

Winfree Meandering in a 2-Dimensional 2-Variable Excitable Medium

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Z. Naturforsch. **34a**, 565–570 (1979); received March 12, 1979

Two-dimensional excitable media, for example the excitable version of the Belousov-Zhabotinsky reaction, are capable of forming spiral-shaped self-sustaining rotating wave patterns (rotors). In order to explain Winfree's experimental observation of an irregular "meandering" of the rotor's core region, we present a numerical simulation of a continuous, two-variable excitable medium in two space dimensions. Two phenomena occur: 1) an irregular motion of the rotor's core; 2) a non-stationary peak inside the core region. Thus, "meandering" is obtained, together with a new phenomenon, the "peak". A sufficient condition for both phenomena is that the underlying (local) system be stiff, that is, admit two time scales for its approximate description. In this case, (1) the "reaching distance" of diffusion is small as compared with the core's radius, and (2) rotation symmetry of the core implies a gradation in local frequencies (increase toward the center), supposing radial decoupling. We propose that both constraints act together to induce a spontaneous breakdown of rotation symmetry under an increase of stiffness. Immediately (or soon) thereafter, the core is no longer synchronized by the wave circling around it; instead, excitation from the surrounding wave penetrates the core along a new path from time to time, causing a non-repetitive short-cut.

Introduction

Excitable media consist locally of excitable systems (monoflops) which by a relatively small exogenous perturbation can be caused to respond with a large-amplitude excitation, followed by a recovery process which re-establishes excitability. Under spatial coupling, a sufficiently large local region, when excited, causes a spread of excitation through the medium. Winfree [1a], following Zeeman [2], called the waves of excitation so formed "trigger waves". Heart tissue, with the pace-maker system removed, provides a classical example (see van der Pol and van der Mark [3], Wiener and Rosenblueth [4], Swain and Yanagita [5], Balakovsky [6], and Krinsky [7]). A quantitative description of trigger waves as "moving catastrophes" [8, 9] was recently given by Feinn and Ortoleva [10].

Two-dimensional excitable media are known to support spiral-shaped wave patterns that regenerate themselves. These were, in a discrete state model, termed "reverberators" [6] and, in continuous systems, called "spiral wave-reverberators" [11] and "rotors" [12], respectively. In the cardiological literature, the term "circus movement excitation" is customary (cf. [13]).

The spiral has in its outer region approximately the form of an involute around a circle, circling

around a core [14]. In most numerical studies, a rotation-symmetrical situation was found. However, Gul'ko and Petrov [15] showed that the position of the core region may be drifting, and Karfunkel [16] pointed out that a "slow drift" may be expected in general. Winfree's [1, 8] experimental observation of a quite irregular, "meandering" behavior of the core (in a thin layer of the Z-reagent) came as a surprise. A possibly analogous observation in a piece of heart tissue was made by Allesie et al. [13], see [12].

In the following, a digital numerical simulation reproducing the phenomenon is presented and a qualitative explanation attempted.

Numerical Results

The following equations were simulated:

$$\begin{aligned}x_t &= D_1 \nabla^2 x + a + bx - cyx/(x + K) - dx^2, \\y_t &= D_2 \nabla^2 y + \mu(x - ey). \quad (1)\end{aligned}$$

The corresponding local system ($D_1 = D_2 = 0$) has been indicated before as a simplified model of the Zhabotinsky reaction [17, 18]. The equations were run in the monostable version, that is, the nullclines had the form shown in Figure 1. The system was started with a spiral-inducing initial condition (Figure 2). After a spiral had developed, the diffusion constants were readjusted to obtain a convenient frame. A "stationary" regime was obtained using $D_1 = 0.1$, $D_2 = 0$. At these parameter values, the spiral was allowed to rotate about

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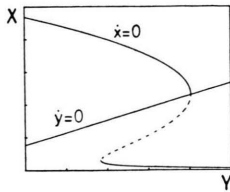


Fig. 1. Nullclines of Eq. (1) in concentration space (at $D_1 = D_2 = 0$). Unstable portion dashed. Parameters: $a = 0.4$, $b = 0.6$, $c = K = 1$, $d = 0.04$, $e = 2.28493$, $\mu = 1/3000$. Axes: 1 ... 3.5 for x and 0 ... 15 for y .

