Running tails as codimension two quasi-solitons in excitation taxis waves with negative refractoriness.

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(Dated: June 26, 2007)

We describe a new type of wave phenomena observed in reaction-taxis systems of equations. This is "running tail", a localized stable perturbation steadily moving laterally along the back of a plane wave. This phenomenon is related to "negative refractoriness", a property observed in some excitable systems with cross-diffusion instead of usual diffusion. We suggest a simple mechanism of such running tails for the Keller-Segel model describing chemotaxis of bacteria on the nutrient substrate. We also demonstrate that collision of running tails may happen by "quasi-soliton" and "half-soliton" scenarios.

PACS numbers: 87.10.+e

Introduction Reaction-diffusion systems are the most studied class of models describing waves and patterns in spatially distributed systems [1]. However, mechanisms of spatial interaction in real system vary widely beyond simple diffusion. For instance, "cross-diffusion" [2] is important in the propagation of forest boundary [3], in chemical and biological pattern formation [4, 5], turbulence-shear flow interaction in plasmas [6], and displacement and velocity interact cross-diffusively in the Burridge-Knopoff model of tectonic slips [7]. A characteristic feature of living systems is their ability to react to changes of the environment, and to move towards, or away from, an environmental stimulus, behavior known as taxis. Of special interest are population taxis waves. Mathematical description of those includes nonlinear cross-diffusion [8–10]. If the usual diffusion is supplemented or replaced with taxis of cross-diffusion terms in an excitable system of equations, the properties of propagating waves can change radically [11–15].

In this paper we describe a new phenomenon in this kind of models. We consider distributed populations in a predator-prey relationship with each other. Spatial evolution is governed by two processes: positive taxis of predators up the gradient of prey (pursuit) and negative taxis of prey down the gradient of predators (evasion), yielding nonlinear "cross-diffusion" terms. The resulting mathematical model of "reaction-taxis" is a system of two partial differential equations, We consider a two-dimensional version of the model, studied earlier in [13, 14]:

$$\begin{aligned}\frac{\partial P}{\partial t} &= f(P,Z) + h_- \nabla\left(P\nabla Z\right), \\ \frac{\partial Z}{\partial t} &= g(P,Z) - h_+ \nabla\left(Z\nabla P\right), \qquad (1)\end{aligned}$$

where $P(x,y,t)$ and $Z(x,y,t)$ are biomass densities of the prey and predator populations. In system (1) h_- is the coefficient determining the taxis of prey down the gradient of predators (evasion), h_+ is the coefficient determining the taxis of predators up the gradient of prey (pursuit). The nonlinear functions $f(P,Z)$ and $g(P,Z)$ describe local dynamics,including growth and interaction of the species. We assume that this local interaction takes the Truscott-Brindley [16] form,

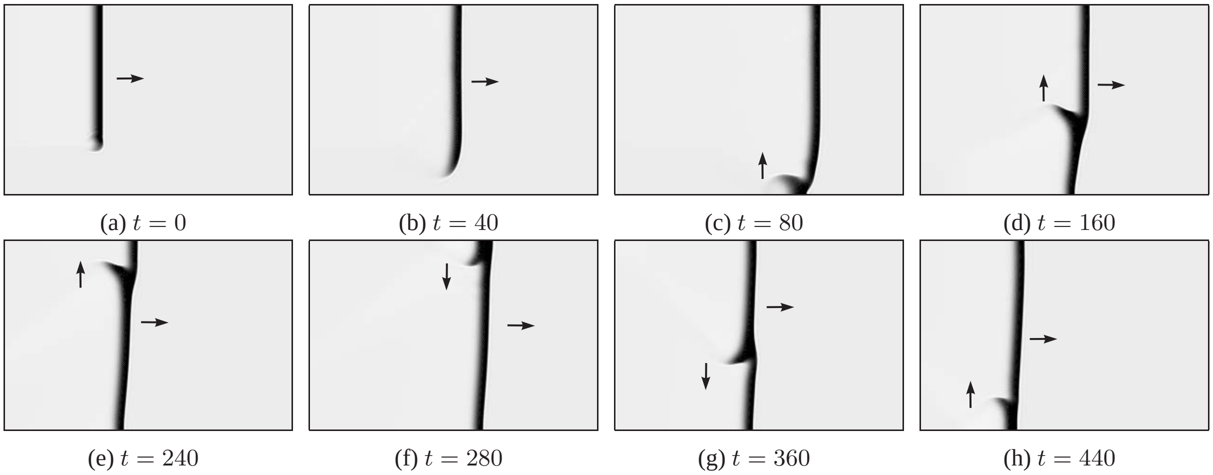
$$\begin{aligned}f(P,Z) &= \beta P(1-P) - ZP^2/(P^2+\nu^2), \\ g(P,Z) &= \gamma ZP^2/(P^2+\nu^2) - wZ, \qquad (2)\end{aligned}$$

