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Periodical survival or decay of traveling impulse in a model of a one-dimensional reaction-diffusion system

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A two-variable model of a one-dimensional (1D), open, excitable reaction-diffusion system describing space-time evolutions of traveling impulses is investigated. It is shown that depending on the size of the system, the traveling impulse can survive or decay. Continuous increase of the size of the system causes periodical repetitions of surviving and decay of the impulse. The qualitative properties of the model, which allow us to expect the phenomenon, are described. Numerical solutions confirm this expectation. The chemical reaction scheme is realistic and may be a stimulus for seeking the phenomenon in experiments.

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I. INTRODUCTION

Two-variable reaction-diffusion (RD) models in one-dimensional infinite (1D) systems for initial value (Cauchy) problems are minimal models, in which asymptotic solutions in the form of traveling impulses can exist. Excitability of the system is the necessary condition for the existence of the traveling impulse. A simple example of an excitable system has an S-shaped (or N-shaped) nullcline for one variable (activator). In the simplest case, a nullcline for the other variable (inhibitor) has only one intersection point with one of the two attracting branches of the S-shaped nullcline. In another case, the nullcline for the inhibitor intersects the S-shaped nullcline in three points; one of them is situated on the attracting branch (a stable node), and the remaining two on a repelling branch (a saddle point and an unstable node or focus). Such models have been elaborated to describe in a qualitative way specific phenomena observed in biological [1,2], chemical [3,4], and physical [5] systems. If diffusion coefficients for both variables are sufficiently close to each other, then the traveling impulse spreads with constant velocity and invariant shape in excitable systems, both with one as well as three stationary states. It is noteworthy that the traveling impulse in 1D systems is defined as an asymptotic solution of the corresponding initial value (Cauchy) problems for infinite systems $-\infty < x < +\infty$. For finite systems, the corresponding initial-boundary value (Fourier) problems can be investigated. Their solutions evolve increasingly close to the traveling impulse for the Cauchy problem, if the size of the system continuously increases to larger values. In the case of equal or close diffusion coefficients and zero-flux boundary conditions, one can observe the traveling impulse exclusively in a finite interval of time. If the traveling impulse approaches an impermeable boundary, then its front and subsequently back are continuously absorbed, and the system becomes homogeneous. Also, the collision of two impulses leads to their annihilation and homogenization of the system.

However, if a reaction model is excitable but the diffusion coefficients differ substantially, then nontrivial effects appear in 1D reaction-diffusion systems [6–20]. The reflection of impulses from impermeable boundaries can appear, as well as when they collide. Moreover, traveling impulses can divide during their spreading. Interplay between these effects and annihilation in the 1D system can generate various spatiotemporal evolutions, such as consecutive reflections of the traveling impulse from boundaries [6,10,20], stationary periodical structures [6–9,11–13,16–20], spatiotemporal patterns isomorphic to the Sierpinski gasket [14] and spatiotemporal chaos [8,15,18].

In the present paper, we present another possibility, which, to our best knowledge, has not been described so far. In a finite excitable system with three stationary states (one of them is a stable node and the two remaining ones are a saddle point and an unstable focus), for a proper ratio of the diffusion coefficients, we have found that the traveling impulse can survive and continue its evolution or decay depending on the size of the system. With continuous increase of the size, surviving and decay of the traveling impulse succeed periodically. This phenomenon is illustrated by an example of a realistic chemical model.

Let us mention that for equal or close diffusion coefficients a traveling impulse with constant velocity and invariant shape is the asymptotic solution to a nonlinear excitable RD system, but for a diffusion coefficient of the activator sufficiently smaller than that of the inhibitor the impulse divides periodically into itself and a pulse of excitation behind it, generating a large amplitude stationary periodical structure [6–9,13,16,18–21]. Therefore, from the theorem about the continuous dependence of solutions to nonlinear RD systems on parameter values it follows that one can expect that the pulse behind the traveling impulse will appear but will not survive for some intermediate values of the diffusion coefficients ratio. A qualitative analysis of the competition between diffusion and kinetic terms around the front and the back of the traveling impulse, and around a local minimum between them in the concentration profile for the activator when the front approaches the impermeable boundary, allows for the prediction of the discussed effect. Signs of the diffusion terms are well defined in these regions. The competition

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may affect the further evolution of the traveling impulse in a qualitatively different way depending on the actual curvature of its shape. When the front approaches the impermeable boundary, its shape changes slightly, but its velocity decreases to zero. The front velocity is determined by the threshold for excitation. The threshold depends on the actual value of the inhibitor concentration (p) before the front. In the presented model, the threshold increases when the value of p before the front decreases.