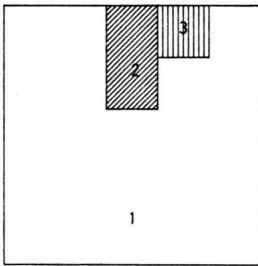


Fig. 2. Initial conditions chosen for Equation (1). $D_1 = 0.02$, $D_2 = 0$. Mesh size: 0.02 length units. Whole area: unit square. Region 1: near steady state concentrations (6.9, 3.0) for (x, y) ; region 2: refractory (10, 2); region 3: excited (0.2, 3).

four times (till $t = 5.15$). A typical plot obtained thereafter is shown in Figure 3.

Figure 4 shows the corresponding computer printout for x (using five grayness values (concentration ranges)). One level line of the wave front (in the region of the steepest slope of the first variable) is emphasized. Thirty plots of this type were obtained, ten in intervals of 0.025, from $t = 5.15$ to $t = 5.4$, twenty in intervals twice as long, till $t = 6.4$.

Figure 5 shows a pair of subsequent level lines. The intersection point of two such lines, separated by a short time interval, approximates the "point of inflection" (point q of Gul'ko and Petrov [15]) which separates the region of active propagation (bold lines) and the region of local recovery, that is, passive propagation (broken lines in Figure 5). This point has been chosen for convenience. If the asymptotic regime were rotation symmetric, point q would have to be either stationary or confined to a circular movement.

Entering all subsequent positions of q into one picture, a meandering movement of the core region is found: see Figure 6. The effect seems to be real

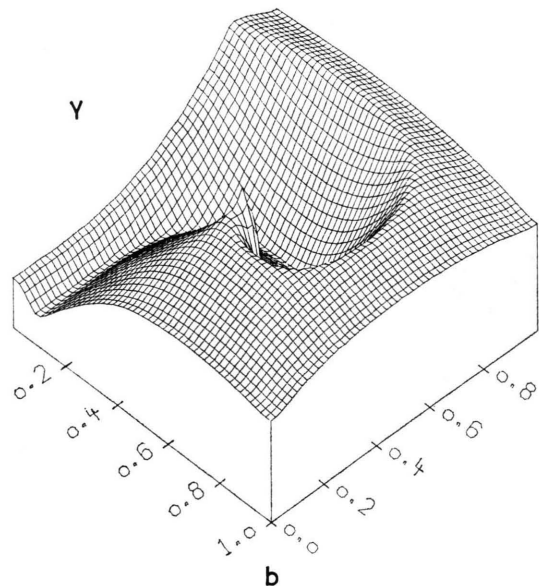
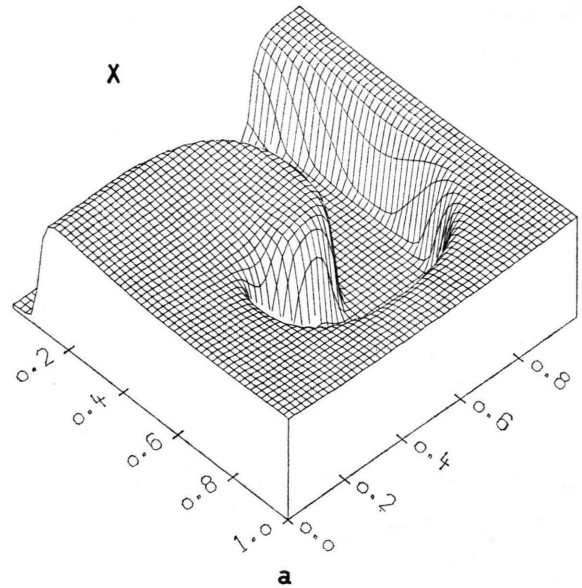


Fig. 3. Concentration profiles of x and y at time $t = 6.40$. Note the "peak" in the second variable. Numerical simulation of Equation (1) with the parameters of Figure 1 and $D_1 = 0.1$, $D_2 = 0$ (see text), using an integration routine based on the ADI Crank Nicolson algorithm (Karfunkel [16a]). The simulation program [16] was run on a CDC 3300 and a TR 440 in the Computing Center of the University of Tübingen.

in spite of the numerical approximations involved (finite mesh size; finite time steps; finite area).

