Large Amplitude Stationary Waves in an Excitable Lateral-Inhibitory Medium

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LARGE AMPLITUDE STATIONARY WAVES IN AN EXCITABLE LATERAL-INHIBITORY MEDIUM*

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Abstract. Pattern formation in a system of reaction-diffusion equations which exhibit both lateral inhibition and excitability is investigated. The system studied is derived from the FitzHugh–Nagumo nerve conduction model. The existence of solitary and periodic stationary wave solutions is proved. Numerical computations show that some of these waves are stable as solutions of the partial differential equations. Further, arguments are given which indicate that these patterns arise as a result of excitability of the system and not as a result of a Turing mechanism.

1. Introduction. One of the most important problems in developmental biology is to determine the mechanisms responsible for pattern formation. In the early 1950's, two landmark papers were published on this topic. The first of these consists of the celebrated Hodgkin–Huxley model of nerve conduction. The Hodgkin–Huxley equations describe the formation and propagation of an electrical impulse along the nerve axon. At about this same time, Turing [10] was investigating the formation of stationary, nonpropagating patterns. He considered a physical system whose temporal component has a stable equilibrium state. Under the proper conditions he showed that the effects of introducing diffusion into the system can destabilize the steady state and lead to the formation of stationary spatial patterns. That is, in an appropriate class of reaction-diffusion equations, as one of the diffusion coefficients passes through a critical value, the steady state loses stability and there occurs a bifurcation of small amplitude stationary wave solutions.

In this paper we investigate a mechanism for pattern formation in a system of reaction-diffusion models which is substantially different from that considered by Turing. Briefly, we consider a two variable system in which u is considered to be an activator and w acts as its inhibitor. By calling u an activator we mean that u is autocatalytically involved in its own production. Similarly, the inhibitor w causes a decrease in the production of u. Next, we assume that the system is excitable. That is, there is a globally attracting steady state, (u_0, w_0), as well as a threshold of excitation. With these basic assumptions in mind we first consider the case in which the rate of diffusion of w is negligible relative to that of u. Then a local perturbation in u which exceeds threshold can grow into a large peak. Subsequently, this large excursion in u quickly spreads to neighboring regions, triggering them to undergo a large excursion in u. In this way, a wave of u can form and propagate through the medium. As explained by Hodgkin and Huxley [4], this mechanism is responsible for the formation and propagation of nerve impulses. Suppose, however, that the rate of diffusion of w is large relative to that of u. Again, a local perturbation in u which exceeds threshold can form into a large, local peak. However, this peak may be prevented from propagating due to the rapid diffusion of the inhibitor w into the surrounding region. This mechanism, popularly known as "lateral inhibition," has been proposed by Meinhardt [7], and Gierer and Meinhardt [3] as possibly playing a role in the formation of complex

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linear structures such as blood vessels, leaf veins and dendrites of nerve cells. It has been suggested that lateral inhibition may also contribute to pattern formation in plankton populations [8], the budding of hydra and yeast [3], and the formation of localized peaks of electrical activity in neural net models for short term memory [1].

In this paper we study a prototype model which exhibits both lateral inhibition and excitability. This model consists of an extension of the FitzHugh–Nagumo [9] equations, namely

$$u_t = u_{xx} + u(1-u)(u-a) - w, \qquad (1)$$
$$w_t = Dw_{xx} + \varepsilon(u - \gamma w)$$

where $u, w \in R$, $t \geqq 0$, $-\infty < x < \infty$, $D \geqq 0$, $\varepsilon > 0$, $\gamma > 0$, and $0 < a < 1/2$.

Our main goal is to investigate (1) for the existence and stability of stationary spatial patterns. To ensure that equations (1) have a unique equilibrium solution we assume that $0 < \gamma < \gamma_1$ where $1/\gamma_1 > \max_{u>0}(u-a)(1-u)$. Further, if we take $\varepsilon > 0$ to be small, then the point $(u, w) = (a, 0)$ acts as a threshold of excitation in the kinetic system

$$u_t = u(1-u)(u-a) - w, \qquad (2)$$
$$w_t = \varepsilon(u - \gamma w).$$

That is, if we keep $w(0) = 0$ (the resting level of w) and let $u(0) > 0$, then the following occurs:

(i) if $0 < u(0) < a$ and $\varepsilon > 0$ is small, then (u, w) decays to rest (possibly with damped oscillations),

(ii) if $a < u(0) < 1$ and $\varepsilon > 0$ is small, then u quickly approaches a peak value near $u = 1$ followed by the return of the solution to rest.

In § 2 we describe our main results and state two theorems concerning the existence of periodic and nonperiodic stationary wave solutions of Eqs. (1). We discuss numerical computations which suggest that some of these solutions are stable.

The proofs of our theorems are found in §§ 3 and 4.

2. Statement of main results. Stationary waves are time independent solutions of (1). Therefore we set $u_t \equiv 0$ and $w_t \equiv 0$, and consider the system

$$u'' + f(u) - w = 0, \qquad Dw'' + \varepsilon(u - \gamma w) = 0 \qquad (3)$$

where $' \equiv d/dx$, $f(u) = u(1-u)(u-a)$ and $0 < a < \frac{1}{2}$. Lateral inhibition requires that we take $D > 0$ to be large. Since the kinetic equations (2) are excitable, we also assume that $\varepsilon > 0$ is small. Recall that we let $0 < \gamma < \gamma_1$ in order to guarantee that (2) and (3) have a unique equilibrium solution.

It is convenient to require that solutions satisfy the initial condition

$$u'(0) = w'(0) = 0. \qquad (4)$$

From (3) and the transformation $\hat{x} = -x$ it follows that solutions which satisfy (4) are symmetric about the origin $x = 0$. Thus, condition (4) greatly simplifies our investigations since it allows us to restrict both our mathematical proofs and numerical computations to the interval $0 \leqq x < \infty$.

In our first theorem we describe stationary wave solutions which tend to equilibrium at $\pm\infty$.

THEOREM 1. *Let $\gamma \in (0, \gamma_1)$. If $\varepsilon/D > 0$ is sufficiently small, then the problem* (3)–(4) *has at least two nonconstant, bounded solutions each of which satisfies the following*:

(i) $\lim_{|x|\to\infty}(u, u', w, w') = (0, 0, 0, 0)$;

(ii) *$u(x)$ and $w(x)$ have exactly one relative maximum on* $(-\infty, \infty)$ *which occurs at* $x = 0$.

Our second main result concerns the existence of periodic stationary wave solutions.

THEOREM 2. *Let* $0 < \gamma < \gamma_1$. *If* $\varepsilon / D > 0$ *is sufficiently small, then the problem* (3)–(4) *has a continuum of periodic solutions.*

Discussion of results. At this point we find it illuminating to discuss numerical results which indicate the stability properties of solutions found in Theorems 1 and 2. That is, we determine classes of initial data for (1) which evolve (as $t \to +\infty$) either into a periodic or a solitary stationary wave. For these simulations we use the collocation solver PDECOL [6] which solves a general system of nonlinear parabolic partial differential equations in time and one space dimension. All computations were done on the University of Pittsburgh DEC-10 computer.

For ease of computation (i.e. minimal cost and maximal speed per run) we split the effects of D and ε by the scaling $x = sD^{1/2}$, and solve the system

$$u_t = \frac{1}{D} u_{ss} + f(u) - w, \qquad w_t = w_{ss} + \varepsilon(u - \gamma w). \tag{5}$$

By way of example, we let $a = .25$ and $\gamma = .1$. For these values there is a unique equilibrium solution, $(u, w) = (0, 0)$. To reflect lateral inhibition we let $D = 10^2$ and $\varepsilon = 10^{-2}$.

All of our computations are restricted to the interval $0 \leqq s \leqq 28$ with Neuman boundary conditions at each end. The grid size was $\Delta s = 0.1$ so that the entire interval was broken into 280 points. In most simulations we set $w(s, 0) \equiv 0$ for $s \in [0, 28]$, and $u(s, 0) \equiv 0$ on $[0, 28]$ except for a small subinterval where $u(s, 0) \equiv 0.65 > a$, the threshold. These perturbations evolve into stationary solutions on the finite interval $[0, 28]$. By symmetry, we can extend these to periodic solutions on the whole line. An isolated pulse peak centered at $s = 0$ was considered to represent the solitary pulse although the domain was only finite. Earlier numerical investigations indicate that for other domain sizes, this isolated solution still exists.