If the traveling impulse of the activator $-s(t,x)$ reaches the boundary at the very beginning of its division, its continuation may be prevented. The positive diffusion term in the region of initiation of the division may be able to prevail over the negative kinetic term for the activator in the region of initiation of the division. Moreover, the negative diffusion terms around the front of the traveling impulse, as well as around the back, may not be able to prevail over the positive kinetic terms for the activator in these regions. Consequently, the division of the traveling impulse may be stopped, and then reversed. After a complex evolution accompanied by changes of the front of the impulse to the back of it and vice versa, the traveling impulse can survive and then spread to the opposite boundary.

However, if the traveling impulse reaches the boundary when its division is more advanced, then the kinetic term for the activator around the minimum between the front and the back becomes stronger and may prevail over the positive diffusion term in this region, and the division may be completed. Moreover, the negative diffusion terms around the pulse and the impulse may be sufficiently large to prevail over the positive kinetic terms, and, consequently, the pulse and next the impulse itself may decay.

If the traveling impulse reaches the boundary when its division is much more advanced than in the previous case, then it splits into the impulse and the pulse. The negative diffusion term around the maximum of the pulse may be sufficiently large to prevail over the positive kinetic term and, consequently, the pulse decays. However, the kinetic term for the impulse may be so strong that it prevails over the negative diffusion term and, consequently, the impulse may survive.

The possibilities mentioned above may be realized in systems of a proper size. Continuous increase of the size of the system causes the front of the traveling impulse to approach the boundary at different steps of the advance of its division. Note that the division of the traveling impulse occurs periodically. Therefore, the three possibilities mentioned above should also appear periodically, provided the size of the system is continuously increased. The evolution of the traveling impulse, which has survived the reflection, is quite complex and we had to limit ourselves to numerical calculations only.

In the next section, the model and the results of numerical calculations will be presented. The last section presents our conclusions.

II. MODEL AND RESULTS

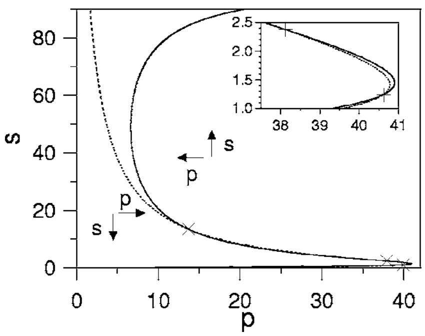

FIG. 1. The nullclines for s (continuous line) and p (dotted line) on the phase plane (p,s) for Eqs. (1) and (2) with neglected diffusion terms. The unstable focus positioned at (13.364 314 68, 13.885 593 25) is visible. The inset shows that the nullclines have two additional intersection points: the stable node with coordinates (40.585 927 8, 1.227 542 47) and the saddle point at (38.144 272 305, 2.362 912 366).

Our model describes an open chemical system in which two catalytic (enzymatic) reactions occur. One of the reactions is inhibited by an excess of the reactant (activator) and the product (inhibitor), and the other reaction occurs in its saturation regime. The chemical scheme consists only of elementary, monomolecular, and bimolecular chemical reactions (excluding autocatalysis). The details of the system have been described elsewhere [16,21,22].

The space-time behavior of the system for dimensionless concentrations of the reactant s and the product p is described by the following equations:

$$\frac{\partial s}{\partial t} - D_s \frac{\partial^2 s}{\partial x^2} = A_1 - A_2 s - \frac{s}{(1 + s + A_3 s^2)(1 + p)}, \tag{1}$$

$$\frac{\partial p}{\partial t} - D_p \frac{\partial^2 p}{\partial x^2} = B\left(- B_1 - B_2 p + \frac{s}{(1 + s + A_3 s^2)(1 + p)} \right), \tag{2}$$

where t and x are dimensionless time and space coordinates, respectively. D_s and D_p are dimensionless diffusion coefficients. The parameters A_1, A_2, A_3, B, B_1, and B_2 are related to the rate constants of the chemical reactions and to the total concentrations of both catalysts (enzymes).