Figure 7 shows the trajectory in local phase space of an arbitrarily picked point in the core region. The trajectory is not closed.

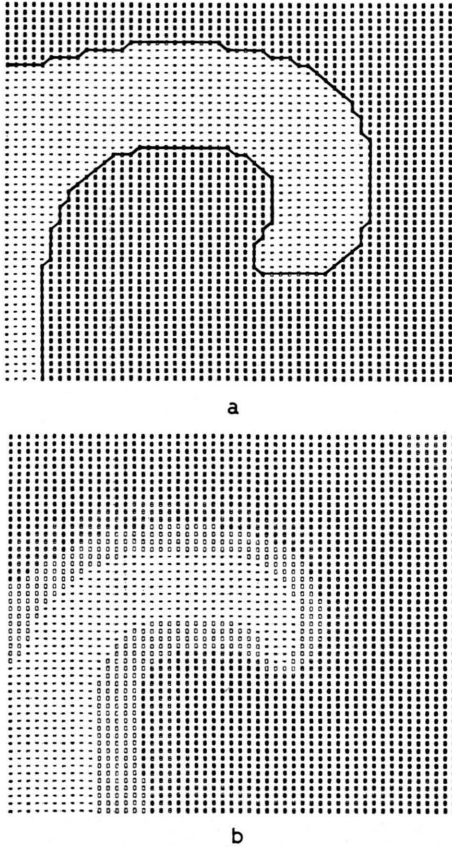


Fig. 4. Computer printouts of the kind used for the subsequent Figures (where only x will be used). The two pictures shown correspond directly to those of Figure 3. One level line in the x -plot is emphasized.

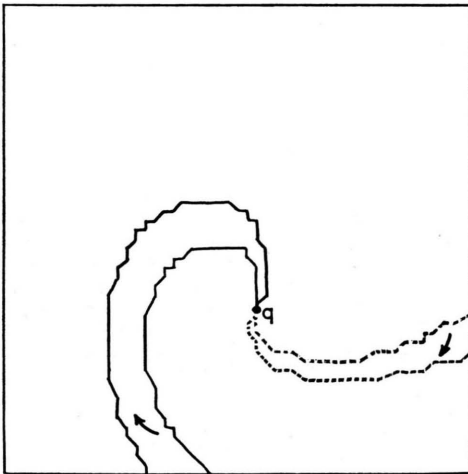


Fig. 5. Two subsequent level lines. They correspond to times $t = 5.375$ and $t = 5.4$, respectively. The arrows mark the direction of rotation. q = intersection point (see text).

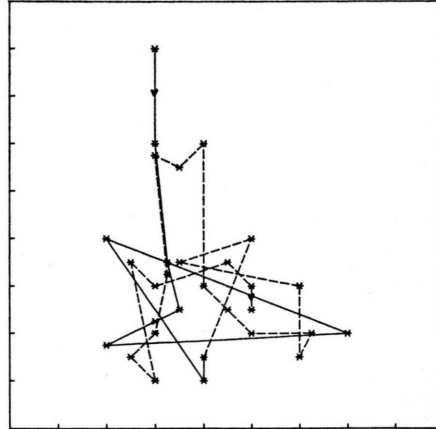


Fig. 6. Meandering of subsequent positions of point q (as defined in Fig. 5), from time $t = 5.15$ to time $t = 6.4$. Solid line: time step size $\Delta t = 0.025$; dashed line (starting at $t = 5.4$): $\Delta t = 0.05$. Axes: $0.46 \dots 0.64$ (horizontal) and $0.32 \dots 0.5$ (vertical).