In Figs. 1, 2 and 3 we follow the evolution of a single square impulse as $t \to \infty$. Figure 1 shows initial data consisting of two square impulses centered at $s = \pm 5.5$ and

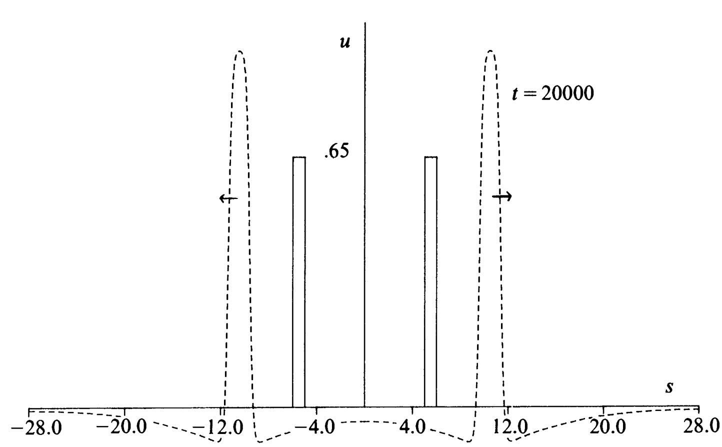

FIG. 1. *Initial perturbation is* $w(s, 0) \equiv 0$, *and* $u(s, 0) \equiv 0$ *on* $[-28, 28]$ *except for the intervals* $[-6, -5]$ *and* $[5, 6]$ *where* $u(s, 0) \equiv .65$. *Dotted curve denotes the evolution of the initial condition into a wave after* $t = 20{,}000$ *time steps.*

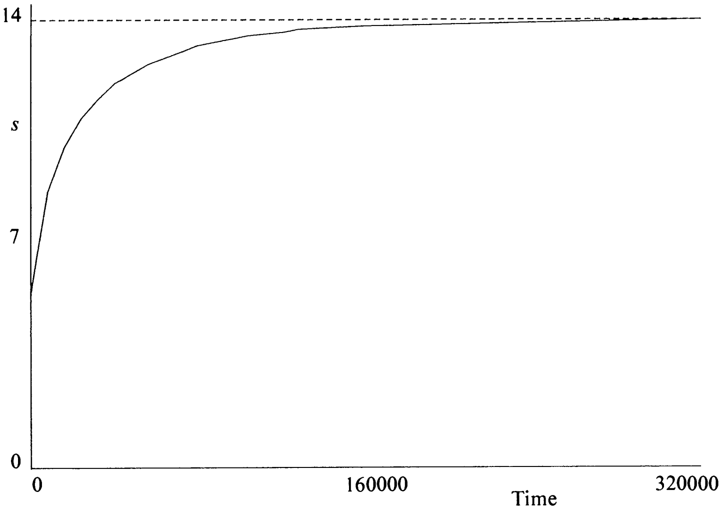

FIG. 2. *Given $t > 0$, $s(t)$ denotes the positive value at which the wave has a peak* (*e.g.* $s(20{,}000) = 11.4$). *Numerical experiments show that $s \to 14.0$ at $t \to \infty$ and the stationary periodic wave has formed.*

having width $\Delta s = 1$. As t increases, the initial data evolves into a large amplitude solution with two peaks. After 20,000 time steps the peaks have spread out and are centered at $s = \pm 11.4$. However, the peaks continue their slow movement for still larger values of t. Thus, in Fig. 2, we compute the positive value s at which the peak occurs as a function of t and find that $\dot{s}(t) > 0$ for all $t > 0$, and it appears that $\lim_{t\to\infty} s(t) = 14$. (Similarly, the negative s value at which a peak occurs satisfies $\dot{s} < 0$ for all $t > 0$, with $\lim_{t\to\infty} s(t) = -14$.) In Fig. 3, the solution has ultimately evolved into a large amplitude stationary wave which is periodic in s with period 28. This is a two peak periodic solution on a finite domain. But if we identify the endpoint $s = -28$ with the point $s = +28$, we see that the peaks are actually periodic with period 28. In this manner we can patch together these solutions to obtain a solution on the infinite line. Our results, however, tell us nothing of the stability of this solution in the infinite domain. Furthermore, we conjecture that such a periodic solution could only evolve from initial data which was infinite in extent.

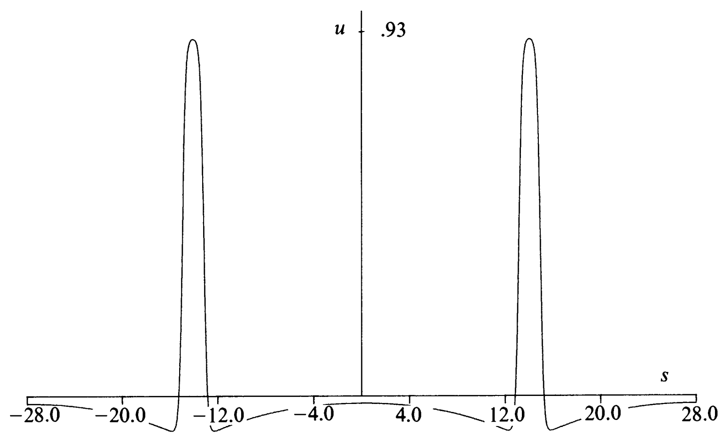

FIG. 3. *After* 36,000 *time steps the wave solution shown in Fig.* 1 *evolves into a two peak periodic solution as $t \to \infty$, with peaks at $s = \pm 14$.*

Figures 4 and 5 show that there are other large amplitude, stable, periodic stationary wave solutions with periods $18\frac{2}{3}$ and 14. (See figure legends for further details.) That we can find "periodic" solutions of these particular periods is not at all surprising when one takes into account that we have proven the existence of a continuum of solutions. That is, for any sufficiently large number, P, there is a solution to (3)–(4) which has period P. We have found solutions of period 28, $18\frac{2}{3}$, and 14 numerically, representing 56/2, 56/3 and 56/4 periodic solutions.

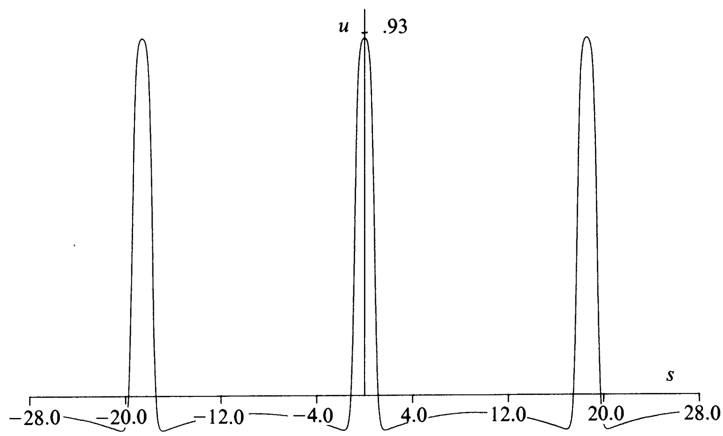

FIG. 4. *Initial conditions* $w(s,0)\equiv 0$ *on* $[-28,28]$, *and* $u(s,0)\equiv 0$ *on* $[-28,28]$ *except on the intervals* $[-16,-15]\cup[-1,1]\cup[15,16]$ *where* $u(s,0)\equiv .65$. *This initial perturbation evolves into a three-peak periodic stationary wave as t increases, with period* $t=18\frac{2}{3}$.

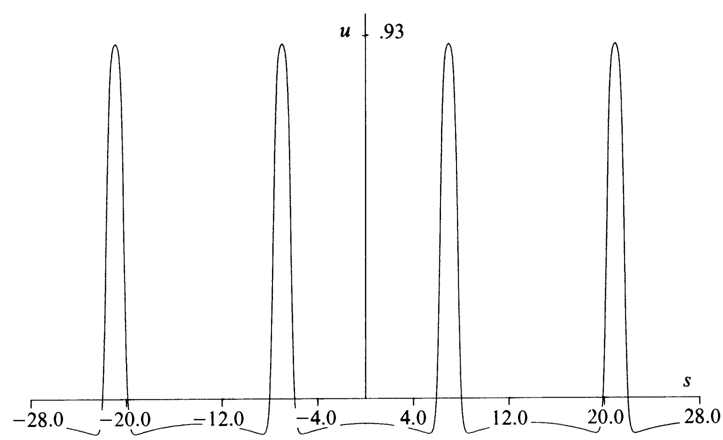

FIG. 5. *Initial conditions* $w(s,0)\equiv 0$ *on* $[-28,28]$, *and* $u(s,0)\equiv 0$ *on* $[-28,28]$ *except on the intervals* $[-21,-20]\cup[-11.5,-10.5]\cup[10.5,11.5]\cup[20,21]$ *where* $u(s,0)\equiv .65$. *The initial perturbation grows into a four-peak periodic stationary wave as t increases, with period* $t=14$.

