Evidence of Soliton-Like Behavior of Solitary Waves in a Nonlinear Reaction-Diffusion System

Henry C. Tuckwell

SIAM Journal on Applied Mathematics, Vol. 39, No. 2. (Oct., 1980), pp. 310-322.

Stable URL:
http://links.jstor.org/sici?sici=0036-1399%28198010%2939%3A2%3C310%3AEOSBOS%3E2.0.CO%3B2-I

SIAM Journal on Applied Mathematics is currently published by Society for Industrial and Applied Mathematics.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/siam.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Sun Oct 21 03:07:58 2007

SIAM J. APPL. MATH.
Vol. 39, No. 2, October 1980

0036-1399/80/3902-0011 $01.00/0

EVIDENCE OF SOLITON-LIKE BEHAVIOR OF SOLITARY WAVES IN A NONLINEAR REACTION-DIFFUSION SYSTEM*

HENRY C. TUCKWELL†

Abstract. Many systems of nonlinear reaction-diffusion equations have been found in which stable traveling solitary waves annihilate one another on collision. A two-component reaction-diffusion system with this property is constructed from the equations in a model of spreading cortical depression, in which the components are the concentrations of potassium and calcium ions in the extracellular compartment of nervous tissue. The solitary wave orbit is studied in relation to the source functions in the reaction-diffusion system. The trajectories of the solutions are studied at various spatial points during the collision of the annihilating waves. During the collision interaction, parts of the plane of values of the components are visited that have not arisen during the passage of the solitary waves. The source functions are modified off the solitary wave trajectory, and it is found that two solitary waves emerge from the collision whose wave forms and speeds are identical to those of the colliding waves. The numerical computations thus suggest that the modified system of reaction-diffusion equations has solitary wave solutions with soliton-like properties. With slightly asymmetric initial data, when two solitary waves collided, only one emerged from the collision.

1. Introduction. In this paper a pair of coupled nonlinear reaction-diffusion equations of the form

$$\begin{aligned} u_t &= D_1 u_{xx} + F(u, v), \\ v_t &= D_2 v_{xx} + G(u, v), \end{aligned} \tag{1}$$

where D_1 and D_2 are positive constants, will be shown by numerical computation to possess solitary wave solutions which do not annihilate each other on collision: that is, the solitary waves display soliton-like behavior.

In their comprehensive review article, Scott, Chu, and McLaughlin [16] defined a soliton as a solitary wave which asymptotically maintains its shape and velocity after a collision with other solitary waves. Solitons which travel in the same direction as each other have been shown to exist by numerical computation for the Korteweg-deVries equation

$$u_t = -u_{xxx} - u u_x, \tag{2}$$

by Zabusky and Kruskal [21], and subsequently explicit expressions were obtained for two soliton solutions by Zabusky [20]. A scalar wave equation that admits of soliton solutions traveling in opposite directions is the Boussinesq equation

$$u_{tt} = u_{xx} + u_{xxxx} + 6(u^2)_{xx}. \tag{3}$$

Numerical evidence and analytic expressions for soliton solutions of this equation were found by Hirota [7].

Solitons have been associated with the inverse scattering method, pioneered by Gardner, Greene, Kruskal, and Miura [6] and subsequently generalized and extended by Lax [10] and Ablowitz, Kaup, Newell, and Segur [1]. Nonlinear evolution equations solvable by this method have been characterized by an infinite number of conservation laws. These do not appear to exist for nonlinear reaction-diffusion systems; thus soliton-like behavior in such systems had not been considered possible.

---

* Received by the editors March 7, 1979, and in final form December 3, 1979. The work was supported in part by the National Research Council of Canada under grants A4559 and A9259.

† Department of Biomathematics, School of Medicine, University of California, Los Angeles CA 90024.

A particularly well known example of a system of nonlinear reaction-diffusion equations is that of Hodgkin and Huxley [8],

$$V_t = DV_{xx} + \sum_i k_i g_i(V - V_i) + I(x, t), \tag{4}$$

where $V(x, t)$ is the depolarization of a nerve axon, D contains electrical constants, the V_i are equilibrium membrane potentials for various ions, the k_i are constants, $I(x, t)$ is the input current, and the g_i are the conductances for various ions which are obtained from the system of associated ordinary differential equations. This system possesses solitary wave solutions, but analysis is difficult, so that most studies have been numerical (see Cooley and Dodge [5], for example). Annihilation of solitary waves occurs when two such waves meet each other head on.

A simpler system of equations whose solutions mimic those of the Hodgkin-Huxley system was devised by Nagumo et al. [14]; it can be written as a coupled two-component reaction-diffusion system:

$$\begin{aligned} u_t &= Du_{xx} + u(u - a)(b - u) - cv, \\ v_t &= u, \end{aligned} \tag{5}$$

where a, b and c are positive constants. The system (5) shares with (4) the properties of possessing solitary wave solutions and annihilation of such waves on collision. For studies on the stability of traveling waves for this kind of system and use of singular perturbation theory, see the papers of Cohen [4], McKean [13], and Casten et al. [3].

Another solitary wave phenomenon from neurobiology is that of spreading cortical depression. This was discovered first in the rabbit brain by Leao [11] and is noticeable as a slowly moving (typically 3 mm/minute) wave of surface-negative potential. Subsequent experiments demonstrated concomitant changes in the membrane potentials of neurons and glial cells (see for example Sugaya et al. [17]), and more recently changes in the concentrations of the sodium, potassium, calcium and chloride ions in the extracellular space of the cortical tissue (Kraig & Nicholson [9], Nicholson et al. [15]). The interested reader may see the book by Bures et al. [2] for a wealth of experimental results and some preliminary theoretical studies on spreading depression.