We assume the following values for the parameters: $A_1 = 10^{-2}$, $A_2 = 10^{-4}$, $A_3 = 0.505$, $B = 0.5$, $B_1 = 7.99 \times 10^{-3}$, $B_2 = 4.65 \times 10^{-5}$, $D_s = 10^{-5}$, and $D_p = 2.7 \times 10^{-5}$.

The nullclines for the activator and the inhibitor are shown in Fig. 1. Only a small part of the upper attracting branch of the nullcline for s is shown. The arrows on the plane (p,s) show the vector direction fields for s (up or down) and p (left or right). The unstable focus is visible. The inset in Fig. 1 shows that the nullclines have two additional intersection points (the stable node and the saddle point).

The initial-boundary value (Fourier) problem for the 1D system ($x \in [0,L]$) with initial: $s(0,x) = 20$ and $p(0,x) = 35$ for $x \in [0,0.5]$, $s(0,x) = 1.22754$, and $p(0,x) = 40.5859$ for $x \in (0.5,L]$, and boundary conditions: $(\partial s/\partial x)|_0 = (\partial s/\partial x)|_L = (\partial p/\partial x)|_0 = (\partial p/\partial x)|_L = 0$ is solved numerically. The Cranck-Nicolson method is used in numerical solutions of Eqs. (1) and (2) with the time step equal to 1 and the space

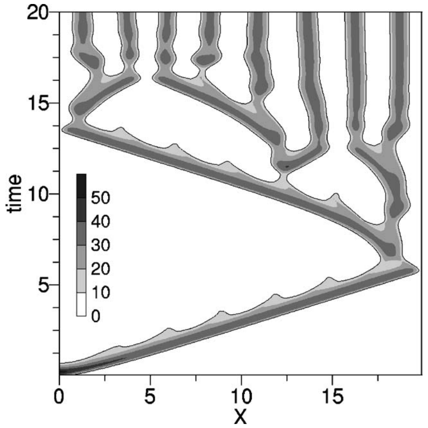

FIG. 2. Space-time evolution of $s(t,x)$ (activator) in the system with $L=19.9$. At this size the traveling impulse reaches the boundary at the very beginning of the sixth division and survives. A large amplitude stationary periodical structure is formed asymptotically (unit of time equals 50 000).

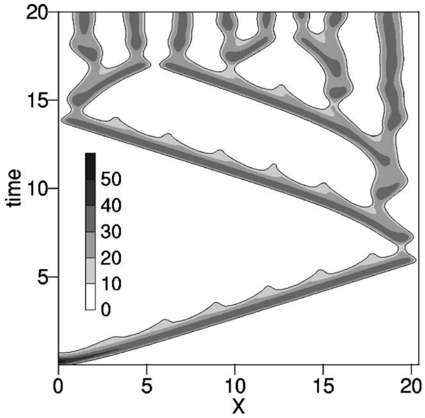

FIG. 4. Space-time evolution of $s(t,x)$ (activator) in the system with $L=20.4$. The traveling impulse attains the boundary when its division is more advanced compared with Fig. 3. A large amplitude stationary periodical structure is generated with the same number of periods as in Fig. 2 (unit of time equals 50 000).

step equal to 10^{-2}. The initial values of s and p on the unexcited interval are approximately equal to their values at the stable node.

The main result of our paper illustrating the surviving or decay of the traveling impulse is presented in Figs. 2–4 for $L=19.9$, 20.0, and 20.4, respectively. Differences in the transient behaviors of the systems are indistinguishable up to the fifth division. It is easy to notice the five periodic divisions of the traveling impulse followed by the five decays of pulses behind it. The qualitative difference in the later evolutions is also very well visible. In order to be more precise, we use the condition that the traveling impulse approaches the right boundary when the velocity of its front changes sign. This condition is approximately satisfied when $p(t,L)$ decreases from its initial value to 25.