In Fig. 6 a single square impulse of width 1 unit and centered at $s=0$ has evolved into a large amplitude solitary stationary wave solution.

Our numerical computations indicate that over a fixed spatial interval and parameter set, (5) have a unique, stable, stationary wave which tends to equilibrium as $x\to\pm\infty$. All other stable patterns are periodic and there are only a finite number of these solutions. However, as D increases, the number of stable periodic solutions increases, their amplitudes remain constant, and the width at the base of each peak

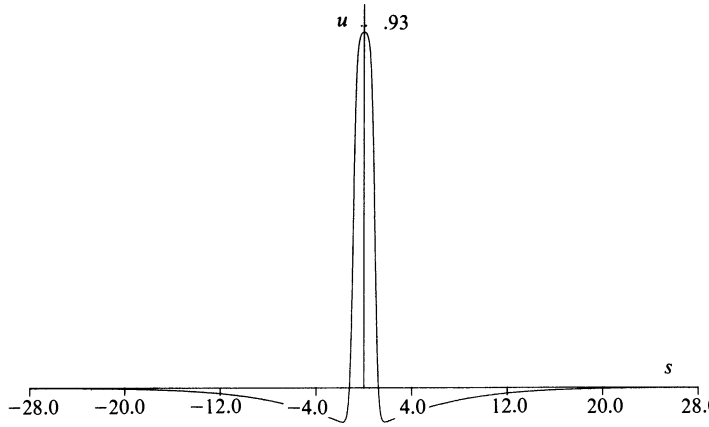

FIG. 6. *Initial conditions* $w(s, 0) \equiv 0$ *on* $[-28, 28]$ *and* $u(s, 0) \equiv 0$ *on* $[-28, 28]$ *except on the interval* $[-1, 1]$ *where* $u(s, 0) \equiv .65$. *This perturbation evolves into a single peak stationary pulse solution as t increases.*

narrows. If we extend the domain to $\pm\infty$, then it is possible that there is a continuum of periodic solutions. This is a problem for further study. Another interesting problem is to determine whether there are stable stationary wave solutions which do not satisfy these conditions. Such solutions would be "nonsymmetric".

3. Proofs. The proofs of our two theorems rely on a shooting method which in turn relies on a functional derived from (3). Thus, we subdivide this section into three parts. First, we develop the mathematical properties of the functional. Following that we give an outline of the shooting method, and then proceed with the final details of the proofs.

Consider the functional

$$P = (u')^2 - \frac{D(w')^2}{\varepsilon} + Q(u, u) \tag{6}$$

where

$$Q(u, w) \equiv \gamma w^2 + 2F(u) - 2uw \tag{7}$$

and

$$F(u) \equiv \int_0^u f(s)\, ds. \tag{8}$$

It easily follows from (3) that $P' \equiv 0$ along solutions. Therefore, $P \equiv c$ where c is a constant. Since we assume that $u'(0) = w'(0) = 0$, it follows that

$$Q(u(0), w(0)) = c. \tag{9}$$

In Theorem 1 we seek solutions which tend to $(u, w) = (0, 0)$ as $x \to \infty$. Therefore, such solutions remain on the surface $P \equiv 0$ and, from condition (4), $(u(0), w(0))$ must satisfy

$$Q(u(0), w(0)) = 0. \tag{10}$$

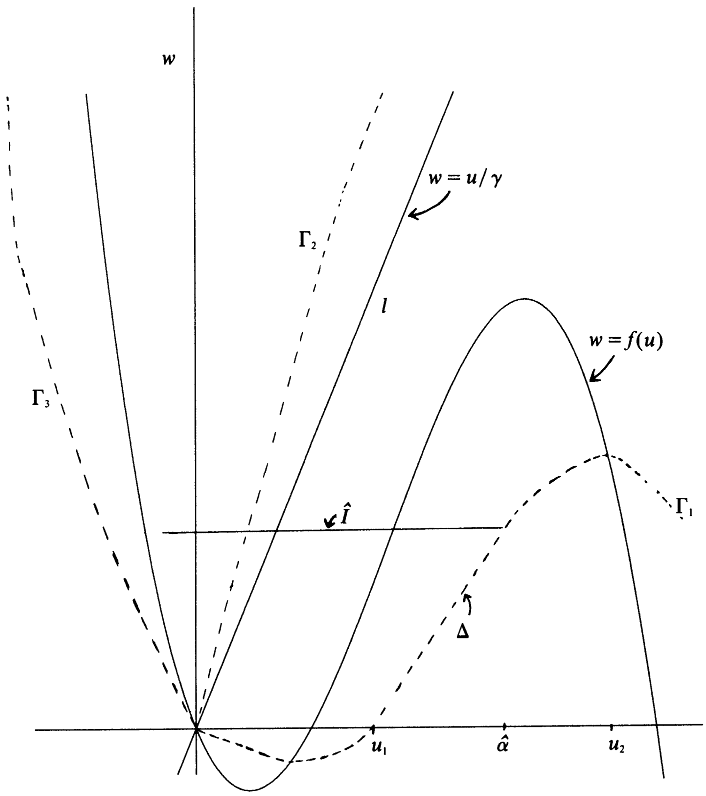

FIG. 7. *The dotted curves* $\Gamma_1, \Gamma_2, \Gamma_3$ *represent solutions of the equation* $Q(u, w)=0$. *For* $\varepsilon=0$ *and* $w\equiv\hat{w}$, *the solution of* (11) *with* $u(0)=\hat{\alpha}$, *is periodic and its trajectory projected onto the* (u, w) *plane is represented by the line segment* $\hat{l}$.

The solutions of (10) consist of the four sets (see Fig. 7)

$$\Gamma_1=\left\{(u, w)\,|\,u\geqq 0,\ w=g_1(u)\equiv\frac{u}{\gamma}+\frac{1}{\gamma}(u^2-2\gamma F(u))^{1/2}\right\},$$

$$\Gamma_2=\left\{(u, w)\,|\,u\geqq 0,\ w=g_2(u)\equiv\frac{u}{\gamma}-\frac{1}{\gamma}(u^2-2\gamma F(u))^{1/2}\right\},$$

$$\Gamma_3=\left\{(u, w)\,|\,u\leqq 0,\ w=g_3(u)\equiv\frac{u}{\gamma}+\frac{1}{\gamma}(u^2-2\gamma F(u))^{1/2}\right\},$$

$$\Gamma_4=\left\{(u, w)\,|\,u\leqq 0,\ w=g_4(u)\equiv\frac{u}{\gamma}-\frac{1}{\gamma}(u^2-2\gamma F(u))^{1/2}\right\}.$$

Each of these sets is a smooth function on an open half line. We make several observations about g_1, g_2 and g_3. (The set Γ_4 is not used in the proofs.)

(a) $g_1'(u)>1/\gamma$ for $u>0$.

(b) Since $\int_0^1 f(u)\,du>0$, then there is a unique u_1 in $(a, 1)$ such that $g_2(u_1)=0$. Also, there is a unique $u_2\in(u_1, 1)$ for which $g_2(u_2)=f(u_2)$, g_2 is increasing for $u\in(u_1, u_2)$ and g_2 decreases on (u_2, ∞).

(c) $g_3'<0$ for $-\infty<u<0$, and $\delta\equiv\sup_{u<0} g_3'(u)$ is negative. We shall assume that $(\varepsilon/D)^{1/2}<-\delta$. (Further restrictions on the size of $(c/D)^{1/2}$ will be required.)