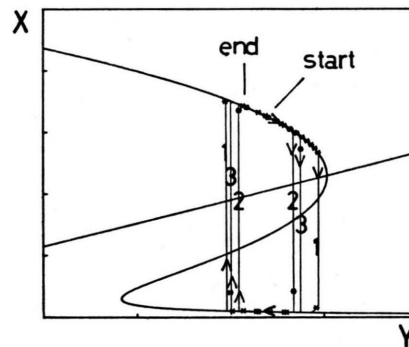


Fig. 7. Trajectory in local concentration space, applying to the point $(0.54, 0.38)$ in real space. Start: $t = 5.15$, end: $t = 6.4$. 1, 2, 3 = successive cycles.

A second series of simulations with a different initial condition and slightly different diffusion coefficients yielded similar results.

A Proposed Explanation

A complete understanding of core behavior in two-dimensional 2-variable excitable systems with fast relaxation has yet to be obtained. A multiple time scales approach (cf. [10]) would be desirable, but is so far applicable only outside the core region. This is because the wave has to be assumed to propagate into a region with invariant excitability properties (so that the velocity of propagation becomes a constant calculable as an eigenvalue of the scaled equation [10]).

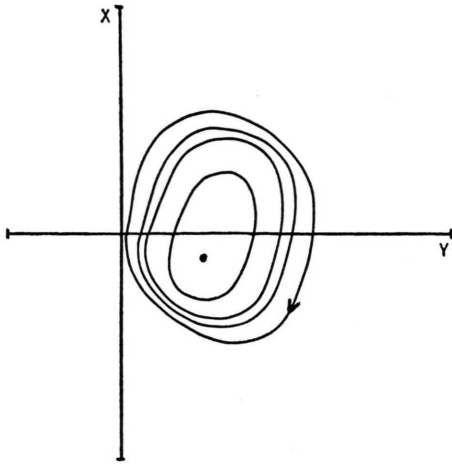


Fig. 8. Trajectories of a representative sample of points in real space, projected into phase space, obtained in a non-stiff system. (Winfree [12], part of Figure 17c.) If μ in Eq. (1) is increased to a value of 0.03, for example, an analogous picture is obtained in place of Figure 7.

Winfree [19, 12] observed that the trajectories in local phase space are all closed in the core region of a non-stiff system, forming a smooth concentric set when the behavior at all local points is entered into the same picture: Figure 8. Extremely stiff systems, on the other hand, can — by local coupling — hardly be forced into the neighborhood of the unstable branch of the fast nullcline. Therefore, the above structure is not likely. Nonetheless, something which looks like a set of concentric narrow windows, all with approximately the same height (x -amplitude), is possible. Reason: large changes of gradient over short distances, if present, can induce a local system to switch while still in a relative-refractory state. This is evident from the local formulation of Eq. (1), which reads

$$\begin{aligned}\dot{x} &= \varphi + a + b x - c y x / (x + K) - d x^2, \\ \dot{y} &= \mu (x - e y).\end{aligned}\quad (2)$$

If φ , the locally forcing flux, is strongly negative, the lefthand nullcline of Fig. 9 applies. The switching threshold for a transition toward the lower state is displaced to the left; and vice versa for positive fluxes (Figure 9). Thus, two different nullclines, one displaced to the left and one to the right, contribute to the formation of the sides of the “windows”; see Figure 7. From the point of view of the undisplaced nullcline (compare Fig. 1), the transitions give the impression that a region seemingly strongly resistant to excitation, is being “tunneled through”.

Slower movement in space unavoidably occurs inside of a rotation symmetric core region. Slower movement, however, leads to steeper gradients and curvatures — and hence to the “tunneling” described above.

One possible way to verify whether there is indeed a slower motion and an increase in tunneling inside a rotation-symmetrical core, is to look at cyclic one-dimensional systems of small circumference. Simulating excitable rings of different sizes, we obtained cycling waves which in local state space corresponded to “windows” of differing widths [20]. In the smaller rings, velocity of propagation was reduced and angular velocity enhanced; frequency was increased. The rings were too short to support a cyclic wave when triggered in the usual way; that is, they corresponded to the internal region of the core.

