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Large pulsating waves in a one-dimensional excitable medium

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Abstract

The term "pulsating wave" has been introduced by Kerner and Osipov for an unmoving wave whose shape changes periodically. Such waves are known to occur in reaction–diffusion systems where stationary waves become unstable. The present paper investigates numerically the properties of pulsating waves in a modified FitzHugh–Nagumo model. In the range of the model parameters the pulsating waves have been shown to appear in the intermediate region between the ones where stationary and propagating waves occur. The mechanisms of the "pulsations" are discussed in terms of the wave front and the wave back dynamics.

1. Introduction

The investigation of nonlinear systems is mostly stimulated by problems in mathematical biology. Simulation of information transfer in biological systems as well as simulation of pattern formation leads to consideration of a reaction–diffusion system of the following type [6,8],

$$\tau_U \partial U/\partial t = l^2 \triangle U - q(U,W),$$
$$\tau_W \partial W/\partial t = L^2 \triangle W - Q(U,W). \qquad (1)$$

These equations describe an excitable medium. The function $q(U,W)$ is sigmoidal; the function $Q(U,W)$ is monotonic; these functions have one crossing point in the phase plane (U,W) corresponding to a stationary state of system (1). Solutions, $U(x,t)$, $W(x,t)$, are searched for in a domain with von Neumann boundary conditions. The variables U and W usually denote concentrations of biochemical reagents, called "activator" and "inhibitor" respectively [8]. These terms mean that U is autocatalytically involved in its own production, but W causes a decrease in the production of U.

Systems of type (1) have two well known types of solutions: propagating waves [6] and stationary waves [5,11]. Propagating waves occur in models of information transfer. They describe the propagation of excitation waves, for instance, in the Belousov–Zabotinskii reaction, nerve or muscle tissues. Stationary waves (or "dissipative structures" [8]) occur when pattern formation is simulated. They describe, for instance, morphogenetic patterns.

A third type of solution of the system (1) has been found recently [10,12]. It is convenient to consider this solution as a destabilized stationary wave whose fronts become movable and exhibit "breathing mo-

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tion". As a result the width (and/or the amplitude) of the wave oscillates. This solution has been called "layer oscillations" in Ref. [12], or "pulsating wave" in Ref. [10]. There are examples of real biological patterns similar to pulsating waves. For instance, hydroidal polyps can exhibit "pulsations" when their sizes change periodically in the course of time [4].

Pulsating waves were predicted in Ref. [9] where the stationary solutions of (1) were shown to become sensitive to periodical noise under the following conditions,

$$\epsilon^2 < \alpha < \epsilon \ll 1, \tag{2}$$

where $\alpha = \tau_U/\tau_W$ and $\epsilon = l/L$. The frequency of the wave pulsations was found to be

$$\omega \sim \sqrt{\epsilon/\tau_U\tau_W}. \tag{3}$$

The results of an analytical investigation of the pulsating wave reported in Ref. [12] confirm both (2) and (3). In addition, it was shown in Ref. [12] that pulsating waves occur via a Hopf bifurcation of the stationary waves when $\alpha \sim \epsilon$, and the amplitude of pulsations increases as α decreases.

The goal of the present paper is to numerically investigate pulsating waves. In this way we check estimations (2) and (3) and study some other wave properties. The qualitative mechanisms causing pulsations and transitions between wave regimes is also considered.

2. Model

We have used for calculations the extension of the FitzHugh–Nagumo equations as used in Refs. [5,11],

$$\partial U/\partial t = \partial^2 U/\partial x^2 - f(U) - W,$$
$$\partial W/\partial t = D\partial^2 W/\partial x^2 + (K_W U - W)/\tau. \tag{4}$$

The term $D\partial^2 W/\partial x^2$, responsible for the inhibitor diffusion, is known to be necessary for both stationary and pulsating wave occurrence [7,8]. Instead of the ordinary cubic function $f(U)$ [6] we used a piecewise linear function [14],

$$\begin{aligned} f(U) &= SU, && \text{if } U \leqslant 0, \\ &= -K_U(U-a), && \text{if } 0 < U < 1, \\ &= S(U-1), && \text{if } U \geqslant 0, \end{aligned} \tag{5}$$

in the limit that S is infinite. Because S is infinite $f(U)$ is defined only on the interval $0 < g < 1$.