In the proof of Theorem 1 we restrict our initial condition to a subset of Γ_2, namely the set

$$\Delta \equiv \{(u, w) \in \Gamma_2 | u \geqq u_1\}. \tag{11}$$

We shall also refer to the half line segment

$$L \equiv \{(u, u/\gamma) | u \geqq 0\}.$$

Outline of the proof of Theorem 1. The first step in our analysis is to consider the case $\varepsilon = 0$ in (3)–(4). This causes w to remain at a constant value, say $\hat{w}$, and the system is reduced to

$$u' = z, \qquad z' = \hat{w} - f(u). \tag{12}$$

Equations (12) can be rewritten as the single equation

$$u'' + f(u) - \hat{w} = 0. \tag{13}$$

If we assume that $0 < \hat{w} < g_2(u_2)$, then there is a unique value $\hat{\alpha} \in (u_1, u_2)$ such that $(\hat{w}, \hat{\alpha}) \in \Delta$. A key step in our analysis is to determine the behavior of the solution of (13) with initial condition

$$u(0) = \hat{\alpha}, \qquad u'(0) = 0.$$

As we shall show, this solution is periodic. Therefore, the set $\hat{I} = \{(u(x), \hat{w}) | x \geqq 0\}$ is a finite line segment (Fig. 7). Furthermore, $\hat{I}$ lies to the right of the curve $\{(u, f(u)) | u \leqq 0\}$, since $u'' > 0$ at a minimum value of u. Also, $\hat{I} \cap \Gamma_3 = \varnothing$ since Γ_3 lies to the left of $w = f(u)$ for $u < 0$.

Further, since $u(x)$ is periodic, the function $(u(x), \hat{w})$ intersects L infinitely often. Thus, from a continuity argument it follows that if $\varepsilon > 0$ is sufficiently small then the solution of (3) with initial value

$$u(0) = \hat{\alpha}, \quad w(0) = g_2(\hat{\alpha}), \quad u'(0) = w'(0) = 0 \tag{14}$$

must intersect L at least 2 times, before either $(u, w) \in \Gamma_3$ or $w = 0$. We let $q_\alpha = (u_\alpha, u'_\alpha, w_\alpha, w'_\alpha)$ denote the solution such that $q_\alpha(0) = (\alpha, 0, q_2(\alpha), 0)$. Then for small $\varepsilon/D > 0$ we define the following nonempty sets:

$$\Omega_1 \equiv \{\alpha \geqq u_1 | \text{there exists } x_1 = x_1(\alpha) > 0 \text{ with } (u_\alpha(x_1), w_\alpha(x_1)) \in L \text{ and } w_\alpha(x) > 0 \text{ for } 0 \leqq x \leqq x_1\},$$

$$\Omega_2 \equiv \left\{ \alpha \in \Omega_1 \middle| \begin{array}{l} \text{there are values } x_2 > x_1 > 0 \text{ with} \\ \text{(i) } (u_\alpha(x_i), w_\alpha(x_i)) \in L \text{ for } i = 1, 2, \\ \quad (u_\alpha(x), w_\alpha(x)) \notin L \text{ for all } x \in [0, x_1) \cup (x_1, x_2), \\ \text{(ii) } (u_\alpha(x), w_\alpha(x)) \notin \Gamma_3 \text{ and } w_\alpha(x) > 0 \text{ for all } x \in [0, x_2] \end{array} \right\}.$$

To proceed with the proof of Theorem 1 we need several auxiliary lemmas. First, for small $\varepsilon/D > 0$ we show that Ω_2 is nonempty, open and bounded, with

$$u_1 < \alpha_2 \equiv \inf \Omega_2 < \alpha^2 \equiv \sup \Omega_2 < \infty.$$

Following that we consider solutions of (3) with either

$$(u(0), w(0), u'(0), w'(0)) = (\alpha_2, g_2(\alpha_2), 0, 0)$$

or

$$(u(0), w(0), u'(0), w'(0)) = (\alpha^2, g_2(\alpha^2), 0, 0).$$

We then show that these two solutions satisfy Theorem 1.

Completion of the proof of Theorem 1. As stated in the outline given above the first step in our analysis is to consider the special case $\varepsilon = 0$. This reduces (3) to

$$u'' + f(u) - \hat{w} = 0. \tag{15}$$

Let $f_{\min} = \min_{0<u<1} f(u)$ and $f_{\max} = \max_{0<u<1} f(u)$. Then for each $\hat{w} \in (f_{\min}, f_{\max})$ there are three distinct roots, $u_L(\hat{w}) < 0 < u_M(\hat{w}) < u_R(\hat{w})$, of the equation

$$f(u) - \hat{w} = 0. \tag{16}$$

Further, $g_2(u_2) < f_{\max}$, $g_2'(u_2) = 0 > f'(u_2)$ and for each $\hat{w} \in (0, g(u_2))$ there is a unique value $\hat{\alpha}$ such that $(\hat{\alpha}, \hat{w}) \in \Delta$. That is,

$$2F(\hat{\alpha}) - 2\hat{\alpha}\hat{w} = -\gamma\hat{w}^2. \tag{17}$$

We further restrict $\hat{w} > 0$ so that

$$\int_{u_L(\hat{w})}^{u_R(\hat{w})} (f(s) - \hat{w})\, ds > 0. \tag{18}$$

Finally, we shall use the two auxiliary functions

$$\mu(\hat{w}) \equiv 2F(u_L(\hat{w})) - 2\hat{w}u_L(\hat{w}) \tag{19}$$

and

$$\eta(\hat{w}) \equiv 2F(u_M(\hat{w})) - 2\hat{w}u_M(\hat{w}). \tag{20}$$

We now consider (15). The qualitative behavior of solutions of (15) is well known. The function $H(u, u') = (u')^2 + 2F(u) = 2u\hat{w}$, is constant along solutions. Suppose that

$$H(u, u') \equiv K \tag{21}$$

where K is constant. If $K = \mu(\hat{w})$, then (20) describes the trajectory of a homoclinic orbit leading to and from the equilibrium point $(u, u') = (u_L(\hat{w}), 0)$. If $K = \eta(\hat{w})$, then the solution (20) consists of the single point $(u, u') = (u_M, 0)$. If $\eta(\hat{w}) < K < \mu(\hat{w})$, then (20) describes the trajectory of a periodic solution of (15). The particular solution which we are interested in satisfies

$$u(0) = \hat{\alpha}, \qquad u'(0) = 0. \tag{22}$$

From (17) and (22) it follows that $H(u, u') = -\gamma\hat{w}^2$. Thus, to show that the solution of (15)–(22) is periodic we need to prove that

$$\eta(\hat{w}) < -\gamma\hat{w}^2 < \mu(\hat{w}). \tag{23}$$

From the definition of $\eta(\hat{w})$ we conclude that

$$\eta(0) = 2F(u_M(0)) < 0 \quad \text{and} \quad \eta'(0) = -2u_M(0) < 0.$$

Therefore, $(\eta(\hat{w}) + \gamma\hat{w}^2)' = -2u_M(\hat{w}) + 2\gamma\hat{w} < 0$ and $\eta(\hat{w}) < -\gamma\hat{w}^2$ for small $\hat{w} > 0$. Since $\mu(\hat{w}) > 0$ for $\hat{w} > 0$, the requirements of (23) are satisfied for small $\hat{w} > 0$ and the solution of (15) and (22) is periodic. Therefore, in the (w, u) plane the functions $(u(x), \hat{w})$ traces out a straight line segment $\hat{I}$ (Fig. 7). An algebraic computation shows that this function intersects the line $w = u/\gamma$ at the point $(\gamma\hat{w}, \hat{w})$ and that

$$\min_{x \geqq 0} u(x) < \gamma\hat{w} < \max_{x \geqq 0} u(x). \tag{24}$$

This concludes our analysis of the case $\varepsilon = 0$.

We now consider the full system, (3) for small $\varepsilon/D>0$. It follows from our discussion of the case $\varepsilon=0$, and the continuity of solutions with respect to parameters, that if $\varepsilon/D>0$ is sufficiently small, then $\Omega_2 \neq \varnothing$. We will show that Ω_2 is a proper open subset and that Ω_2 has at least two boundary points. These boundary points have the following properties:

(i) They correspond to solutions which tend to equilibrium as $x \to \pm\infty$.

(ii) The u and w components of these solutions have exactly one positive relative maximum which occurs at $x=0$, and $u(0)>a$.

From the properties described in (i)–(ii) above it follows that there are at least 2 homoclinic orbits of (3).

A further restriction which we need to make on the size of the parameters ε and D is to assume that

$$(\varepsilon/D)^{1/2} < \min\{-\delta, 1/\gamma\}. \tag{25}$$

In the following three lemmas we show that any solution of (3) which intersects either of the curves L or Γ_3 must cross those curves. These properties are crucial in showing that our "shooting" sets Ω_1 and Ω_2 are open.