System (1) have large parametric regions where excitation waves interact in a "quasi-soliton" way: they can penetrate through each other, and also reflect from impermeable boundaries [11, 12, 14]. Sometimes "half-soliton" interaction is possible, when of two colliding waves, one annihilates and the other continues to propagate[13].

Here we describe a new wave phenomenon in system (1), "running tail", and show that such running tails can exhibit both quasi-soliton and half-soliton interaction with each other.

Running tail. We studied system (1,2) numerically, at the same parameter value as in [12]: $\nu = 0.07$, $\beta = 1$, $w = 0.004$, $\gamma = 0.016$ and for varying h_- and h_+. In a two-dimensional domain, $(x,y) \in [0,L_x] \times [0,L_y]$, we initiated a propagating taxis wave in the x direction, independent on the y coordinate. Then we "cut out" a stripe $[0,L_x] \times [0,L_1]$, where $L_1 < L_y$, by setting both variables to the resting state values, $P = P_0 = 0.04$, $Z = Z_0 = 0.155$ within that stripe. In fact, we considered effectively $x \in [-\infty,+\infty]$, which was achieved by shifting the whole calcultion domain along x axes each time the wave approached the right boundary to a certain distance $L_{shift} = 25$. We used "upwind" scheme to approximate the taxis terms, see [12] for details, with discretization steps $\delta x = \delta y = 0.5$ and $\delta t = 0.001$. Selected control experiments used smaller steps, down to $\delta x = \delta y = 0.25$ and $\delta x = \delta y = 0.1$.

Germination of the free end of the broken wave, see fig. 1(a,b), and its interaction with the impermeable boundary $y = 0$, leads to formation of a "tail", a short wavelet attached to the back of the mother wave which is now restored and whole, see fig. 1(c). This "tail" wavelet propagates along the back of the mother plane wave as it goes ahead. In doing so,


(a) $t = 0$ (b) $t = 40$ (c) $t = 80$ (d) $t = 160$

(e) $t = 240$ (f) $t = 280$ (g) $t = 360$ (h) $t = 440$

FIG. 1: Formation of a wavelet and propagation of the running tail along the back of a plane wave, and its reflection from impermeable boundaries. Arrows show direction of propagation of the mother wave and the running tail. The parameters are $h_- = 4, h_+ = 2.3$; $L_x \times L_y = 150 \times 100$, $L_1 = 25$. The domain is effectively infinite in the x direction.

the tail is reflected from the impermeable boundaries $y = L_y$ and $y = 0$, see fig. 1(d-h). This process of propagation and reflection continues without decay. In our simulations we have followed it up to $t = 2500$.

To check whether the running tail is a transient of the interactions with boundaries or a truly stable and persistent phenomenon, we performed simulations with periodic boundary conditions along the y direction, i.e. $(P, Z)(x, 0) = (P, Z)(x, L_y)$, $\left(\frac{\partial P}{\partial y}, \frac{\partial Z}{\partial y}\right)(x, 0) = \left(\frac{\partial P}{\partial y}, \frac{\partial Z}{\partial y}\right)(x, L_y)$. The initial conditions for such simulations were the running tail solutions obtained in a similar domain with non-flux boundaries; that is, we changed boundary conditions from non-flux to period at a certain time moment. These simulations have shown that the propagating tail is stable and reflections from impermeable boundaries is not necessary for it to persist.