Calculations were performed in a one-dimensional array using the explicit Euler method of integration with a space step $h_x = 0.5$ and a time step $h_t = 0.025$ [14]. Von Neumann's "no flux" conditions were imposed on the boundaries of the array. Test runs with $h_x = 0.25$ and $h_t = 0.006$ show a minute deviation in the values of the space and time parameters measured. This confirms reliability of the computational method. For calculations we have used the following basic set of parameters: $a = 0.05, K_U = 1, K_W = 1, \tau = 8, D = 3.2$, the size of the medium is $M = 70$.

3. Results

Views of the pulsating waves are shown in Fig. 1. A stimulation of the central region causes the excitation propagating from there. The propagation rate is not constant, it changes periodically from positive to negative. As a result, the size of the excited area changes as well, and pulsations are observed. Comparison of the pulsating waves presented in Figs. 1A and 1B shows that their shapes for piecewise and cubic functions $f(U)$ are qualitatively similar.

Calculations have shown that pulsating waves occur and are stable when the inhibitor diffusion (D) is in a limited range, $D_2 < D < D_1$. If the diffusion D is higher than the critical value D_1, classical dissipative structures are observed. On the other hand, a decrease of the diffusion D to below the critical value D_2 makes the pulsating waves unstable; they vanish after a few pulsations. A further decrease of D to below a third critical value D_3 leads to the appearance of propagating waves. Thus, four different wave regimes in system (4) can be observed as the inhibitor diffusion D is varied. Fig. 2 shows the planes τ–D, and a–D divided into four regions by curves D_1, D_2, and D_3. One can see that an increase in τ (Fig. 2A) or a decrease in a (Fig. 2B) both cause an increase in the diffusion critical values.

The transitions of the wave regimes when D crosses critical values D_1 and D_2 can be explained by the de-

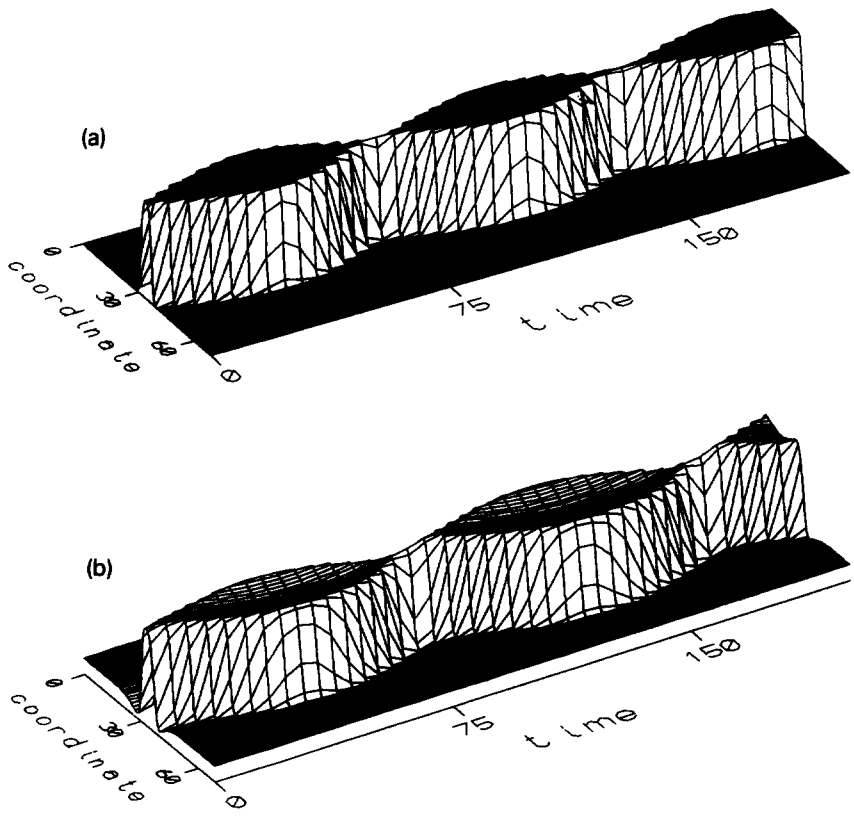


Fig. 1. View of pulsating waves in system (4) (the solutions $U(x,t)$ are presented). The medium in (A) is described by the piecewise function $f(U)$ (5), in (B) by the cubic function $f(U) = 4.8U(U-a)(1-U)$. $D = 3.2$ in (A) and $D = 2.8$ in (B).