Figure 2 corresponds to the situation when the traveling impulse approaches the boundary at the very beginning of the sixth division and reflects from it. Its later spreading is not as simple as the earlier one, when the traveling impulse runs from the left to the right boundary. Just after reflection, a division of the traveling impulse occurs. The pulse does not decay, but survives, and after some time divides again, generating two pulses, which survive. In the meantime the traveling impulse divides twice. The pulse formed in the first division decays, but the pulse formed in the second one survives, and next divides into two pulses. The right of them moves slightly to the right and stops, but the left one divides two times, leaving behind two surviving pulses. The traveling impulse still continues spreading to the left boundary and divides three times, but this time all three pulses formed behind it decay. Next, the traveling impulse approaches the right boundary, reflects from it, and then divides into two surviving pulses. After this complex evolution all the surviving pulses asymptotically form a large amplitude stationary periodical structure.

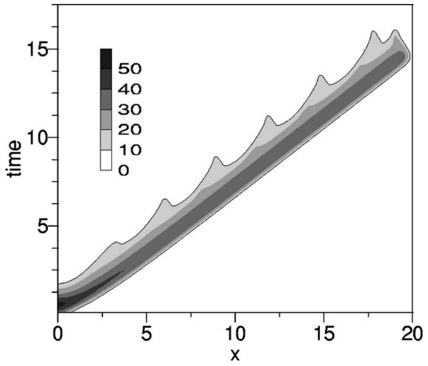

FIG. 3. Space-time evolution of $s(t,x)$ (activator) in the system with $L=20.0$. At this size the traveling impulse attains the boundary when the beginning of the sixth division is more advanced than in Fig. 2. The traveling impulse decays and the system becomes homogeneous (unit of time equals 50 000).

Figure 3 shows the space-time evolution of the traveling impulse when its sixth division is more advanced as compared with Fig. 2. In this case, the traveling impulse decays.

The space-time evolution of the system for $L=20.4$ is shown in Fig. 4. At this size, the traveling impulse divides six times and all the six pulses generated behind it decay. After reflection, the traveling impulse divides similarly as in Fig. 2, but then it spreads to the left boundary, leaving behind the decaying pulses. The surviving pulse divides itself, generating a child pulse, which survives and does not change substantially, and a child traveling impulse spreading to the left boundary. This impulse divides three times. Its first and third divisions generate surviving grandchild pulses, whereas the grandchild pulse formed in the second division decays. In the meantime the traveling impulse approaches the left boundary and reflects from it. After the reflection, it divides, generating two surviving child pulses. The right of them meets the child traveling impulse and both of them stop. Later, evolution leads to a large amplitude stationary structure with the same number of periods as in Fig. 2.

Our expectations that the surviving and decay of the traveling impulse occur periodically with the continuous increase of the size of the system have been fully confirmed by numerical calculations. The surviving, as well as the decay, repeats with the period close to 3.0 space units. We have checked this periodicity at sizes of the system in which the traveling impulse divides at least 25 times. The subinterval in which the traveling impulse decays equals approximately 0.4 space units. In the remaining complementary subinterval (about 2.6 space units) of the whole period, the traveling impulse survives. These values are correct for sufficiently long systems ($L > 14$), in which the traveling impulse approaches its asymptotic form. This condition seems to be fulfilled in the case of systems in which the traveling impulse has been divided at least four times.

The subsequent steps of the scenario caused by the increase of the size of the above-mentioned system are shown in detail in Figs. 5–7. The evolutions of the traveling impulse only in the region close to the boundary are shown. Our expectations concerning the competition between the reaction term and the diffusion term around the maximum of the traveling impulse have been confirmed. In order to show this confirmation we present selected shapes of the traveling impulse for s and p, as well as their projections on the plane (p,s). Figures 5(a) and 5(b) show the distributions of the reactant $s(t,x)$ and the product $p(t,x)$ at four selected times, taken from the interval of time at which the traveling impulse reaches the boundary. The initial steps in the division of the impulse are illustrated by curves 1 and 2. Curve 1 shows the traveling impulse when the velocity of the front is close to zero, because the value of p at the right boundary is close to 25 [see Fig. 5(b)]. The continuation of the division is stopped and then reversed, as shown by curves 3 and 4. The traveling impulse survives and then continues spreading to the left boundary. In order to explain the influence of the kinetic term for s on the distributions $s(t,x)$ and $p(t,x)$, Fig. 5(c) shows their projections on the "phase" plane (p,s). The projections are taken at the same times as the distributions shown in Figs. 5(a) and 5(b).