The running tail seen in fig. 1 moves simultaneously in two directions: in the direction of mother wave propagation, along the x axis, and along the back of the mother wave, along the y axis. So the absolute speed of the running tail is higher than the speed of the plane wave. Remember that in reaction-diffusion excitable systems, a back of a propagating wave has a zone of absolute refractoriness where initiation of another wave is impossible, and a zone of relative refractoriness where such initiation is impeded and a new wave propagates slower. So here in our cross-diffusion model we see a new phenomenon, “negative refractoriness”, where a new wave in the wake of an existing one propagates faster rather than slower.

Negative refractoriness is related to the unusual shape of the dispersion curve in this system. Fig. 2 shows the propagation speed of plane waves in (1) with periodic boundary conditions as a function of the period, for selected values of parameters. Method of calculation was as in [14]: a wave was initiated in an interval of large length L with no-flux boundaries, then boundary conditions changed to periodic, then L was decreased in small steps and the established wave speed $v(L)$ measured at each value of L. Fig. 2 shows that if $h_+ > 0$, then $v(L) > v(\infty)$ for short L, that is, waves closely following each other, propagate faster than a solitary plane wave.

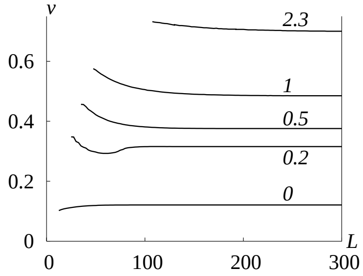
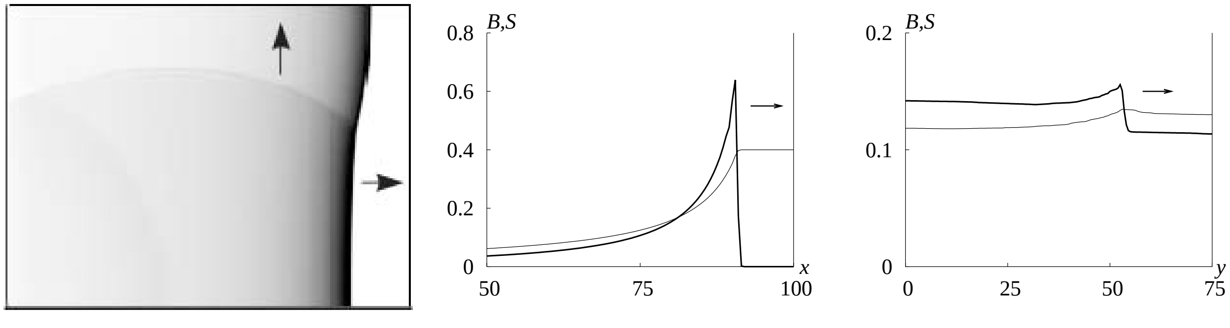


FIG. 2: Dispersion curves of periodic plane waves in system (1): propagation speed v as function of spatial period L, for fixed $h_- = 4$ and values of h_+ shown as labels at curves.

The detailed mechanisms of these unusual phenomena require further investigation. A simple qualitative explanation of the running tail could be done for bacterial population waves due to chemotaxis of bacteria to the gradient of the nutrient substrate described by a variation of Keller and Segel model [8, 9] of the form:

$$\begin{aligned} \frac{\partial B}{\partial t} &= \gamma f_1(S) B - h_+ \nabla \left(B \nabla f_2(S)\right), \\ \frac{\partial S}{\partial t} &= -\beta f_1(S) B, \end{aligned} \tag{3}$$

where $B(x, y, t)$ is biomass density of bacteria; $S(x, y, t)$ is concentration of substrate; functions $f_i(S) = S/(S + c_i)$, γ, β, c_1, c_2, h_+ are constants. The spatial gradient of the substrate is caused by its consumption by bacteria. This model also has running tail solution, as illustrated in fig. 3(a). A