That more “internal” cyclic motions should have a higher frequency than more external ones follows also from Figure 9: The frequency of each motion along a “window” is determined by its width, that is, the y -amplitude, since the vertical motions are fast. So if there are any “more narrow” paths, they are bound to have a higher frequency [21]. This tendency toward faster rotation inside of a symmetric rotor is going to be enhanced with increasing stiffness.

There is another (synergistic) effect which comes into play: with increasing stiffness the spatial “reaching distance” of diffusion (as compared with the core diameter) goes down, due to the occurring relative compression in space of the high-curvature zones (compare the flat plateaus and the steep descents in Figure 3a). For the core diameter grows

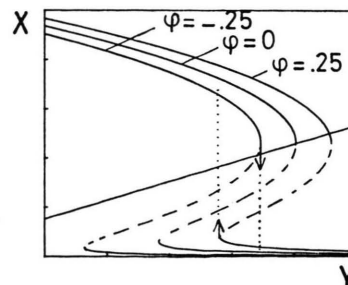


Fig. 9. Nullclines of Eq. (2) for 3 different values of the local flux φ . Parameters and conventions as in Figure 1. Arrows = displaced transition thresholds. Note that the displaced nullclines apply in the original system (Eq. (1)) only to zones of high curvature in the x -concentration (that is, to the regions of the cliffs in Figure 3a).

with $1/\mu$ while the local coupling remains unchanged. Synchronization has to be mediated by diffusion, however.

Both effects taken together mean that under an increase of stiffness (that is, decrease of μ) a breakdown of rotation symmetry is bound to occur — somewhere in between the situations depicted in Figures 8 and 7.

The special properties of the type of symmetry breaking thus predicted have yet to be studied. Winfree's [12] topological method may prove helpful (although in this case $D_1 = D_2$ is required, a situation which has yet to be simulated). We conjecture that a "scrambling" of trajectories in local phase space occurs at — or soon after — the onset of instability. Figure 7 numerically supports this view.

Discussion

Our results appear to reproduce Winfree's [1, 8] experimental finding of meandering.

Gul'ko and Petrov's [15] early analogue computer studies of a 3-variable excitable system [22] in a sense foretell our results: there, point q also was not stationary, but made a slowly drifting, otherwise "circular" movement (see the pictures in [15]). Winfree's experiment was nonetheless necessary to draw attention to the possibility of an even more complicated behavior.

One special feature, present in the above simulations, has apparently not been noted before in chemical or computer experiments: the "peak" of y visible in Figure 3b. It is present in the core region for most of the time, and its movement appears to be irregular. We interpret it as a visible

corollary to our hypothesis, sketched above, that there exist non-concentric paths in local concentration space: the peak marks a region in which no "tunneling" has occurred for a while. "Meandering" and "peak formation" appear to go hand in hand, as two aspects of the same reality.

The present computer study, designed to reproduce an experimental phenomenon, at the same time had its roots in a more abstract problem: is it possible to have a "flashing eye" inside the cyclone formed in an excitable medium? This question was motivated by the obvious discrepancy between Winfree's early, very regularly shaped core [14] on the one hand, and the zero volume core-analogue of comparable circumference found earlier in discrete studies [7] on the other hand (see [23]). The gap should be bridged by a sequence of intermediate forms. One element of the sequence, resembling "irregular flashing", has now been found.

A more general mathematical problem is the relationship between a stiff excitable medium on the one hand and a cellular automaton of the type considered by Swain and Yanagita [5], Burks [24] and Greenberg et al [25] on the other. The possibility of "tunneling", discussed above, does not exist in the automata theoretic situation. None the less, an analytical "bridge" may be sought.

The question whether meandering is chaos (Winfree, personal communication 1975; [26]) has to await further understanding of the bifurcations at and beyond symmetry breaking. For reviews of different types of chaos in two-variable reaction-diffusion media of different kinds, see [27] and [28].

We thank Heinz Karfunkel for kindly providing a copy of his simulation program.

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