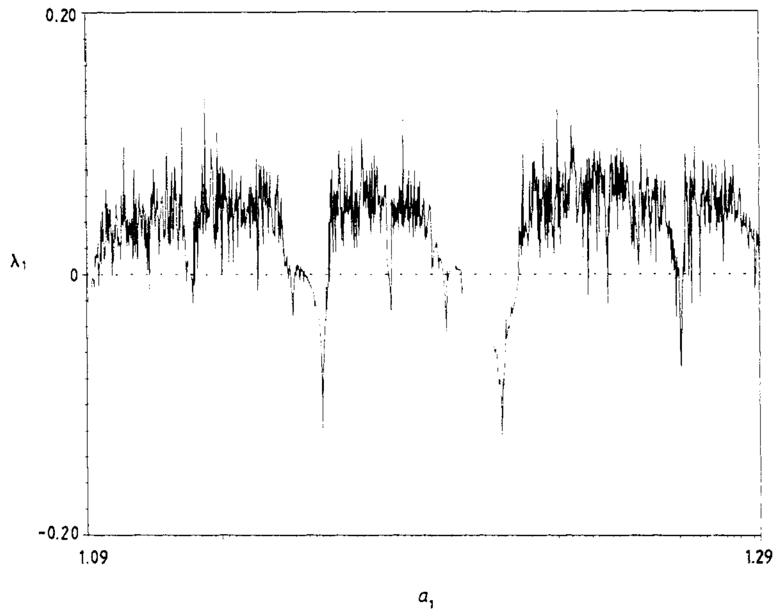

Figure 6. The largest Lyapunov exponent against the excitation amplitude a_1 corresponding to figure 3.

The impulse is the indivisible unit of nervous activity, and its presence or absence in a nerve membrane, according to the magnitude of the stimulus, constitutes the threshold phenomenon [4, 5]. From figures 1-3, we see that such a threshold for the stimulus exists at $a_0 = 0.7490$. When $a_1 < a_0$ we have only small amplitude synchronised oscillations, subthreshold responses to the stimulus, which undergo a transition to chaos from period-doubling, and there are no impulses (the definition of an impulse is a large pulse-shaped action potential, not a subthreshold response). When just past $a_1 = a_0$ we see a bifurcation from a subthreshold chaotic attractor to a superthreshold attractor. This bifurcation is called an interior crisis by Grebogi *et al* [11], and is a saddle-node bifurcation.

When $a_1 > a_0$ the superthreshold responses undergo chaos, reversed period-doubling window, chaos, reversed period-doubling bifurcation to period 1. This period-n behaviour corresponds to the n-shaped impulse (n different wave-shaped impulses) trains which code the signal of single nerve fibres in neural tissue [8], and the chaotic state of the BVP model corresponds to the infinite-shaped-impulse trains.

To summarise the results presented above we concluded that the ordinary and reversed period-doubling bifurcation, as well as chaotic behaviour is due to the interaction between the BVP oscillations and the periodic stimulating current. The mode-locking state is due to the equilibrium of the BVP oscillations and the periodic stimulating oscillations, and corresponds to 4-shaped-impulse trains. Finally, this mode-locking of BVP (equations (1) and (2)) is even stronger than in the case of van der Pol's equation [3].

A more detailed calculation and analysis will be given in another publication.

I thank Professor Xixian Yao for introducing me to work on non-linear physics and Professor D F Brewer and Dr D S Betts for inviting me to work at Sussex University, and Dr A L Thomson and Dr Renzhi Ling for helping me with this work while staying there. All computations have been carried out on a VAX-8530 in the Computer Centre of Sussex University.

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