A mathematical model for spreading depression has been devised [19]. The physiological basis of the model is briefly as follows. Potassium ions diffuse into a region of cortex and depolarize neuronal (and glial) membrane. Transmitter substance is released as calcium ions flow into specialized presynaptic membrane. The transmitter causes changes in conductance to potassium ions so that these are released and diffuse to the uninvaded cortex. The wave thus propagates, and in its wake the active transport mechanisms (pumps) return the ionic concentrations to their original levels. In this treatment we ignore some other sources of ions, such as action potentials, as it is known that spreading depression propagates without these when the cortical structure is treated with tetrodotoxin. The simplified model considers only the changes in potassium and calcium ions: the movements of sodium and chloride ions depend upon these former ions, and the fundamental phenomenon can be studied without them. The transmitter concentration does not appear explicitly in the final simplified model equations, which take the following form:

$$K_t^0 = D_1 K_{xx}^0 + k_1 g(V)(V - V_C)(V - V_K) - k_2(1 - \exp(-k_3(K^0 - K_R^0))) \tag{6a}$$

$$K_t^i = -k(k_1 g(V)(V - V_C)(V - V_K) - k_2(1 - \exp(-k_3(K^0 - K_R^0)))), \tag{6b}$$

$$C_t^0 = D_2 C_{xx}^0 + k_4 g(V)(V - V_C) + k_5(1 - \exp(-k_6(C^i - C_R^i))), \tag{6c}$$

$$C_t^i = -k(k_4 g(V)(V - V_C) + k_5(1 - \exp(-k_6(C^i - C_R^i)))), \tag{6d}$$

where K^0, K^i, C^0, C^i are the extracellular (outside) and intracellular concentrations of potassium and calcium ions, D_1 and D_2 are diffusion coefficients for the ions in the extracellular space, K_R^0 and C_R^i are the resting values of K^0 and C^i, and $k, k_1, \cdots, k_6$ are constants. The potentials V, V_K and V_C are respectively the membrane potential, the potassium equilibrium potential and the calcium equilibrium potential:

$$V = 58 \log_{10}((K^0 + k_7)/(K^i + k_8)), \tag{7a}$$

$$V_K = 58 \log_{10}(K^0/K^i), \tag{7b}$$

$$V_C = 29 \log_{10}(C^0/C^i), \tag{7c}$$

where k_7 and k_8 are additional constants. In addition, the function $g(V)$ represents the dependence of the calcium ion conductance on membrane potential and, based on available experimental evidence, is chosen as

$$g(V) = (1 + \tanh(k_9(V + V_T)))H(V - V^*), \tag{8}$$

where k_9 is a constant, V_T is a (constant) threshold type voltage and V^* is a (constant) cutoff voltage to ensure that the source terms become zero at and close to resting ion concentrations, H being the unit step function.

The reaction-diffusion system (6a)–(6d) has been integrated numerically with an initial stimulus consisting of a local elevation of extracellular potassium [19]. Two solitary traveling waves emerge from the stimulus, one moving to the left and one to the right. A collision between two solitary waves was observed for the reaction-diffusion system, and the end result was their mutual annihilation with an eventual return to resting levels for the two ions.

2. The two-component reaction-diffusion system. For reasons of computational efficiency, it was decided to first reduce the system to two equations whose solutions are practically identical to those of (6a)–(6d). As the solitary wave solutions of (6a)–(6d) pass through a region of space, the value of K^i changes only a little and, despite the diffusion of C^0, there is at any value of x an approximate conservation of total calcium. (In fact the solitary waves are not much different if $D_2 = 0$). Let $u(x, t)$ be the value of the extracellular potassium ion concentration, and regard the internal potassium ion concentration as fixed. This is equivalent to letting the intracellular space, which is much larger than the extracellular compartment, be infinite. Since k in (6b) is the ratio of the extracellular to intracellular volumes, this is the same as letting $k = 0$. Let $v(x, t)$ be the extracellular concentration of calcium ions, and let C_R^i be the resting value of intracellular calcium ion concentration. Then if calcium is conserved locally we have from (6d):

$$C^i(x, t) = C_R^i + k(C_R^0 - v(x, t)), \tag{9}$$

which enables the sink term in (6c) and V_C to be found from the value of v.

We now have a two-component reaction-diffusion system:

$$u_t = D_1 u_{xx} + F(u, v), \tag{10a}$$

$$v_t = D_2 v_{xx} + G(u, v), \tag{10b}$$

where

$$F(u, v) = c_1 g(V)(V - V_C)(V - V_K) - c_2(1 - \exp(-c_3(u - u_0))), \tag{11a}$$

$$G(u, v) = c_4 g(V)(V - V_C) + c_5(1 - \exp(-c_6(v_0 - v))), \tag{11b}$$

with $c_1, \cdots, c_6$ being constant and u_0, v_0 the resting values of u and v. We now have

$$V = V(u) = 58 \log_{10}((u + c_7)/c_8), \tag{12a}$$

$$V_K = V_K(u) = 58 \log_{10}(u/c_9), \tag{12b}$$

$$V_C = V_C(v) = 29 \log_{10}(v/c_{10} - kv)), \tag{12c}$$

where $c_7, \cdots, c_{10}$ are constants and k has the same meaning as before. The function

$$g(V) = g(V(u)) = (1 + \tanh(c_{11}(V(u) + V_T))), \tag{13}$$

is essentially unchanged and is multiplied by the step function $H(u - u^*)$.