We should stress that the correct phase plane for all reaction-diffusion models has an infinite, uncountable number of dimensions, but for our qualitative explanations the projections of the distributions from the infinite dimensional space to the two-dimensional reagents space are helpful. The beginning of the division of the traveling impulse is illustrated by curve 1. The part of the distribution around the front of the traveling impulse (the very top of curve 1) is positioned on both sides of the nullcline for s. In this region of the phase plane (p,s), the term for the activator s is small and changes sign from positive values (to the right of the nullcline for s) to negative ones (on the other side of the nullcline s). Therefore, it is not able to prevail over the negative diffusion term, and the maximal value of s at the front decreases (compare curves 1 and 2). In the part of the distribution around the back of the traveling impulse (the maximum of curve 1 positioned at $p \approx 12.5$), the negative diffusion term is almost compensated by the positive kinetic term and, consequently, the changes of the maximal value of s at the back are small (compare curves 1 and 2). The part of the distribution between the front and the back of the traveling impulse (the local minimum on curve 1 at $p \approx 10$) has a positive diffusion term, but it is positioned in the region of the phase plane (p,s) where the kinetic term for s is negative. The curvature of this part of the distribution of s is small and, therefore, the positive diffusion term is not able to prevail over the negative kinetic term. Consequently, the local minimal value of s decreases and the division process is continued (compare curves 1 and 2). However, continuation of the division leads to such a significant increase of the positive curvature in the region around the minimum of $s(t,x)$ that the kinetic term is fully compensated by the diffusion term and the division is stopped. The positive kinetic terms around the front and back of the impulse shift $s(t,x)$ to the region on the phase plane where the kinetic term is posi-

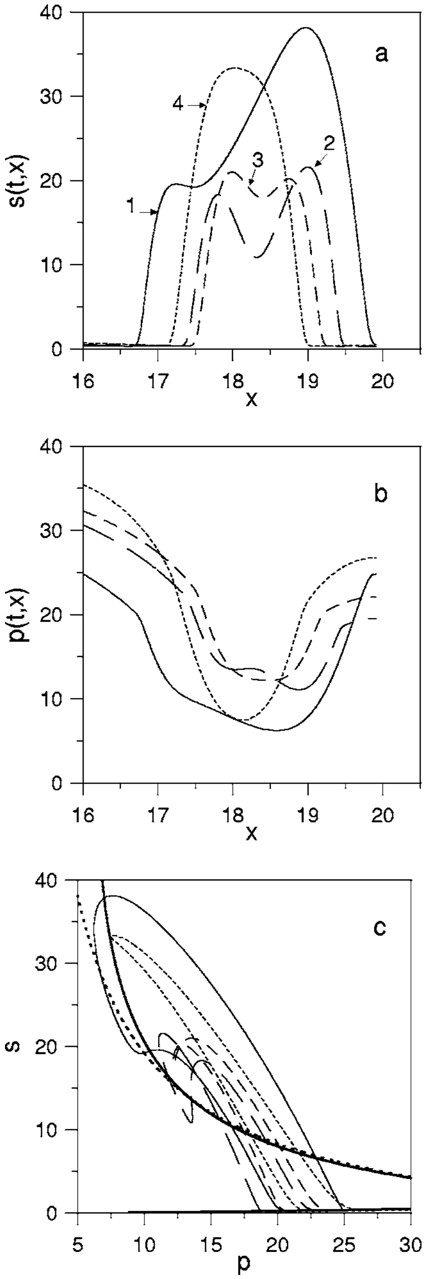

FIG. 5. Details of the spatiotemporal evolution of s (a) and p (b) for $L = 19.9$ and their projections on plane (p,s) (c) for the following times: line 1, $t = 285\,500$; line 2, $t = 308\,000$; line 3, $t = 317\,000$; line 4, $t = 350\,000$; solid line, nullcline for s; point line, nullcline for p.