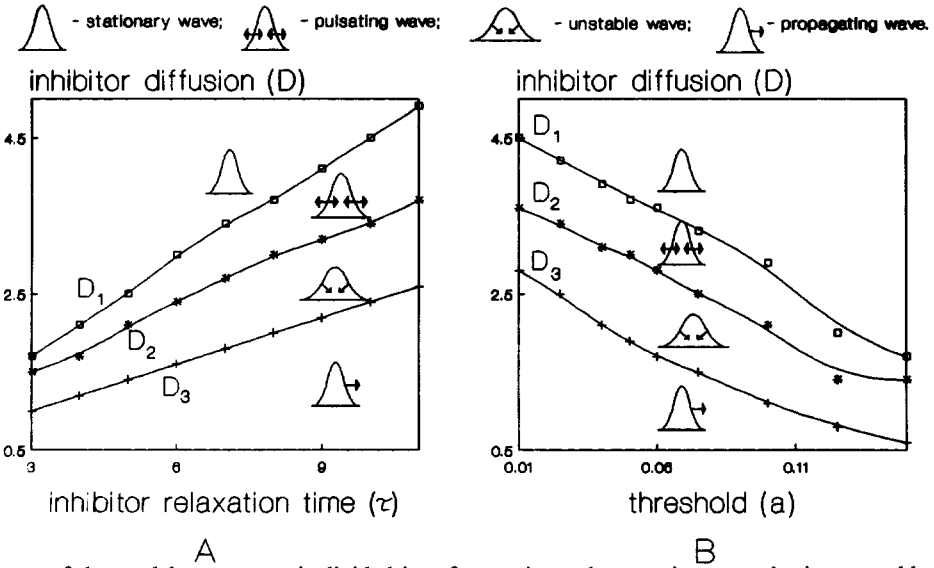


Fig. 2. The range of the model parameters is divided into four regions where stationary, pulsating, unstable or propagating waves are observed. These regions in the planes τ–D (A), and a–D (B) are shown.

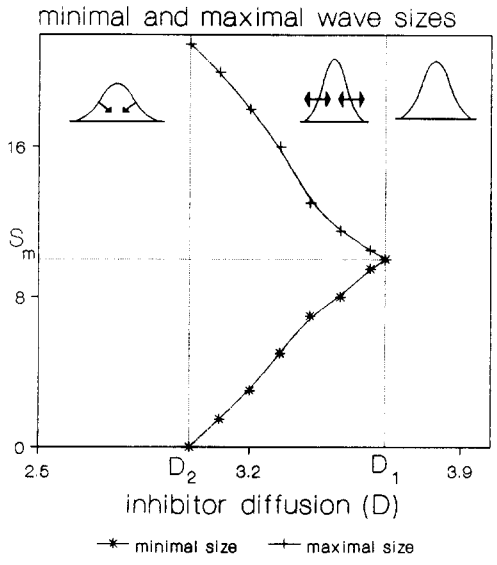
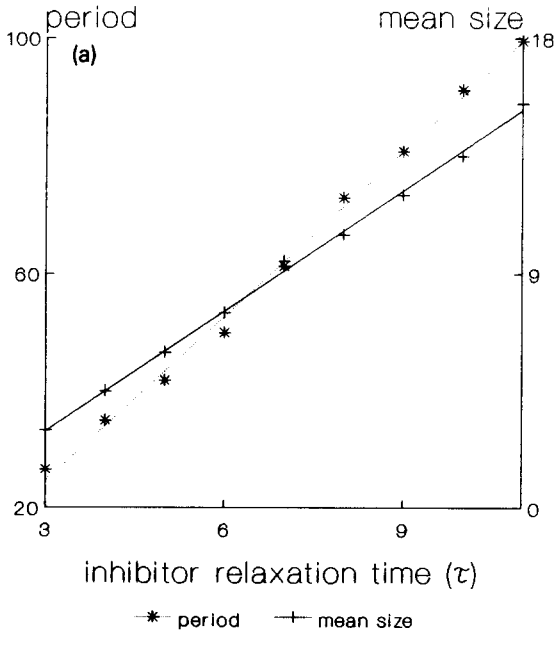