Numerical solutions of the equations (10a) and (10b) were obtained with the values of the various parameters and constants shown in Table 1. The numerical scheme was a slight modification of Lees' adaptation of the Crank-Nicolson procedure [12], devised by Davis Cope and found to be very efficient for this kind of system. Solutions of (10a) and (10b) were found to be practically the same as those for K^0 and C^0 in the system (6a)–(6d). The overall space interval was (0, 1) with 100 equally spaced subintervals, and the time increments were .005. In the actual computations the sink term for u and the source term for v were multiplied by $H(u - u_0)$ and $H(v - v_0)$ respectively, which made the resting values more stable. The response was first computed to the following initial data:

TABLE 1
Values of parameters, system (10).

Parameter	Value	Parameter	Value	Parameter	Value
c_1	−.75	c_7	9	D_1	.0025
c_2	52	c_8	180	D_2	.00125
c_3	10	c_9	140	u_0	2
c_4	.075	c_{10}	.3	v_0	1
c_5	.52	c_{11}	.11	V_T	45
c_6	10	k	.25	u^*	2.2

$$u(x, 0) = u_0 + 8 \exp\left(-\left(\frac{x - .5}{.025}\right)^2\right), \tag{14a}$$

$$v(x, 0) = 1, \tag{14b}$$

i.e., a Gaussian type elevation of u (potassium) at the center of the interval. The boundary conditions employed were

$$u(0, t) = u(1, t) = u_0, \tag{15a}$$

$$v(0, t) = v(1, t) = v_0. \tag{15b}$$

Solitary waves consisting of an elevation of u (potassium ion concentration) and a depression of v (calcium ion concentration) emerged from the initial stimulus, one traveling to the left, the other to the right. These waves are sketched in Fig. 1. The constants c_1, c_2, c_4 and c_5 were chosen such that the total width of the solitary wave (of u and v) was about .1. The velocity of the waves in the system (10a) and (10b) is a spatial increment of .15 in one unit of time. Translated back to the velocity of spreading depression in brain structures, this corresponds to a velocity of about 1.4 mm/minute,

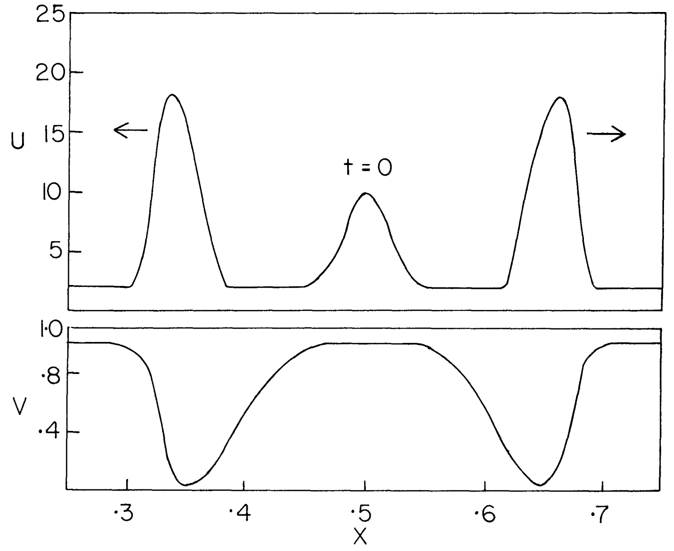

FIG. 1. *Solitary wave solutions of the two-component reaction-diffusion system* (10)–(13). *The initial data is shown consisting of a local elevation of u, with v at its resting level of* 1.0.

close to the experimental range of velocities. To see this, let the equation for $u(x, t)$ with x in cm and t in sec be

$$u_t = Du_{xx} + F(u, v), \tag{16}$$

where D is the actual diffusion coefficient for potassium ions in aqueous solution at about 2.5×10^{-5} cm^2/sec [19]. Now scale distance and time with $X = ax$ and $T = bt$, so that

$$u_T = (Da^2/b)u_{XX} + (F/b). \tag{17}$$

The value of b was set at .025 in order to make the rates of change of u and v about the same as in experimental reports. This gives, since the diffusion coefficient employed in the calculations was 2.5×10^{-3}, $a = (2.5)^{1/2}$. The actual velocity is thus $.15/(40 \times (2.5)^{1/2})$ cm/sec, which is the stated value. The two-component model described by equations (10), (11), (12) and (13) thus satisfactorily predicts the same wave forms and velocities as the original system.

To understand how the reaction-diffusion system gives rise to solitary waves, it is instructive to do two things. One is to plot the solitary wave trajectory (i.e., the set of (u, v) values at a given space point as a function of time as the solitary wave passes that space point) in the (u, v)-plane, and the other is to evaluate the source functions $F(u, v)$ and $G(u, v)$ at various parts of the (u, v)-plane that embrace the solitary wave trajectory. This is done in Fig. 2. The curves along which $F(u, v) = 0$ and $G(u, v) = 0$ are shown as dashed lines, and the regions are indicated where these functions are positive or negative. Note that on the v-axis are three linear scales: one between .01 and .05, one between .05 and .10 and a third between .1 and 1.0. The reason for this is to expand the small v values which are important for studying the collision of two solitary waves. The solitary wave trajectory is marked as a heavy line on Fig. 2, with arrows indicating the direction of increasing time.