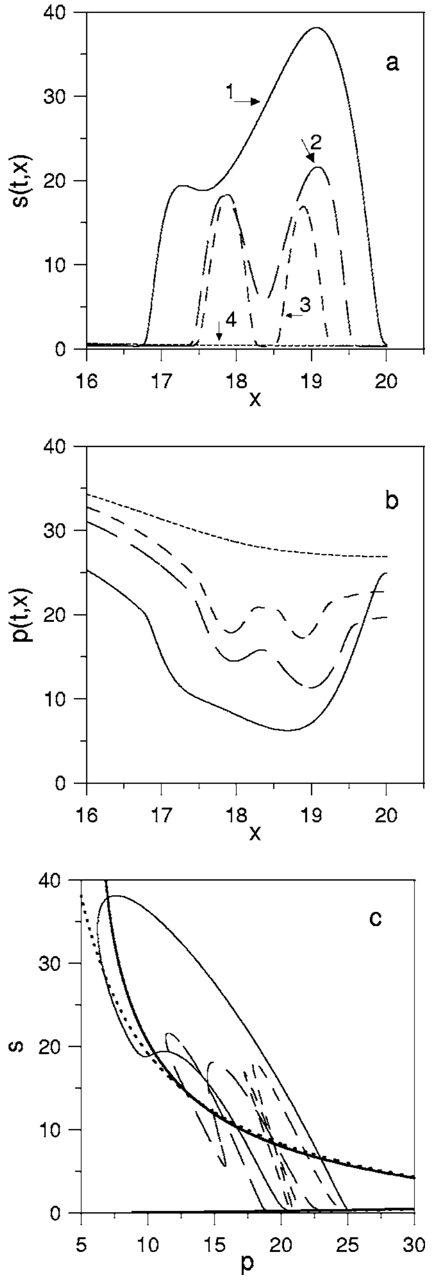

FIG. 6. The same as in Fig. 5 but for $L=20.0$: line 1, $t=287\,000$; line 2, $t=310\,000$; line 3, $t=320\,000$; line 4, $t=330\,000$.

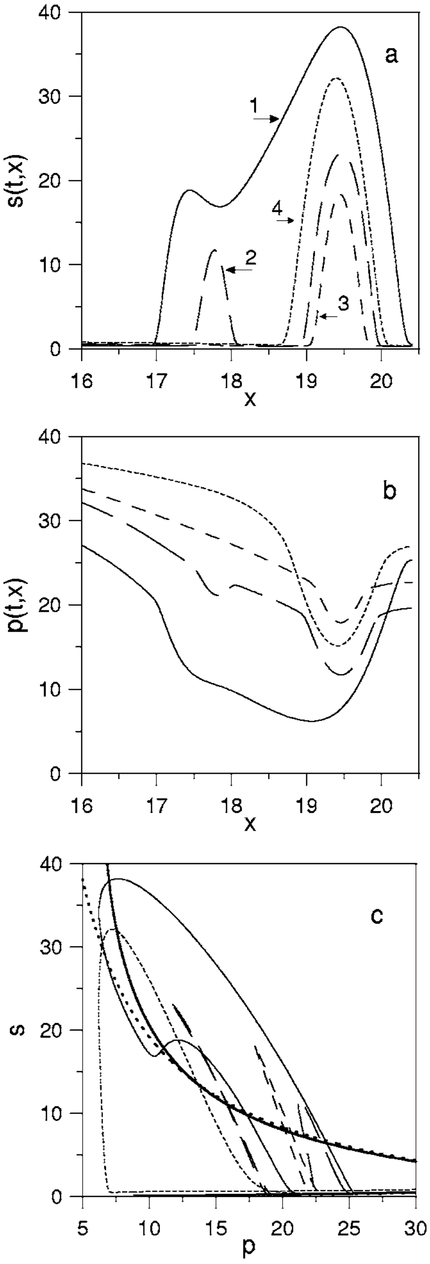

FIG. 7. The same as in Fig. 5 but for $L=20.4$: line 1, $t=293\,000$; line 2, $t=316\,000$; line 3, $t=326\,000$; line 4, $t=350\,000$.

tive. Consequently, the minimum in $s(t,x)$ disappears (see curve 3). Further evolution follows in the increase of $s(t,x)$ at the front, which is now the previous back of the impulse (compare curves 3 and 4).