LEMMA 1. *If* $(u_\alpha, w_\alpha) \in L$ *for some* $x_0>0$, *and* $u_\alpha(x_0)>0$, *then* (u_α, w_α) *crosses* L *at* x_0.

Proof. Since $P \equiv 0$ along solutions, and $Q<0$ on L then $(u'(x_0))^2 - D(w'(x_0))^2/\varepsilon > 0$. This, and the restriction (25) imply that $|w'_\alpha(x_0)/u'_\alpha(x_0)| < (\varepsilon/D)^{1/2} < 1/\gamma$. Thus, (u_α, w_α) cannot be tangent to L at x_0, and therefore must cross L at this point. This proves the lemma.

LEMMA 2. *If* (u_α, w_α) *intersects* Γ_3 *at some* $x=x_0$, $(u'(x_0), w'(x_0)) \neq (0,0)$, *and* $u_\alpha(x_0)<0$, *then* (u_α, w_α) *crosses* Γ_3 *at* x_0.

Proof. Since $0<(\varepsilon/D)^{1/2}<-\delta$, then the lemma follows by the same type of argument used in the proof of Lemma 1.

In the next lemma we consider the possibility that $(u, w)=(0,0)$ for some finite $x>0$. For this we need to define $g_3'(0^-) = \lim_{u\to 0, u<0} g_3'(u)$. From the definition of δ it follows that $g_3'(0^-) \leqq \delta$.

LEMMA 3. *Let* L_1 *denote the entire line* $u=\gamma w$ *and set*

$$T = \{(u, w) \mid \textit{if } u \leqq 0 \textit{ then } w = q_3(u), \textit{ while if } u \geqq 0 \textit{ then } w = g_3'(0^-)\}.$$

If $(u_\alpha, w_\alpha)=(0,0)$ *for some first* $x_0>0$ *then* (u_α, w_α) *crosses both* L_1 *and* T *at* x_0.

Proof. If there is a first $x_0>0$ for which $(u_\alpha(x_0), w_\alpha(x_0))=(0,0)$, then $P(x_0)=Q(u_\alpha(x_0), w_\alpha(x_0))=0$. From this and uniqueness of solutions it follows that $u'_\alpha(x_0)\neq 0$, and therefore $|w'(x_0)/u'(x_0)| = (\varepsilon/D)^{1/2}$. Since both L_1 and T have slopes greater than $(\varepsilon/D)^{1/2}$, then the result follows.

Using Lemmas 1 and 2, we now prove:

LEMMA 4. Ω_1 *and* Ω_2 *are open.*

Proof. That Ω_1 is open follows immediately from Lemma 1 and continuity of solutions with respect to initial conditions. Next, let $\alpha_0 \in \Omega_2$. Then there are values $x_2>x_1>0$ for which $(u_{\alpha_0}(x_i), w_{\alpha_0}(x_i)) \in L$ for $1 \leqq i \leqq 2$. From the definition of Ω_2 we observe that each of these intersections with L is nontangential, $(u_\alpha, w_\alpha) \notin \Gamma_3$ for any $x \in [0, x_2]$, and $w_\alpha>0$ for all $x\in[0, x_2]$. Thus, the result follows from Lemmas 1 and 2, and continuity of solutions with respect to initial conditions.

In the following lemma we show that each Ω_2 is bounded.

LEMMA 5. $\Omega_1 \subseteq (u_1, 1)$.

Proof. By definition, $\Omega_1 \subseteq (u_1, \infty)$. To show that $\Omega_1 \subseteq (u_1, 1)$ we consider a solution of (3) with initial conditions satisfying $u(0) > 1$, $w(0) = g_2(u(0))$, $u'(0) = w'(0) = 0$. Then $u'' > 0$ and $w'' < 0$ for $x > 0$ as long as $w > 0$ and $u > 1$. This proves the lemma.

We have now shown that each set Ω_j $(j = 1, 2)$ is nonempty, open and contained in the interval $(u_1, 1)$. Therefore, Ω_2 has at least two distinct limit points $\alpha_2 \equiv \inf \Omega_2$ and $\alpha^2 \equiv \sup \Omega_2$. We consider the solutions of (3) which satisfy either

$$u(0) = \alpha_2, \quad w(0) = g_2(\alpha_2), \quad u'(0) = w'(0) = 0 \tag{26}$$

or

$$u(0) = \alpha^2, \quad w(0) = g_2(\alpha_2), \quad u'(0) = w'(0) = 0. \tag{27}$$

We need to show that each of these two solutions has the following properties:

(i) $\lim_{x \to \infty} (u, u', w, w') = (0, 0, 0, 0)$,

(ii) u and w have a unique maximum in $[0, \infty)$ which occurs at $x = 0$, and $u(0) > a$, the threshold for the kinetic system (2).

For convenience we restrict our attention to solutions which satisfy property (26). The arguments for solutions satisfying (27) are similar and are therefore omitted. Suppose, first of all, that $w = 0$ at some first $\bar{x} > 0$ before $(u, w) \in L$. Then equations (3) imply that $w'(\bar{x}) < 0$ and (u, w) crosses the line $w = 0$ at $x = \bar{x}$. By continuity the same thing happens for values of α near α_2, contradicting the definition of α_2. If $w > 0$ and $(u, w) \notin L$ for all $x \in [0, \infty)$, then (3) imply that $(u, w) \to (0, 0)$ as $x \to \infty$ and $0 < w < u/\gamma$ for all $x \geqq 0$. However, this is not possible since a linearization of (3) shows that the stable manifold of solutions leading to $(u, w) = (0, 0)$ does not point into the region $u > 0, 0 < w < u/\gamma$. Therefore, (u, w) must intersect L at some first $x_1 > 0$, and by Lemma 1, this intersection is nontangential. Lemmas 1 and 2, and a continuity argument imply that $(u, w) \notin \Gamma_3 \cup L$ for any $x > x_2$. Next, consider the set $S = \{(u, w) | w > 0, g_3^{-1}(w) < u < \gamma w\}$. We have just shown that (u, w) cannot intersect the boundary of S at a point where $w > 0$. Suppose, therefore, that there is a first $\tilde{x} > x_1$ where $(u(\tilde{x}), w(\tilde{x})) = (0, 0)$. Recall that $P(x) \equiv 0$ for all $x \geqq 0$. Since $Q(u, w) > 0$ for all $(u, w) \in S$, it follows from (6) and (25) that $|w'(\tilde{x})/u'(\tilde{x})| \geqq \min\{1/\gamma, -\delta\} > (\varepsilon/D)^{1/2}$. Thus, $P(\tilde{x}) \neq 0$, a contradiction. Therefore, (u, w) remains in S^0, the interior of S, for all $x > x_1$. To complete the proof we need to show $w' < 0\ \forall x \geqq x_1$. Thus, for the sake of contradiction, we suppose that there is a value $\tilde{x} > 0$ such that $w'(\tilde{x}) \geqq 0$. If $w'(\tilde{x}) = 0$, then $w''(\tilde{x}) > 0$. Thus, from the definition of S, and (3) it follows that $w' > 0\ \forall x \geqq \tilde{x}$ and (u, w) must enter the set (Fig. 8)

$$R \equiv \{(u, w) | w \geqq 2f_{\max}, g_3^{-1}(w) < u < \gamma w\} \tag{28}$$

at some $\hat{x} \geqq \tilde{x}$. Thus, $w(\tilde{x}) = 2f_{\max}$ and $w'(\tilde{x}) > 0$. To eliminate this possibility we need the following:

LEMMA 6. *If* $(u(\hat{x}), w(\hat{x})) \in R$ *and* $w'(\hat{x}) > 0$ *for some* $\hat{x} \geqq 0$, *then* (u, w) *must leave* R *through the set* $\Gamma_3 \cup L$.