The takeoff from the rest point R is through a region where $F < 0$ and $G > 0$, and since u is increasing and v is decreasing, the reason must be that $D_1 u_{xx}$ is positive and

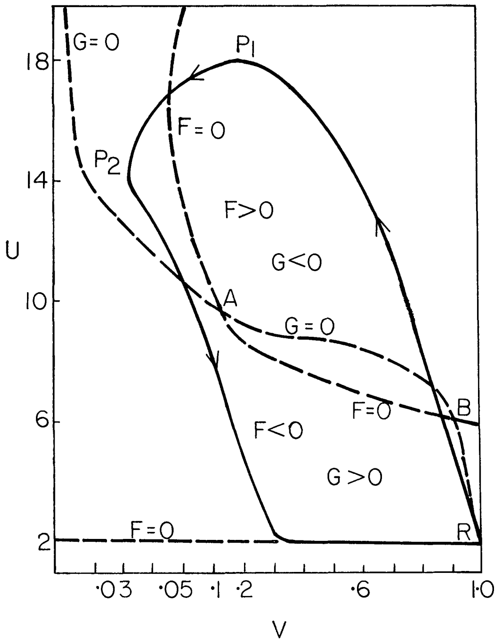

FIG. 2. *The heavy line marked with arrows is the solitary wave trajectory at fixed x. Regions where the source functions for u and v are negative and positive are indicated.*

D_2v_{xx} is negative as potassium (u) diffuses forward and calcium (v) diffuses backwards as the wave enters the region for the first time. The trajectory passes to the left of the equilibrium point $B(F=G=0)$, and swings upward into a region where $F>0$ and $G<0$, so that u increases as v decreases. The peak of the u-wave occurs at P_1 and, since at this point $F>0$, we must have $D_1u_{xx}<0$ at and just subsequent to the point P_1. Meanwhile G is still negative, so v continues to decrease and the trajectory is taken towards P_2, where $F<0$ and u is achieving its minimum value. Since at P_2, G is slightly negative and v begins to increase, D_2v_{xx} must be positive and responsible for the instigation of the recovery of v. Once the trajectory passes the curve $G=0$, it enters a region where $F<0$ and $G>0$, whereupon it swings downward and to the right. The value of u reaches 2 where $F=0$, but v has not yet returned to its resting value, which it does subsequently along $u=2$ where $G>0$. The trajectory thus ends up at R, the rest state.

It is noteworthy that the solitary wave trajectory narrowly misses the point A at which $F=G=0$. This point is presumably a stable equilibrium point for the corresponding ordinary differential equations (i.e. the system (10a) and (10b) with $D_1=D_2=0$), because when other computer runs were performed with not very different parameter values, waves were obtained with exceedingly long tails where (u, v) values did not return to resting values in the course of the computer run but stayed at or near the values of (u, v) at the point A.

3. Collision of solitary waves and modifications to $F(u, v)$ and $G(u, v)$ that give rise to non-annihilating pulses. The reaction-diffusion system defined by equations (10)–(13) has solitary waves which annihilate one another on collision. A collision between two such solitary waves is shown in Fig. 3. In order to observe a collision, symmetric (about $x=.5$) initial data consisting of two fully developed solitary waves traveling towards $x=.5$ were employed. The peaks of the u-waves were initially at

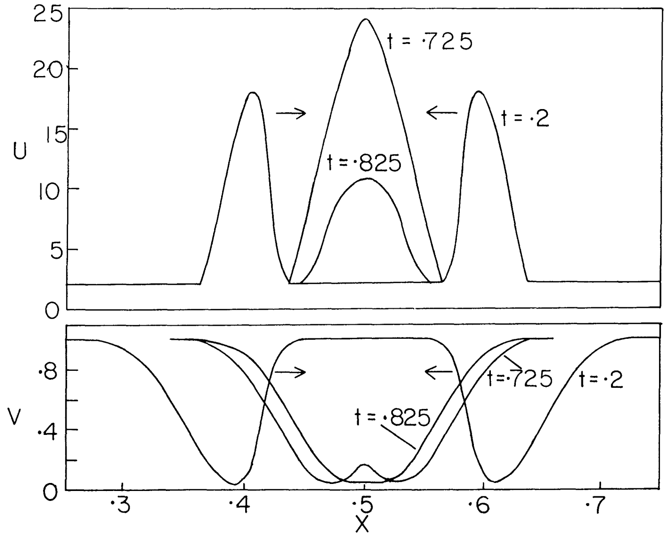

FIG. 3. *Collision of solitary waves in the system* (10)–(13). *At* $t = 0$ *the solitary waves were at* $x = .68$ *and* $x = .32$, *the collision taking place at about* $t = .650$. *The u waves have merged at* $t = .725$, *and the resultant envelope collapses down to the resting value* $u = 2$. *The v waves have also merged at* $t = .725$, *and eventually v returns to its resting value of* 1.0 *everywhere.*

$x = .38$ and $x = .62$. The same space grid, time increment and boundary conditions were employed as previously. The waves begin to interact at $t = .650$, and at $t = .725$ the u-waves have merged to form a profile which is larger than either solitary u-wave, the maximum value of u being 23.06. The profile for v at this time has a slight peak at $x = .5$ with a value of .158, dropping to .025 at $x = .5 \pm .03$ and then rising to achieve the resting value of 1.0 at $x = .5 \pm .16$. The u-profile subsequently falls so that at $t = .825$ its peak value (at $x = .5$) is 1.7, dropping to the rest value of 2 at $x = .5 \pm .06$. At this value of t the value of v at the collision center has begun its return to resting value. The u-profile has returned uniformly to $u = 2$ by about $t = .900$, whereas the v-profile does not return to the rest state ($v = 1$) uniformly in space until about $t = 1.25$ (actually at this t value, v at the collision center is .92).