(a) (b) (c)

FIG. 3: Running tail in bacterial population waves model (3). (a) A snapshot of the bacterial population density. (b) Instant profiles of the variables across the mother wave. (c) Instant profiles of the variables along the back of the mother wave, at the distance $l = 15$ from its front, across the running tail. In (b) and (c), the bold lines are for B and thin line for S. Parameters: $\gamma = 0.002$, $\beta = 0.02$, $c_1 = 0.3$, $c_2 = 0.01$, h_+ = 40, $L_x \times L_y = 100 \times 75$

shoot of bacterial wave, formed on reflection from the impermeable boundary, creates a gradient of substrate concentration, fig. 3(c), which stays after passage of the mother plane wave, fig. 3(b).

Interactions of running tails We initiated two-tail solution similarly to single tail solutions, this time cutting out two stripes, $0 \leq y \leq L_1$, $L_y - L_2 \leq y \leq L_y$. We illustrate here two cases. The first case, $L_1 = L_2$, is shown on fig. 1. The two running tails were formed, fig. 1(a-c). They interacted in a quasi-soliton manner: penetrated through each other, and also reflected from impermeable boundaries fig. 1(d-h).

The second case, shown in fig. 5 is for assymmetric initial conditions, with $L_1 < L_2$. The two running tails first demonstrate quasi-soliton interactions in collisions with impermeable boundaries and with each other (panels a–e). Then they experience a half-soliton interaction where only one of two colliding tails survives and the other decays (panels f–h). This is analogous to the interaction of taxis waves we described in [13], when interaction of two waves of different widths could result in the thicker one suppressing propagation of the thinner one. Notice that the shape and thickness of the tails is significantly affected by the curvature of the mother wave. As this curvature smoothens out, a difference in the shapes and thicknesses of the two tails emerges. This difference is due to non-synchronous collisions of the tails with the boundaries. So the second impact of the two tails (panel f) the thinner one decays and the thicker one continues to propagate (panels g, h).

Conclusion We have described new types of wave phenomena in an excitable cross-diffusion system of equations modelling a predator-prey system. These are codimension two waves or “waves running along waves”. They have some apparent similarity to the spin flames, when intensive reaction sites move along a combustion front [17, 18].

The negative refractoriness may look similar to “supernormal excitability” observed in some cardiac and neural tissues, where there is a period after an action potential when the excitation threshold is lower than in the resting state. However the phenomenon described here is different, as it is not due to special local properties of the medium constituents, but to special form of spatial interaction.

Formation of a “tail shoot” was observed in experiments with quasi-soliton interaction of bacterial waves [19], and also in two-dimensional numerical simulations of partial reflection of taxis waves [14]. However, in those works the tail shoot did not move along the mother wave. Possibly, some analogy of quasi-soliton interaction of running tails is observed in developmental waves in myxobacteria, where in early stages of their development, starving myxobacteria organize their motion to produce a periodic pattern of traveling cell density waves. Myxobacteria waves appear to pass through one another unaffected [20].

Authors are grateful to O.A. Mornev for inspiring discussions. This study was supported by RFBR grant 07-04-00363.