Proof. We assume, for the sake of contradiction, that $(u, w) \in R\ \forall x \geqq \hat{x}$. Then equations (3) imply that $w' > 0$ and $u'' > f_{\max} > 0\ \forall x \geqq \hat{x}$. Thus, there exists $x \geqq \hat{x}$ such that $u \geqq 12\sqrt{\varepsilon\gamma}$ and $f(u) \leqq -u^3/3\ \forall x \geqq \bar{x}$. From these observations and (3), it follows that

$$u'' \geqq 4\varepsilon\gamma u \quad \text{and} \quad w'' < \varepsilon\gamma w \quad \forall x \geqq \bar{x}.$$

An integration of each of these inequalities shows that, for sufficiently large x,

$$\frac{u'(x)}{u(x)} > \sqrt{3\varepsilon\gamma} \quad \text{and} \quad \frac{w'}{w} < \sqrt{2\varepsilon\gamma}. \tag{29}$$

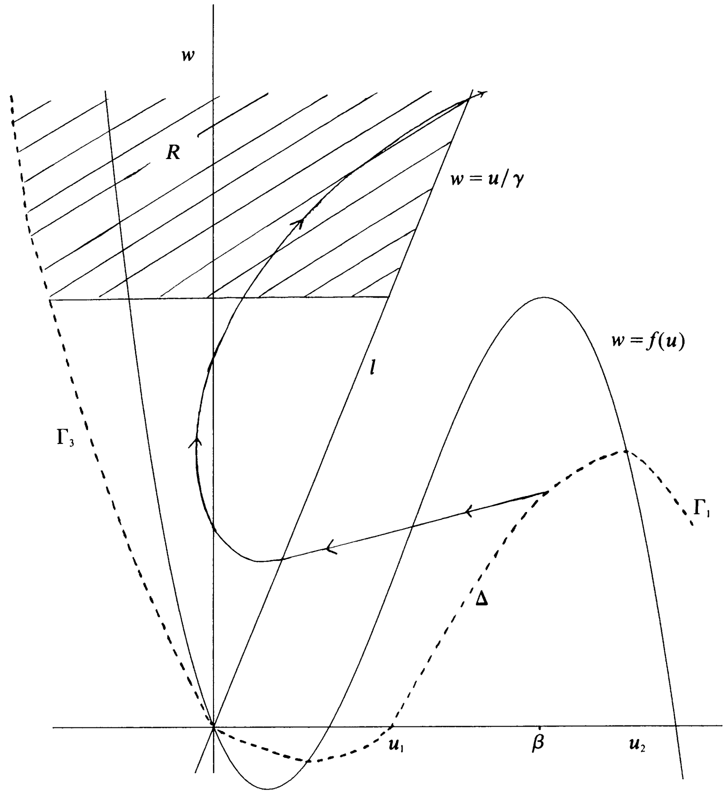

FIG. 8. *A solution entering R (shaded region) at some $x=\hat{x}$ must leave R either through Γ_3 or across the line L.*

A further integration of (29) shows that there are values $A_1>0$, $A_2>0$ and $\bar{\bar{x}}>\hat{x}$ such that

$$u(x)>A_1\,e^{\sqrt{3\varepsilon\gamma x}} \quad \text{and} \quad w(x)<A_2\,e^{\sqrt{2\varepsilon\gamma x}} \quad \forall x\geqq \bar{\bar{x}}. \tag{30}$$

Combining (29) and (30), we obtain

$$\frac{w'(x)}{u'(x)}\leqq\frac{\sqrt{2}\,A_2}{\sqrt{3}\,A_3}\,e^{\sqrt{\varepsilon\gamma}(\sqrt{2}-\sqrt{3})x} \quad \forall x\geqq\bar{\bar{x}}.$$

Thus, $w'/u'<1/\gamma$ for all large x and (u, w) must leave R through L, contradicting our suppositions that $(u, w)\in R$ for $x\geqq\hat{x}$.

We now continue with our proof. From Lemmas 1, 2 and 6 we conclude that (u, w) leaves R across Γ_3 or L. Either of these possibilities, together with a continuity argument, contradicts the definitions of α_2. Therefore, it must be the case that $w'<0\,\forall x\geqq x_1$. From this, and (3), it follows that $\lim_{x\to\infty}(u, u', w, w')=(0, 0, 0, 0)$. This completes the proof of Theorem 1.

Proof of Theorem 2. To prove the existence of periodic solutions we use a shooting method similar to that used in the proof of Theorem 1. First, in order to avoid the possibility that a solution tends to an equilibrium point at $+\infty$, we assume that $P(x)\equiv 2c$, c being a small negative constant. From this, and the condition $u'(0)=w'(0)=0$, it follows that

$$Q(u(0), w(0))=2c. \tag{31}$$

Thus, our solution starts on the solution set of the equation

$$Q(u, w) = 2c. \tag{32}$$

Before describing the solution set of (32), we need to determine the behavior of the related function

$$\rho(u, c) \equiv 2\gamma \int_0^u \left(\frac{s}{\gamma} - f(s)\right) ds + 2\gamma c. \tag{33}$$

If $c = 0$, then ρ has a double root at $u = 0$, $\partial\rho(u, 0)/\partial u < 0$ for all $u < 0$, $\partial\rho(u, 0)/\partial u > 0$ for all $u > 0$, and $\lim_{|u|\to\infty} \rho(u, 0) = \infty$. Therefore, for $c < 0$ it follows that there are exactly two real zeros of ρ, $\tilde{u}(c) < 0 < u_0(c)$. Furthermore, $\partial\rho(u, c)/\partial u < 0$ for all $u < \tilde{u}(c)$, $\partial\rho(u, c)/\partial u > 0$ for all $u > u_0(c)$, and

$$\lim_{|u|\to\infty} \left|\frac{\partial\rho(u, c)}{\partial u}\right| = +\infty.$$

From these observations on ρ, and the definition of $Q(u, w)$ (see (7)) it follows that the solution set of (32) consists of the four sets (Fig. 9)

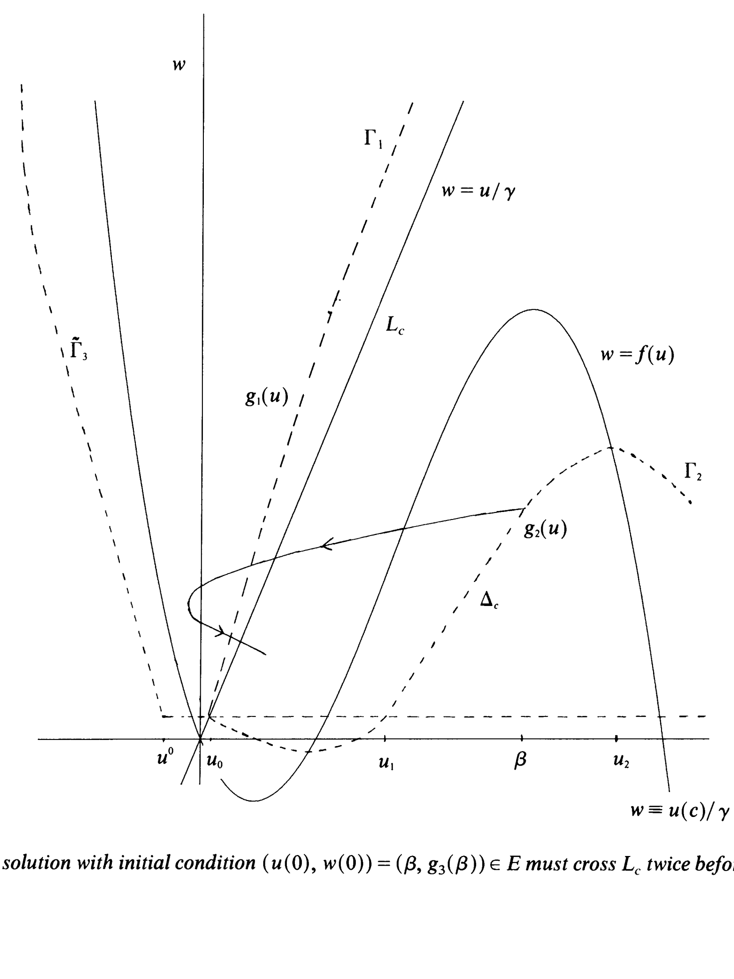

FIG. 9. *A solution with initial condition* $(u(0), w(0)) = (\beta, g_3(\beta)) \in E$ *must cross* L_c *twice before* $(u, w) \in \tilde{\Gamma}_3$ *or* $w = g_3(u_0)$.