It is of direct interest to plot the (u, v) pairs that arise as time progresses during the collision of the annihilating solitary waves. This is done for $x = .50, .50 \pm .02, .50 \pm .04$ and $x = .50 \pm .08$ in Fig. 4. Arrows on the various curves represent the direction of increasing time. It can be seen that the trajectory at distances greater than or equal to .08 from the center of the collision is practically indistinguishable from the solitary wave trajectory shown in Fig. 2. The collision trajectory at $x = .46$ and $x = .54$ is indistinguishable from the solitary wave trajectory until $u = 10$, $v = .07$ on the descending portion of the path, whereupon it ventures into a region of lower v-values for given values of u. At $x = .48$ and $x = .52$, closer to the collision center, the collision trajectory departs much sooner (relative to (u, v) pairs on the orbit) from the solitary wave trajectory, the separation being evident at $u = 13$, $v = .05$ on the ascending branch. The departure becomes more pronounced and the rest of the collision trajectory at these space points is quite distinct from the solitary wave trajectory until the return to the rest state along $u = 2$. At the center of the collision the trajectory is almost entirely distinct from the solitary wave orbit on both ascending and descending portions. This path goes to values of u much greater than those seen during the passage of the solitary wave, and on the descending part, values of v occur which are much smaller than in the solitary

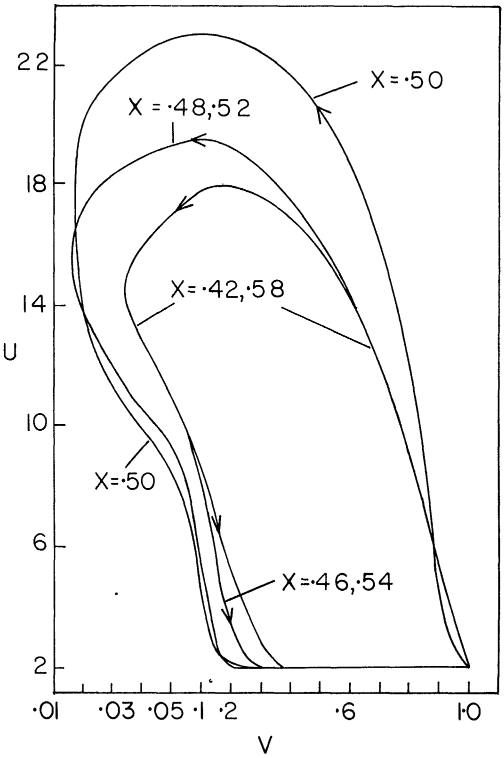

FIG. 4. *The trajectories at various space points in the collision of the solitary waves that annihilate each other on collision. The trajectory at* $x = .42$ *is indistinguishable from the solitary wave trajectory.*

wave. We thus find that during the collision, in the neighborhood of the collision center, solutions of this solitary wave system with annihilation traverse parts of the (u, v)-plane which are quite different from those on the solitary wave trajectory.

The latter observation suggest the possibility of non-annihilating solitary waves (solitons) in a reaction-diffusion system. The question to be answered was: If during the collision, values of (u, v) arise which are not on the solitary wave trajectory, is it possible to change $F(u, v)$ and $G(u, v)$ at those points in such a way that when the solitary waves collide, instead of a mutual annihilation, a rearrangement occurs such that two solitary waves are emitted after the collision? It seems that it is possible to accomplish this with only a few changes to F and G.

It was noted that at $t = .825$, in the collision, $u(x, t)$ was very similar in appearance to the $u(x, 0)$ of equation (14a). The (u, v) values at this time were (10.7, .0338), (10.4, .0375), (9.3, .0536), (7.1, .0998), (3.8, .1934) and (2.3, .3206) at $x = .5$, $.5 \pm .01$, $.5 \pm .02$, $.5 \pm .04$ and $.5 \pm .05$ respectively. These (u, v) values did not arise at or near the solitary wave trajectory. The values of (u, v) which arose just subsequently ($t = .850$) were noted, and estimates were made of the time derivatives of u and v at each space point in the interval $.46 \times .54$ on the numerical grid for (10)–(13). The aim was now to adjust the source functions off the solitary wave trajectory but on the collision trajectories, in order to hold $u(x, t)$ about where it was at $t = .825$ and to elevate $v(x, t)$ from its value at $t = .825$. Hence at parts of the (u, v)-plane which embraced the (u, v) values at $t = .825$ and $.45 \leqq x \leqq .55$, the functions $F(u, v)$ and

$G(u, v)$ were changed so that the reaction-diffusion system became

$$u_t = D_1 u_{xx} + F_1(u, v), \tag{18a}$$

$$v_t = D_2 v_{xx} + G_1(u, v), \tag{18b}$$

$$F_1(u, v) = F(u, v) + \sum_{i=1}^{6} a_i I_{A_i}(u, v), \tag{18c}$$

$$G_1(u, v) = G(u, v) + \sum_{i=1}^{6} b_i I_{A_i}(u, v); \tag{18d}$$

here I_A is the indicator function of the set A, defined through

$$I_A(u, v) = \begin{cases} 1, & (u, v) \in A, \\ 0, & (u\,v) \notin A, \end{cases} \tag{19}$$

the sets A_i being

$$A_i = \{(u, v) | u \in (u_i^1, u_i^2), v \in (v_i^1, v_i^2)\}, \tag{20}$$

and the a_i and b_i being constants. Specific values are shown in Table 2.