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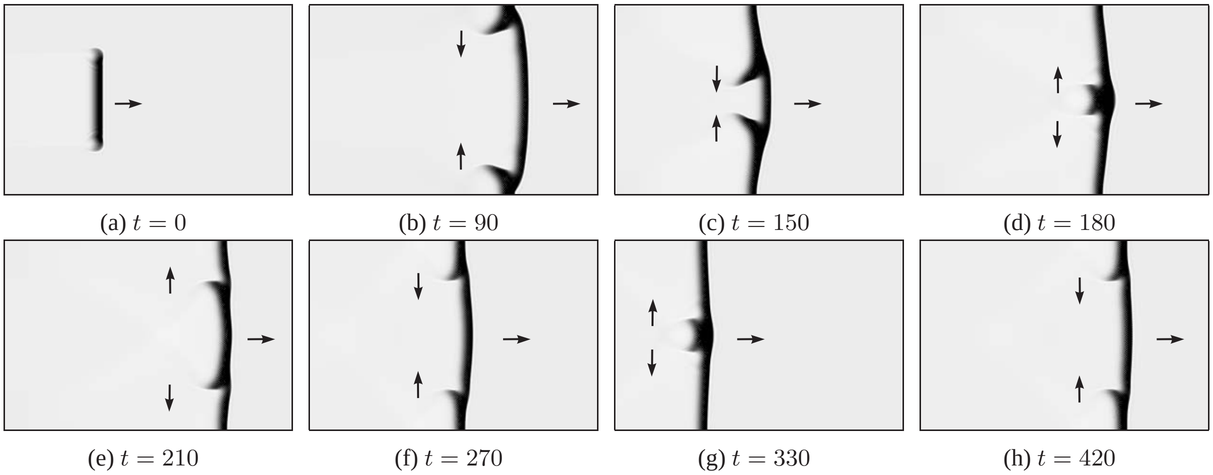
(a) $t = 0$ (b) $t = 90$ (c) $t = 150$ (d) $t = 180$
(e) $t = 210$ (f) $t = 270$ (g) $t = 330$ (h) $t = 420$

FIG. 4: Quasi-soliton interaction of running tails. Parameters $h_- = 4, h_+ = 2.3$, $L_x \times L_y = 150 \times 100$, $L_1 = L_2 = 25$. The domain is effectively inifinite in the x direction.

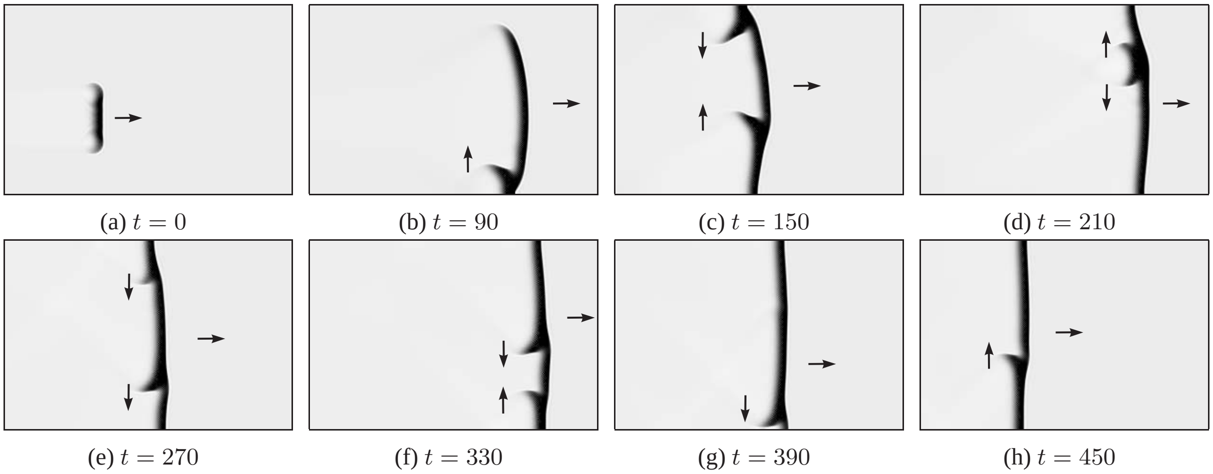
(a) $t = 0$ (b) $t = 90$ (c) $t = 150$ (d) $t = 210$
(e) $t = 270$ (f) $t = 330$ (g) $t = 390$ (h) $t = 450$

FIG. 5: Half-soliton interation of running tails. $h_- = 4, h_+ = 2.3$; $L_x \times L_y = 150 \times 100$, $L_1 = 25, L_2 = 45$. The medium is effectively infinite in the x direction.

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