Fig. 3. Minimal and maximal wave sizes (during a pulsation) versus inhibitor diffusion, D (wave size is measured as a size of the region were $U = 1$). It is possible to see that the mean wave size, S_m, does not change. Stable pulsating waves are observed when $D_1 < D < D_2$. If $D < D_1$ the waves are unstable (they vanish in the course of time), and if $D > D_2$ the waves are stationary.

pendence of the amplitude of the pulsations on the inhibitor diffusion D, shown in Fig. 3. When $D = D_2$ the amplitude is so high that the wave size in the phase of its maximal constriction is about zero and a small increase of the pulsation amplitude makes the pulsating wave vanish. The increase of the inhibitor diffusion to the value $D = D_1$ causes the pulsation amplitude to decrease to zero, and hence pulsating waves become stationary waves.

The effect of the inhibitor diffusion on the period of pulsations (T_p) and on the wave mean size (S_m) (half of the sum of the minimal and maximal wave sizes, see Fig. 3) is negligible. However, further calculations have shown that T_p and S_m increase linearly with inhibitor relaxation time τ (see Fig. 4A). It has been found that an increase of the medium excitability (by a decrease of the threshold of medium excitability a or of the slope K_U of the function $f(U)$) also causes an increase in T_p and S_m.

Calculations have shown that pulsating waves initiated in the same medium are influenced by their interactions. Similary, a solitary wave is influenced by the medium boundaries. Since von Neumann boundary conditions are used the influence of the boundary is similar to that of an imaginary wave located at the



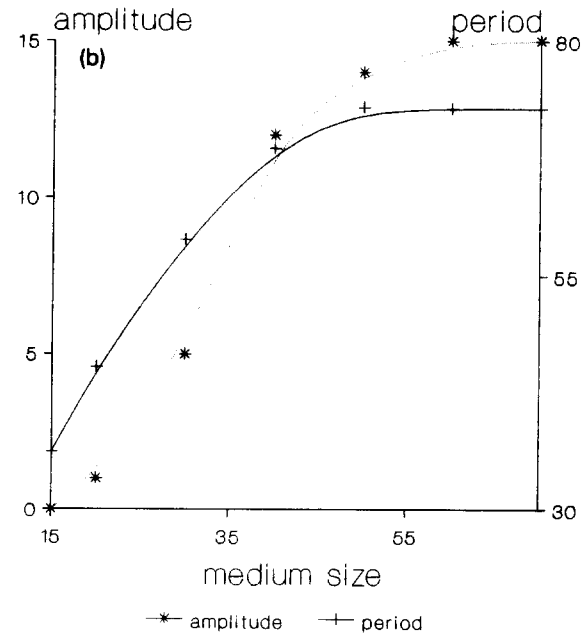


Fig. 4. (A) Dependence of the pulsation period and the wave mean size on the inhibitor relaxation time, τ. (B) Dependence of the period and the amplitude of pulsations on the size of the model medium.

same distance but outside the boundary. As a result the pulsating wave parameters depend on the medium size (see Fig. 4B). The amplitude of pulsations decreases with a decrease of the medium size, and there is a critical size of the medium when the amplitude of pulsation becomes zero and a stationary wave occurs. If the medium is large enough, the boundaries do not influence the pulsation.

4. Mechanism of the wave pulsation

The qualitative explanation of the pulsation phenomenon is based on the following statements:

(1) The velocity of the wave front decreases when the inhibitor concentration, W_{fr}, increases on the wave front [6].

(2) The inhibitor is produced in the excited region and destroyed outside of it.

(3) The diffusion of the inhibitor is faster than that of the activator ($D > 1$).

(4) The rate of inhibitor kinetics is less than that of the activator ($\tau > 1$).