TABLE 2

Values of parameters, system (18).

Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value
a_1	100	b_1	84	u_1^1	10.6	u_2^1	10.2	v_1^1	.0320	v_2^1	.0360
a_2	108	b_2	82	u_1^2	10.8	u_2^2	10.5	v_1^2	.0350	v_2^2	.0390
a_3	120	b_3	78	u_1^3	9.1	u_2^3	9.5	v_1^3	.0510	v_2^3	.0560
a_4	124	b_4	73	u_1^4	6.8	u_2^4	7.2	v_1^4	.0975	v_2^4	.1025
a_5	60	b_5	68	u_1^5	3.5	u_2^5	3.9	v_1^5	.1900	v_2^5	.1950
a_6	5.2	b_6	62	u_1^6	2.2	u_2^6	2.4	v_1^6	.3150	v_2^6	.3250

With solitary wave as initial data the computation was performed again. Because on the solitary wave trajectory $F(u, v) = F_1(u, v)$ and $G(u, v) = G_1(u, v)$, the solitary waves propagated unaltered to the center of the interval and collided. The collision profiles for the systems (18) and (10) are of course identical until $t = .825$, but differ thereafter. For (18) the profiles of u and v at $t = .850$ are sketched in Fig. 5. After $t = .850$ the u and v profiles for (18) returned eventually to their resting values, so (18) did not have solitons. It was noted that the (u, v) values at $t = .850$ in the collision region for (18) are (14.2, .3869), (13.4, .3961), (1.9, .4430) and (6.8, .9462) at $x = .5, .5 \pm .01$, $.5 \pm .02$ and $.5 \pm .03$ respectively. These pairs of values did not occur at or near the solitary wave trajectory. The (u, v) values that arose at $t = .875$ for (18) for the values of x at and around the collision center were used to estimate the time derivatives of u and v. The aim was again to try, by changing the source functions off the solitary wave trajectory, to approximately restore the initial conditions that would lead to the emission of two solitary waves after the interaction. This leads to the system of equations

$$u_t = D_1 u_{xx} + F^*(u, v), \tag{21a}$$

$$v_t = D_2 v_{xx} + G^*(u, v), \tag{21b}$$

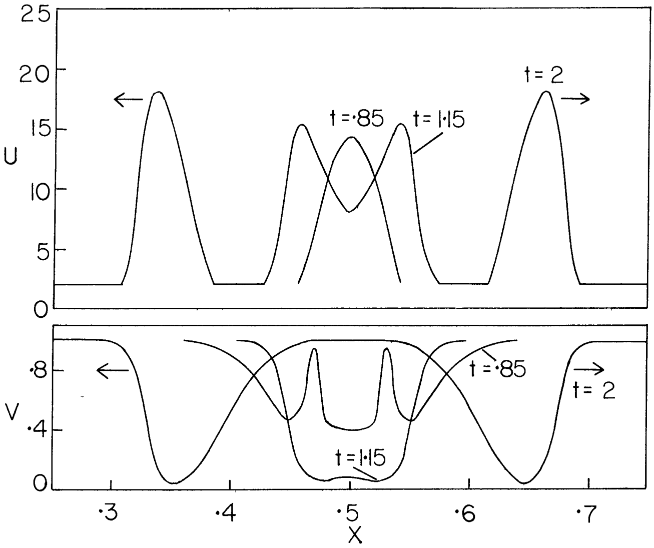

FIG. 5. *The result of a collision of solitary waves in the reaction-diffusion system* (21). *Until* $t=.825$ *the solutions are as in Figure* 3. *By* $t=2$ *two fully developed solitary waves are seen traveling outward from the collision with the same shapes and speed as the incident waves.*

where the new source functions are

$$F^*(u,v)=F_1(u,v)+\sum_{i=7}^{10} a_i I_{A_i}(u,v), \tag{22a}$$

$$G^*(u,v)=G_1(u,v)+\sum_{i=7}^{10} b_i I_{A_i}(u,v), \tag{22b}$$

with values as shown in Table 3.

TABLE 3
Values of parameters, system (21).

Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value
a_7	−120	b_7	65	u_1^7	13.9	u_2^7	14.5	v_1^7	.3750	v_2^7	.3900
a_8	−120	b_8	65	u_1^8	13.2	u_2^8	13.6	v_1^8	.3900	v_2^8	.4000
a_9	−120	b_9	65	u_1^9	10.7	u_2^9	11.2	v_1^9	.4100	v_2^9	.4500
a_{10}	20	b_{10}	65	u_1^{10}	6.4	u_2^{10}	6.9	v_1^{10}	.4700	v_2^{10}	.4950

The original solitary waves were again employed as initial data for the new system (21). Since $F^*(u,v)=F(u,v)$ and $G^*(u,v)=G(u,v)$ on the solitary wave trajectory, the solitary waves propagated unaltered in shape to the center of the interval. At $t=.825$ the systems (10), (18) and (21) have the same u and v profiles, and at $t=.850$ the systems (18) and (21) have the same u and v profiles. Unlike the system (18), however, in the system (21) subsequent to $t=.850$ solitary waves began to form just outside the collision center, and propagated outward with the same shapes as the initially colliding waves. These are sketched in Fig. 5. The system (21) thus appears to have soliton-like solutions. The original aim of restoring the initial data was not achieved, but this was no longer necessary because the solitary waves had (somewhat amazingly) come out of the collision in the system (21).

Since the source functions have been tampered with, the question now arises, whether the system (21) would give solitary waves in response to the initial values of (14a) and (14b). To check this, the reaction-diffusion system (21) was integrated numerically with the initial data (14a) and (14b). The result consisted of two solitary waves of the same shapes and speed as those found for (10) traveling to the right and left from the initial stimulus. Hence the system (21) has, based on numerical computations, (a) solitary waves in response to a local elevation of u and (b) solitary waves emerging from the collision of two solitary waves (solitons).

It is of interest to examine the trajectories in the (u, v)-plane at those space points in the collision region for the system (21) and to compare them with those for the system (10). The set of (u, v) values that occur at $x = .50$ during the collision of the solitons is shown in Fig. 6. The trajectory is the same as in Fig. 4 at $x = .5$ until the system 'sees' the new source functions around the point A. The dashed line in Fig. 6 shows the trajectory for the original system (10) after passing by the point A. The solid line emerging from near A is for (21), and it can be seen that the path loops around and crosses previous parts of the trajectory. It misses the point A the second time around, and returns to the resting values, meanwhile having contributed to the emergence of two solitary waves from the collision. That the trajectory crosses itself may seem curious. Apparently at the points of intersection the (u, v) values at neighboring x are different on the intersecting paths, so that even though the source functions have the same values, the contributions to the time derivatives of u and v from the second space derivatives are different, so the

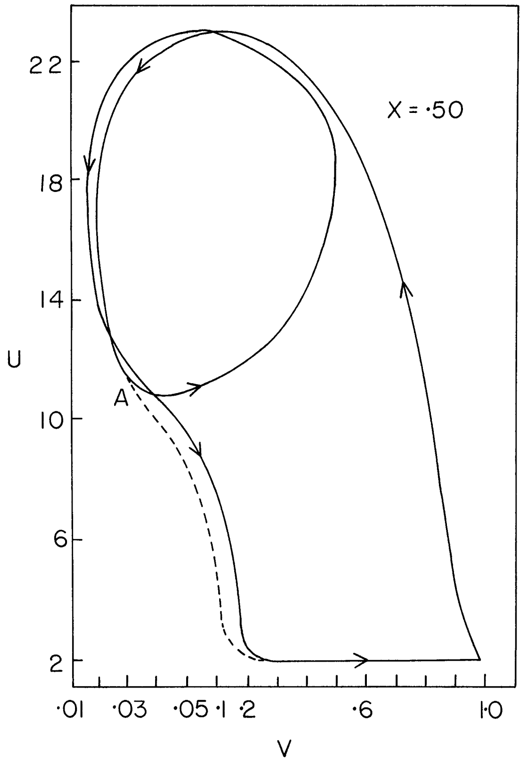

FIG. 6. *The trajectory at* $x = .5$ *in the system* (21) *which apparently has soliton-like solutions. The dashed line is the corresponding trajectory in the system* (10).

directions of motion are also different at the points of intersection. The collision trajectories for (21) for other values of x near the collision center differ from those of (10) in a similar way to that at $x = .5$, in that they loop around and then return to resting values. They are not shown in the figure to avoid overcrowding.

It seems important to consider the way in which the trajectory at $x = .5$ for (21) misses the little rectangle $\{(u, v)|u \in (10.2, 10{,}5),\ v \in (.0360, .0390)\}$ near the point A, after it has looped around and intersected itself. That this rectangle was missed the second time around cannot be due to numerical error, because the accuracy of the methods used here excludes this possibility. Furthermore, the rectangle can be made as small as one pleases as long as it contains the point (10.7, .0338) so that if the diffusion contributions on each visit near A are only slightly different the behavior that gives rise to solitons will be preserved. It might be thought that one could check the existence of solitons by making the grid of space and time points finer in the numerical solution of the reaction-diffusion equations. This would not be the case, however, because one would simply need to increase the number of terms in the sums that occur in the modified source functions F^* and G^*. The problem remains, however, that in a continuous system of trajectories which loop around on themselves, it may not be possible for all the infinitesimal rectangles to be missed on the second time around in the trajectories near the collision center.

However, the way in which solitons were found here is clearly only one of a large number of ways. In particular, it was not accomplished in the way initially intended: to achieve soliton solutions by restoring approximately the initial data (locally elevated u, v at about resting level). On the way to doing so the non-annihilating pulses appeared somewhat unexpectedly.