Figure 6 shows the details of the space-time evolution of the system with $L=20.0$. The traveling impulse attains the boundary when the division is more advanced than in Fig. 5 (compare curves 1 in Figs. 5 and 6). The positive diffusion term around the minimal value of s is not able to compensate the negative kinetic term. The division is completed and the pulse behind the traveling impulse appears (compare curves 2 and 3 in Figs. 5 and 6). The negative diffusion terms around the maximal values of s around the pulse and the impulse prevail over the positive kinetic terms and, consequently, the pulse and the impulse decay (compare curves 3 and 4 in Figs. 5 and 6). The last projection of $s(t,x)$ and $p(t,x)$ on the plane (p,s) is so close to the nullclines that the fourth curve in Fig. 6(c) is invisible.

Figure 7 shows the details of the evolution of the system with $L=20.4$. The traveling impulse attains the boundary when the division is more advanced than in Fig. 6 (compare curves 1 in Figs. 6 and 7). The positive diffusion term around the minimal value of s is not able to compensate the negative kinetic term (see curve 2). The division is completed and the pulse appears behind the traveling impulse (see curve 3). The negative diffusion term around the maximal value of s at the pulse prevails over the positive kinetic term and, consequently, the pulse decays (see curves 3 in Figs. 6 and 7).

However, the maximal value of s at the front of the impulse is now in a so much stronger vector field for the activator (compare curves 3 in Figs. 6 and 7) that the positive kinetic term for s is able to prevail over the negative diffusion term. Consequently, the impulse survives (see curve 4 in Fig. 6) and continues its further evolution.

III. CONCLUSIONS

The periodical survival or decay of the traveling impulse as the result of the influence of the impermeable wall is the main effect shown in this paper. Two mechanisms of the surviving of the traveling impulse are presented. One of them prevents continuation of the division of the impulse. The other one operates when the division of the traveling impulse is completed, but the negative diffusion term around the front of the impulse is too small to prevail over the kinetic term for the activator. The decay of the impulse and the pulse appears periodically between the above-mentioned mechanisms if the size of the system is continuously increased and the system evolves to the homogeneous distributions of reagent concentration.

Infinitesimal changes of the right-hand sides of (1) and (2) as well as diffusion terms do not cause the vanishing of the effect of the periodic survival or decay of the traveling impulse. Therefore, Eqs. (1) and (2) with zero-flux boundary conditions are structurally stable and the discussed phenomenon exists in some range of the given values of the parameters and the diffusion coefficients. Preliminary calculations show that for the codimension one problem with B as the bifurcation parameter at $D_p/D_s=2,7$ the periodic survival or decay exists in the range $0.488<B<0.509$. Similar calculations for codimension one problem for $B=0.5$ with changed values of the ratio of the diffusion coefficients show that the discussed effect exists in the range $2.65<D_p/D_s<2.74$. Outside the structural stability region the behavior of the system is qualitatively different. For $B<0.488$ the traveling impulse always decays before the impenetrable wall, whereas for $B>0.509$ the traveling impulse periodically divides leaving behind surviving pulses. For $D_p/D_s<2.65$ the traveling impulse vanishes, whereas for $D_p/D_s>2.74$ the impulse survives and after reflection generates the large amplitude stationary periodical structure.

Let us mention that large amplitude stationary periodical structures created by subsequent divisions of the traveling impulse have been obtained in this model [16]. Moreover, 2D stationary patterns mimicking all capital Latin [21] as well as old Hebrew [22] letters have been generated in the same model. In the present paper the model remains the same, but the values of parameters are different from those used previously.