Expansion of the wave leads to an increase of the inhibitor production. The inhibitor diffuses quickly and its concentration on the wave front increases (see Fig. 5A). It causes a decrease of the front velocity, so that after some time the wave stops (this phenomenon is known as "lateral inhibition" [8]). This stationary wave is not stable. Due to the slow production of the inhibitor the front velocity decreases further and then becomes negative (the wave front becomes the wave back). Now the wave constricts causing a decrease of inhibitor production (Fig. 5B). The inhibitor amount decreases, and after some time the inhibitor concentration on the wave back begins to decrease as well. As a result, the wave back velocity increases. When it becomes positive the wave expands again. The described processes repeat, producing the pulsations.

5. Discussion

Statements (1) and (2) in the previous section are common for the excitable media. Statements (3) and (4) are specific to this model and are responsible for the pulsations. Estimation (2) expresses the latter two statements. This estimation rewritten for system (4) gives that pulsating waves should occur if $1 < D < \tau$. The respective region obtained numerically and pre-

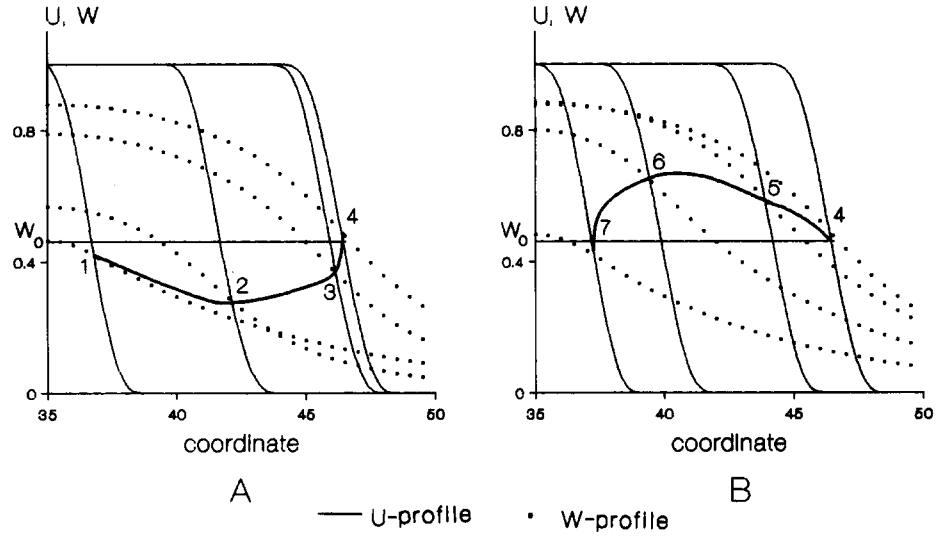


Fig. 5. Profiles of variables on the half of the pulsating wave given in Fig. 2A. Seven pairs of profiles are taken out with an equal time interval during a pulsation. The U- and W-profiles forming each pair are distinguished by the number near their crossing point. Pairs 1, 4, 7 are the profiles of the stopped wave; 2 and 3 the profiles of the expanding wave; 5 and 6 those of the constricting wave. The full line depicts the dynamics of the inhibitor concentration on the wave front, W_{fr}, during a pulsation period.

sented in Fig. 2A qualitatively confirms it. The pulsation period in numerical experiments is in qualitative agreement with estimation (3): $T \sim 2\pi D^{0.25}\tau^{0.75}$. In our computations we have detected no change in the pulsation period by variation of inhibitor diffusion D, and the almost linear dependence of the period on τ.

We have found a new regime of unstable pulsating waves when $D_3 < D < D_2$ (see Fig. 2). It proves that no solitary excitation can exist infinitely long in a medium of this regime. Furthermore, propagating waves occurring in system (4) close to the boundary ($D = D_3$) of this regime exhibit unexpected properties, for example, waves moving towards each other do not annihilate but reflect and move in opposite direction.

Pulsating waves, similar to those studied here, are observed in an open chemical system in Refs. [1,3,13]. However, the mechanism of pulsations in Refs. [1,3,13] is different from the mechanism considered in the present paper. In Refs. [1,3,13] the pulsations occur due to an externally imposed concentration gradient in a system where diffusion of both variables is equal. In contrast, the pulsations considered in our paper are supported internally due to the difference in diffusions and relaxation times of the variables.

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