There is thus some evidence that soliton-like behavior may occur in a reaction-diffusion system whose form is (10) with source functions depending *only* on the components of the system, and not, for example, on the first space derivatives of the components. It can be concluded that "solitons" exist in the discrete system which is employed to numerically compute solutions of the system (21). It may also be stated that the evidence for the existence of "solitons" in a reaction-diffusion system is as strong as the evidence that the system (10) or (21) has stable traveling solitary waves, because the same numerical techniques were used to compute them. As is clear, however, it is not possible to prove by numerical computation that either solitary waves of "solitons" exist in the continuous systems, but only to obtain evidence for their existence. The aim of this investigation was to show that "solitons" could exist for a reaction-diffusion system when solutions were numerically computed, and this has been achieved. It is hoped that analysis will be performed to either reject or support the evidence presented here.

On the way to attaining the apparent "solitons", a curious phenomenon was observed which may be of some significance, especially if the solitary waves correspond to particles of some kind. The computer run just prior to that which gave "solitons" had a slight error in the initial data. The error was at one point on the space grid, in that the value of $v(x, 0)$ was not quite the same as at $v(1-x, 0)$. For this run, two solitary waves propagated towards the center of the interval but only one came out. Thus, with slightly asymmetric initial data, a collision occurred in which one wave (particle) more or less destroyed the other and continued to propagate after the collision.

Acknowledgments. It is a pleasure to thank Davis Cope for many fruitful discussions, and for providing the computer programs for numerically solving the reaction-diffusion systems. Thanks are also due to Betty K. Lang for technical assistance. A preliminary report on this work has appeared [18]. This work was done while the author was at the University of British Columbia, and was supported in part by the National Research Council of Canada under grants A 4559 and A 9259.

REFERENCES

[1] M. J. Ablowitz, D. J. Kaup, A. C. Newell and H. Segur, *The inverse scattering transform-Fourier analysis for nonlinear problems*, Studies in Appl. Math., 53 (1974), pp. 249–315.

[2] J. Bures, O. Buresova and J. Krivanek, *The Mechanism and Application of Leao's Spreading Depression of Electroencephalographic Activity*, Academic Press, New York, 1974.

[3] R. C. Casten, H. Cohen and P. Lagerstrom, *Perturbation analysis of an approximation to the Hodgkin-Huxley theory*, Quart. of Appl. Math., 32 (1975), pp. 365–402.

[4] H. Cohen, *Nonlinear diffusion problems*, Studies in Math., 7 (1971), pp. 27–64.

[5] J. W. Cooley and F. A. Dodge, Jr., *Digital computer solutions for excitation and propagation of the nerve impulse*, Biophys. J., 6 (1966), pp. 583–599.

[6] C. S. Gardner, J. M. Greene, M. D. Kruskal and R. M. Miura, *Method for solving the Korteweg-de Vries equation*, Phys. Rev. Lett., 19 (1967), pp. 1095–1097.

[7] R. Hirota, *Exact N-soliton solution of the wave equation of long waves in shallow-water and in nonlinear lattices*, J. Math. Phys., 14 (1973), pp. 810–815.

[8] A. L. Hodgkin and A. F. Huxley, *A quantitative description of membrane current and its application to conduction and excitation in nerve*, J. Physiol. (Lond.), 117 (1952), pp. 500–544.

[9] R. P. Kraig and C. Nicholson, *Sodium changes: account for electrolyte shifts of spreading depression*, Soc. Neurosci. Abstract, No. 1437, Toronto (1976).

[10] P. D. Lax, *Integrals of nonlinear equations of evolution and solitary waves*, Commun. Pure Appl. Math., 21 (1968), pp. 467–490.

[11] A. Leao, *Spreading depression of activity in the cerebral cortex*, J. Neurophysiol., 7 (1944), pp. 359–390.

[12] M. Lees, in *Numerical Solution of Partial Differential Equations*, W. F. Ames, ed., Barnes and Noble, New York, 1969, p. 193.

[13] H. McKean, *Nagumo's equations*, Advances in Math., 4 (1970), pp. 209–223.

[14] J. Nagumo, S. Arimoto and S. Yoshizawa, *An active pulse transmission line simulating nerve axon*, Proc. IRE, 50 (1962), pp. 2061–2070.

[15] C. Nicholson, G. Ten Bruggencate, R. Steinberg and H. Stuckle, *Calcium modulation in brain extracellular microenvironment demonstrated with ion-selective micropipette*, Proc. Nat. Acad. Sci., 74 (1977), pp. 1287–1290.

[16] A. C. Scott, F. Y. F. Chu and D. W. McLaughlin, *The soliton: a new concept in applied science*, Proc. IEEE, 61 (1973), pp. 1443–1483.

[17] E. Sugaya, M. Takato and Y. Noda, *Neuronal and glial activity during spreading depression in cerebral cortex of cat*, J. Neurophysiol., 38 (1975), pp. 822–841.

[18] H. C. Tuckwell, *Solitons in a reaction-diffusion system*, Science, 205 (1979), pp. 493–495.

[19] H. C. Tuckwell and R. M. Miura, *A mathematical model for spreading cortical depression*, Biophys. J., 23 (1978), pp. 257–276.

[19a] H. C. Tuckwell, *Predictions and properties of a model of potassium and calcium ion movements during spreading cortical depression*, Int. J. Neurosci., 10 (1980), pp. 145–164.

[20] N. J. Zabusky, *Solitons and bound states of the time-independent Schrodinger equation*, Phys. Rev., 168 (1968), pp. 124–128.

[21] N. J. Zabusky and M. D. Kruskal, *Interaction of "solitons" in a collisionless plasma and the recurrence of initial states*, Phys. Rev. Lett., 15 (1965), pp. 240–243.