$$\Gamma_1 = \left\{ (u, w) | u \geqq u_0(c),\ w = g_1(u) \equiv \frac{u}{\gamma} + \frac{1}{\gamma}(\rho(u, c))^{1/2} \right\},$$

$$\Gamma_2 = \left\{ (u, w) | u \geqq u_0(c),\ w = g_2(u) \equiv \frac{u}{\gamma} - \frac{1}{\gamma}(\rho(u, c))^{1/2} \right\},$$

$$\Gamma_3 = \left\{ (u, w) | u \leqq \tilde{u}(c),\ w = g_3(u) \equiv \frac{u}{\gamma} + \frac{1}{\gamma}(\rho(u, c))^{1/2} \right\},$$

$$\Gamma_4 = \left\{ (u, w) | u \leqq \tilde{u}(c),\ w = g_4(w) \equiv \frac{u}{\gamma} - \frac{1}{\gamma}(\rho(u, c))^{1/2} \right\}.$$

We shall only use the sets Γ_1, Γ_2 and part of Γ_3 in our analysis. As in the case $c=0$ we make several observations about the functions g_1, g_2 and g_3: For small $c<0$ there are positive values $u_1(c)$ and $u_2(c)$ such that $0<u_0(c)<a<u_1(c)<u_2(c)<1$, $\lim_{c\uparrow 0} u_0(c)=0$ and

(a) $g_2(u_0)=g_2(u_1)=u_0/\gamma$,
$g_2(u)<u_0/\gamma$ for $u_0<u<u_1$,
$g_2'(u)>0$ for $u_1<u<u_2$, $g_2(u_2)=f(u_2)$ and
$g_2'(u)<0$ for $u>u_2$;

(b) $g_1'(u)>1/\gamma$ for $u>u_0$;

(c) there is a unique $u^0(c)<0$ for which $g_3(u^0)=u_0/\gamma$, $\lim_{c\uparrow 0} u^0(c)=0$, $g_3'(u)<0$ for all $u<u^0$ and $\delta_c \equiv \lim_{u\uparrow u^0} g_3'(u)<0$.

As in the proof of Theorem 1 we assume that

$$(\varepsilon/D)^{1/2} < \min\{-\delta_c, 1/\gamma\}. \tag{34}$$

The initial point $(u(0), w(0))$ lies on the set (see Fig. (10))

$$\Delta_c \equiv \{(u, g_2(u)) | u \geqq u_0(c)\}.$$

We shall refer to the half-line

$$L_c \equiv \{(u, u/\gamma) | u \geqq u_0(c)\}$$

and the line segment

$$l_c \equiv \{(u, u_0(c)/\gamma) | u^0(c) \leqq u \leqq u_0(c)\}.$$

The part of Γ_3 which we use in our analysis consists of the set

$$\tilde{\Gamma}_3 \equiv \{(u, g_3(u)) | u \leqq u^0(c)\}.$$

Outline of proof of Theorem 2. We note that for each $\beta \in (u_1, u_2)$ there exists a unique value $w^\beta \equiv g_2(\beta)$ such that $(\beta, w^\beta) \in \Delta_c$. Let $q_\beta = (u_\beta, u_\beta', w_\beta, w_\beta')$ denote the solution of (3) with $q_\beta(0) = (\beta, 0, w^\beta, 0)$. As in the proof of Theorem 1 it follows from continuity of solutions with respect to initial values and parameters that if $\varepsilon/D>0$ and $c<0$ are sufficiently small, then there exists $\beta \in (u_1(c), u_2(c))$ such that (u_β, w_β) crosses L_c twice before $w_\beta = u_0/\gamma$ or $(u_\beta, w_\beta) \in \tilde{\Gamma}_3$.

Therefore if $\varepsilon/D>0$ and $c<0$ are sufficiently small, then we can define the nonempty set

$$E = \Big\{ \beta \in (u_1(c), \infty) \,\Big|\, \text{there are values } x_2 > x_1 > 0 \text{ with}$$
$$\text{(i) } (u_\beta(x_i), w_\beta(x_i)) \in L_c\ (i=1,2),$$
$$(u_\beta, w_\beta) \notin L_c,\ x \in [0, x_1) \cup (x_1, x_2),$$
$$\text{(ii) } w_\beta > u_0(c)/\gamma \text{ and } (u_\beta, w_\beta) \notin \tilde{\Gamma}_3 \text{ for all } x \in [0, x_2] \Big\}.$$

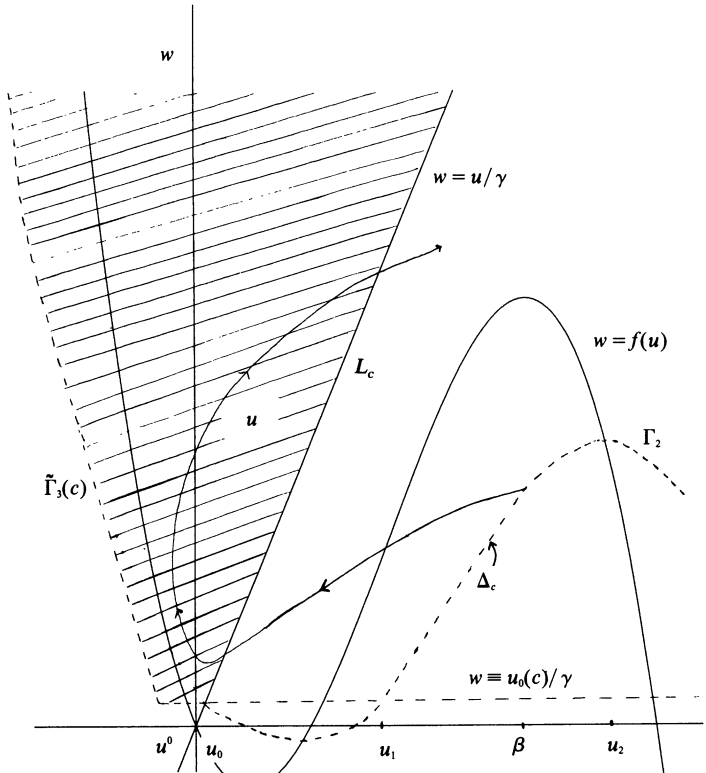

FIG. 10. *If the solution enters* $\mathcal{U}$ *(shaded region) at some* $x=\tilde{x}$, *and* $w'(\tilde{x}) \geqq 0$, *then it must leave* $\mathcal{U}$ *across* $\tilde{\Gamma}_3 \cup L_c$.

In Lemmas 8–13 we prove that E is an open bounded set. Therefore, the numbers

$$\beta_1 \equiv \inf E \quad \text{and} \quad \beta_2 \equiv \sup E \tag{35}$$

are well defined and finite with $u_1 \leqq \beta_1 < \beta_2 < \infty$. In the remainder of the section we show that q_{β_1} and q_{β_2} are periodic solutions of (3).

We now proceed with the details of proving Theorem 2. Lemmas 8–12 give conditions under which a solution that intersects any of the curves $\tilde{\Gamma}_3$, L_c or l_c must cross that curve.

LEMMA 8. *If* $(u_\beta, w_\beta) \in L_c$ *for some* $x_0 > 0$ *and* $u_\beta(x_0) > u_0(c)$, *then* (u_β, w_β) *crosses* L_c *at* x_0.

LEMMA 9. *If* $(u_\beta, w_\beta) \in \tilde{\Gamma}_3$ *for some* $x_0 > 0$, $u_\beta(x_0) < u^0(c)$ *and* $(u'_\beta(x_0), w'_\beta(x_0)) \neq (0,0)$, *then* (u_β, w_β) *crosses* $\tilde{\Gamma}_3$ *at* x_0.

The proofs of Lemmas 8 and 9 are the same as the proofs of Lemmas 1 and 2, and we omit the details.

LEMMA 10. *If* $(u_\beta, w_\beta) \in l_c$ *for some* $x_0 > 0$, *and* $u^0(c) < x_0 < u_0(c)$, *then* (u_β, w_β) *crosses* l_c *at* x_0.

Proof. If (u_β, w_β) is tangential to l_c at $x = x_0$, then $w'_\beta(x_0) = 0$. The definition of l_c implies that $Q(u_\beta(x_0), w_\beta(x_0)) > 2c$. Therefore, it follows that $P(x_0) > 2c$, contradicting the requirement that $P(x) \equiv 2c$.