It is worth noting that the recently discussed concept of scatter (separator) [18–20], which by definition does not depend on the size of the system, is not valid in the description of the periodical surviving or decay of the traveling impulse described in the present paper.

All kinds of traveling impulses known so far satisfy the Hughes principle, in the sense that the shifts of positions of the boundaries do not change their later evolution qualitatively. This principle is violated in our model, in which the continuous increase of the size of the system causes the periodical decay or surviving of the traveling impulse.

In our model, the traveling impulses, after reflection from the boundaries, evolve in a complex way, but they asymptotically approach the stationary periodical structure. The evolutions presented in Figs. 2 and 4 differ substantially from those known so far [6–9,13,16,18–20]. The main difference is that all pulses formed behind the traveling impulse survive and form stationary periodical structures in the models [6–9,13,16,18–20], whereas in our model the surviving of the pulses after reflection of the traveling impulse from the boundary occurs irregularly. The survival of a pulse after reflection looks at a first glance as a random phenomenon. However, this is deterministic effect which depends on actual distributions of s and p formed at the reflection from the impermeable wall. This dependence is complex and it is very difficult to predict which one of succeeding pulses decays or survives.

Our results have been obtained for a sufficiently large excitation located at the left boundary of the system as the initial condition. It is worth noting that reaction-diffusion equations are invariant to translations in space. Moreover, they are also invariant to the change of x to $(-x)$, which follows in the mirror symmetry of their solutions. Therefore, the solutions to Eqs. (1) and (2) on the interval $[-L,L]$ with the initial condition located symmetrically around $x=0$ is equal to the solution on the interval $[0,L]$ and its mirror reflection. Consequently, reflections from the impermeable boundaries are equivalent to scattering of impulses. It is not difficult to foresee the solutions to Eqs. (1) and (2) for nonsymmetrical initial conditions provided initial excitation is not located very close to the boundary. If the initial excitation is located in a subinterval in such a way that both distances from its center to the boundaries belong to the sizes on which the traveling impulse initiated at the center of excitation survives (decays), then both traveling impulses spreading in opposite directions survive (decay). However, if one of these distances belongs to a size for which the traveling impulse initiated at the boundary decays and at the other distance survives, then the first of these impulses will decay, whereas the impulse running in the opposite direction after reflection from the boundary will survive and evolve to a large amplitude stationary periodical structure on the whole system.

It is worth noting that the effect reported in our paper introduces a kind of selection in the set of systems with the same size. In some of them, a sufficiently large local excitation may evolve asymptotically to the homogeneous distributions of reagent concentrations, whereas others asymptotically approach the large amplitude stationary periodical structure. The position of the initial excitation determines the asymptotic state. Moreover, one can expect a similar selection for systems excited at the boundary with sizes belonging to some interval. These results may be useful for explaining various selection phenomena known in biological systems, provided that in biological cells [three-dimensional (3D) systems] one of the three dimensions is substantial only. Such simplification has been used in models of the propagation of electrical excitation in axons. The impermeable boundary conditions may be applicable to sets of contacting cells, if the cell membranes are not permeable for the molecules which play the role of reagents in our model.

Let us mention that the phenomenon described in the present paper can be observed in generic models commonly used to describe the traveling impulses, like the Fitz-Hugh-Nagumo [1,2] and the Gray-Scott [4] models, provided the assumptions described above are fulfilled. It is not excluded that the periodical surviving or decay of traveling impulses may also be observed in the 1D version of the model suggested for description of a surface reaction [CO oxidation on Pt(110)] [8]. This could be a promising possibility, because these phenomena might be observed experimentally, provided the experimental setup would be as close to 1D as possible. Our model is also realistic and could be realized in experiments in 1D continuous-flow, unstirred reactor (CFUR) with two enzymatic reactions. One of them should be inhibited by its reactant and product. There are many enzymes which are inhibited by an excess of their reactants and products. Examples include: invertase inhibited by sucrose (reactant) and by fructose and glucose (products), xantine oxidase inhibited by xantine (reactant) and ureate (product), acetylcholinesterase inhibited by acetylcholine and choline, and many others [23,24]. We hope that our results may be helpful for seeking this phenomenon in real systems.

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