In Lemmas 11 and 12 we determine the behavior of solutions which intersect l_c at either of its endpoints. First we consider the left endpoint. For this we extend the definition of $\tilde{\Gamma}_3$ and define the set

$$V_c=\{(u,w)|\text{ if } u\leqq u^0(c) \text{ then } w=g_3(u), \text{ while}$$
$$\text{if } u\geqq u^0(c) \text{ then } w=\delta_c(u-u^0)+u_0/\gamma\}.$$

LEMMA 11. *If* $(u_\beta, w_\beta)=(u^0, u_0/\gamma)$ *for some* $x_0>0$, *and* $(u'_\beta(x_0), w'_\beta(x_0))\neq(0,0)$, *then* (u_β, w_β) *crosses both* l_c *and* V_c *at* x_0.

Proof. At $x=x_0$ it must be the case that $Q(u_\beta(x_0), w_\beta(x_0))=2c$ and therefore, $(u'(x_0))^2-D(w'(x_0))^2/\varepsilon=0$. From this and the assumption that $(u'_\beta(x_0), w'_\beta(x_0))\neq(0,0)$ it follows that $u'_\beta(x_0)\neq 0$ and $|w'_\beta(x_0)/u'_\beta(x_0)|=(\varepsilon/D)^{1/2}$. This and condition (4.5) imply that (u_β, w_β) crosses V_c and l_c at x_0, completing the proof of the lemma.

In Lemma 12 we determine the behavior of a solution which intersects l_c at its right-hand endpoint, $(u_0(c), u_0(c)/\gamma)$. Since the proof of Lemma 12 is essentially the same as that of Lemma 11 we omit the details. We define

$$L_1=\{(u, u/\gamma)|u\in(-\infty,\infty)\}$$

and

$$L_2=\{(u, u_0/\gamma)|u>u^0(c)\}.$$

LEMMA 12. *If* $(u_\beta, w_\beta)=(u_0(c), u_0(c)/\gamma)$ *for some* $x_0>0$, *and* $(u'_\beta(x_0), w'_\beta(x_0))\neq(0,0)$, *then* (u_β, w_β) *crosses both* L_1 *and* L_2 *at* x_0.

LEMMA 13. *E is open and* $E\subseteq(u_1(c),1)$.

Proof. Let $\beta_0\in E$. Then there are $x_2>x_1>0$ with $(u_{\beta_0}, w_{\beta_0})\notin\tilde{\Gamma}_3$ and $w_{\beta_0}>u_0(c)/\gamma$ $\forall x\in[0,x_2]$, $(u_{\beta_0}(x_i), w_{\beta_0}(x_i))\in L_c$ $(i=1,2)$, and $(u_{\beta_0}, w_{\beta_0})\notin L_c$ for $x\in[0,x_1)\cup(x_1,x_2)$. From this, Lemmas 8–12, and continuity of solutions with respect to initial conditions, it follows that $\beta\in E$ if $|\beta-\beta_0|>0$ is sufficiently small. Thus, E is open. The proof that $E\subseteq(u_1(c),1)$ is exactly the same as the proof of Lemma 5 and is therefore omitted.

From Lemma 13 it follows that the values β_1 and β_2 defined in (45) satisfy $u_1(c)<\beta_1<\beta_2<1$. It remains to be shown that $q_{\beta_1}(x)$ and $q_{\beta_2}(x)$ are periodic. For ease of notation we set $q_1\equiv q_{\beta_1}$. We show that there is a first $x_1>0$ for which $(u_1(x_1), w_1(x_1))\in\tilde{\Gamma}_3\cup l_c$, $w'_1<0$ on $(0,x_1)$, and $u'_1(x_1)=w'_1(x_1)=0$. It then follows from the symmetry of (3), and the translation $\tau=x-x_1$ that q_1 is periodic with period $2x_1$. We shall omit the details for $q_2(x)$ since they follow in a similar fashion.

First, we claim that $(u_1, w_1)\in L_c$ before $(u_1, w_1)\in\tilde{\Gamma}_3$ or $w_1=u_0/\gamma$. If this were false, then there exists $\hat{x}>0$ with $w_1(x)\in(u_0/\gamma, u_1(x)/\gamma)$ for all $x\in(0,\hat{x})$, $w_1(\hat{x})=u_0/\gamma$ and either $u_1(\hat{x})=u_0(c)$ or else $u_1(\hat{x})>u_0(c)$. If $u_1(\hat{x})>u_0(c)$, then equations (3) imply that $w'_1(\hat{x})<0$ $\forall x\in(0,\hat{x}]$, and $u_1>u_0$, $w_1<u_0/\gamma$ for x to the immediate right of $\hat{x}$. But then, by continuity, and (3) it follows that $\beta\notin E$ if $|\beta-\beta_1|>0$ is sufficiently small, contradicting the definition of β_1. Next, we suppose that $u_1(\hat{x})=u_0(c)$. Then Lemma 12 implies that (u_1, w_1) crosses both L_1 and L_2 at $\hat{x}$, and again by continuity, $\beta\notin E$ if $|\beta-\beta_1|>0$ is sufficiently small, a contradiction. Therefore, there is a first $x_0>0$ for which $(u_1(x_0), w_1(x_0))\in L_c$, $w'_1<0$ on $(0,x_0)$ and $w_1(x_0)>u_0/\gamma$.

Next, we determine the behavior of $q_1(x)$ for $x>x_0$ as (u_1, w_1) enters the set (Fig. 10)

$$\mathcal{U}\equiv\{(u,w)|w>u_0(c)/\gamma,\ g_3^{-1}(w)<u<\gamma w\}.$$

From (3) it follows that $w'_1<0$ for $0<x<x_0$, since $w''<0$ on $(0,x_0)$. We claim that $w'_1<0$ for $x>x_0$ as long as $(u_1, w_1)\in\mathcal{U}$. If this were false, then there exists a first $\hat{x}>x_0$ such that $w'_1(\hat{x})=0$ and $(w_1, u_1)\in\mathcal{U}$ for all $x\in(x_0,\hat{x}]$. It then follows from (3) that $w''_1>0$ for $x\geqq\hat{x}$ as long as $(u_1, w_1)\in\mathcal{U}$. Suppose that (u_1, w_1) were to leave $\mathcal{U}$ at some first $\tilde{x} > \hat{x}$, and that $(u_1(\tilde{x}), w_1(\tilde{x})) \in \tilde{\Gamma}_3$. Then $w_1'(\tilde{x}) > 0$, hence Lemma 9 implies that (u_1, w_1) crosses $\tilde{\Gamma}_3(c)$ at $\tilde{x}$. Then again, continuity implies that $\beta \notin E$ if $|\beta - \beta_1| > 0$ is sufficiently small, a contradiction. A similar contradiction arises if we would suppose that (u_1, w_1) leaves $\mathcal{U}$ through L_c. Therefore $(u_1, w_1) \in \mathcal{U}$ and $w_1' > 0$ for all $x > \tilde{x}$. Eventually (u_1, w_1) enters the set R (defined in (28)) at some $\bar{x} > \tilde{x}$, and remains in R for all $x > \bar{x}$. But this is not possible by Lemma 7. Our conclusion must be that $w_1' < 0$ for $x > \hat{x}$ as long as $(u_1, w_1) \in \mathcal{U}$. However, the closure of $\mathcal{U}$ contains no equilibrium points. Therefore, there is a first $x_1 > x_0$ for which $(u_1(x_1), w_1(x_1))$ intersects the boundary of $\mathcal{U}$. Lemmas 8 and 12 and continuity prevent the possibility that $(u_1(x_1), w_1(x_1)) \in L_c$ and $u_1(x_1) \geqq u_0(c)$ unless the solution is periodic. Therefore, we can assume that $(u_1(x_1), w_1(x_1)) \in \tilde{\Gamma}_3 \cup l_c$ and $u_1(x_0) < u_0(c)$.

If $u^0(c) < u_1(x_1) < u_0(c)$, then $(u_1(x_1), w_1(x_1)) \in l_c$ and Lemma 10 forces the solution to cross l_c at $x = x_1$. Again, a continuity argument contradicts the definition of β_1 in this case. Therefore, the only possibility left is that $(u_1(x_1), w_1(x_1)) \in \tilde{\Gamma}_3$. If $(u_1'(x_1), w_1'(x)) = (0, 0)$, then the solution is periodic and the theorem is proved. Otherwise Lemmas 10 and 11 imply that (u_1, w_1) crosses $\tilde{\Gamma}_3$ (if $u_1(x_1) < u^0$) (or V_c and l_c if $u_1(x_1) = u^0$). In either case a continuity argument contradicts the definition of β_1. The proof of Theorem 2 is now complete.

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