

SPATIAL STABILITY OF TRAVELING WAVE SOLUTIONS OF A NERVE CONDUCTION EQUATION

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ABSTRACT A simplified FitzHugh-Nagumo nerve conduction equation with known traveling wave solutions is considered. The spatial stability of these solutions is analyzed to determine which solutions should occur in signal transmission along such a nerve model. It is found that the slower of the two pulse solutions is unstable while the faster one is stable, so the faster one should occur. This agrees with conjectures which have been made about the solutions of other nerve conduction equations. Furthermore for certain parameter values the equation has two periodic wave solutions, each representing a train of impulses, at each frequency less than a maximum frequency ω_{\max} . The slower one is found to be unstable and the faster one to be stable, while that at ω_{\max} is found to be neutrally stable. These *spatial* stability results complement the previous results of Rinzel and Keller (1973. *Biophys. J.* 13: 1313) on *temporal* stability, which are applicable to the solutions of initial value problems.

INTRODUCTION

As models for nerve impulse conduction, various nonlinear partial differential equations have been proposed and studied by Hodgkin and Huxley (15), FitzHugh (11, 12), and Nagumo et al. (20). Numerical calculations (3-5, 12, 15, 16, 20) and analytical results (1, 2, 13) indicate that these equations usually have two solitary pulse solutions with different propagation speeds, and a family of periodic traveling wave solutions. The latter correspond to repetitive firing of a nerve at different frequencies. All these solutions, as traveling waves, satisfy ordinary differential equations. Yet certain of them, for example the slow pulse, have not been observed as asymptotic solutions to appropriate problems for the partial differential equations. On this basis, some of the waves are conjectured to be unstable as solutions to the partial differential equations. However, their stability has not been analyzed. Therefore we have analyzed the stability of the solutions of a simplified FitzHugh-Nagumo equation.

The simplified equation, proposed by McKean (19), exhibits the qualitative features of nerve conduction and it can be solved explicitly. The equation is

$$\begin{aligned}\partial v / \partial t &= (\partial^2 v / \partial x^2) - f(v) - w, \\ \partial w / \partial t &= bv, \quad b > 0\end{aligned}\tag{1}$$

where

$$f(v) = v - H(v - a), \quad 0 < a < 1/2. \quad (2)$$

Here H is the Heaviside step function and f corresponds to a piecewise linear current-voltage relation. Other models which incorporate piecewise linear approximations have been studied by Kunov (18), and Offner et al. (21).

Rinzel and Keller (22) obtained the traveling wave solutions of Eqs. 1-2, for each value of $b > 0$ and each positive $a < a_*(b)$. They found two solitary pulse solutions with different propagation speeds. They also found, for each wavelength larger than some minimum wavelength $P_{\min}(a, b)$, two or more periodic solutions with different speeds. They analyzed the linear temporal stability of these traveling wave solutions and found that each slow solitary pulse was temporally unstable. This confirmed conjectures which had been made for other nerve conduction equations. They further showed that the slower periodic wave trains, and certain of the faster ones, were temporally unstable.

To demonstrate *temporal* instability, they calculated the growth rate with respect to time of perturbations which are bounded in space (i.e., along the length of the axon). Such temporal instability is relevant for initial value problems (cf. Evans [7-10]). However, many problems of physiological interest are naturally posed as signaling problems, and for them temporal instability is not an appropriate concept. Typical of these are repetitive firing of an axon due to injection of a specified current at a fixed location (5, 14, 23) and repetitive firing of a sensory nerve fiber in response to the generator potential developed by the receptor nerve cell (6, 17). Mathematical formulations of such phenomena naturally lead to boundary value problems. For these, one often ignores the transient influence of initial conditions. The spatially localized signal, at say $x = 0$, is specified for all time $-\infty < t < \infty$. Of interest is the relationship between the imposed signal and the response which is transmitted along the nerve to distant locations.

For stability analysis of a traveling wave solution in this context, we assume that the imposed signal generates, at $x = 0$, the waveform plus some perturbation. To study the transmission along the nerve of the perturbed waveform, the notion of spatial stability is appropriate. Here we consider the linear spatial stability of the waves. This requires calculating the growth rates, with respect to distance along the nerve, of perturbations which are bounded in time. We have done this and we shall present our results below. They show that the slower pulse and the slower wave train are spatially unstable while the faster ones are spatially stable. For the wave trains, the transition from instability to stability occurs at the wave train of maximum frequency ω_{\max} , which is neutrally stable.

With respect to *temporal* stability, the transition does not always occur at ω_{\max} . Indeed, numerical results of the temporal stability analysis of these wave trains (22) show that, for $b = 0.005$ and several values of a , the maximum frequency wave is unstable and so are some of the fast waves. Thus there is a difference between the tem-

poral stability and spatial stability of these periodic traveling wave solutions. The *spatially* stable wave trains should be observed in response to spatially localized stimuli.

We remark that our formal approach does not determine the asymptotic response, as $x \rightarrow \infty$, for given boundary data at $x = 0$. Linear stability analysis indicates whether or not infinitesimal perturbations will grow or attenuate with distance from a source. It does not determine the exact perturbed wave for all $x > 0$. Linear stability typically plays a fundamental role in a rigorously complete stability theory; for example, see Sattinger (24). In that case, theorems insure that, for small perturbations, the solution of interest is asymptotically attained if there are no growing solutions to the linear stability problem. Here we assume that such theorems can be provided. For nerve conduction, Evans's work is one example of this for temporal stability of the solitary pulse.

SPATIAL STABILITY ANALYSIS OF SOLITARY PULSES

A traveling wave solution of Eqs. 1-2 is a solution of the form $v(x, t) = v_c(z)$, $w(x, t) = w_c(z)$, where $z = x - ct$. The positive constant c is the propagation speed of the rightward moving wave. It follows that v_c, w_c satisfy the ordinary differential equation

$$\begin{aligned} -cv'_c &= v''_c - f(v_c) - w_c, \\ -cw'_c &= bv_c, \quad c \neq 0. \end{aligned} \quad (3)$$

A solitary pulse must, in addition, satisfy the condition

$$v_c, w_c \rightarrow 0 \text{ as } |z| \rightarrow \infty. \quad (4)$$

Rinzel and Keller (22) determined all these solutions and their speeds as functions of the parameters a and b . They found for given positive values of a and b where $0 < a < a_*(b)$, that Eqs. 1-2 have precisely two pulse-shaped traveling wave solutions. For $a = a_*$, there is a unique pulse with speed c_* . The speed curve, c vs. a , for $b = 0.05$ is shown in Fig. 1. The fast (upper) and slow (lower) branches of the speed curve coalesce at the knee whose coordinates are a_*, c_* . The fast pulse for $b = 0.05$, $a = 0.15$ is illustrated in Fig. 2. It is obtained by evaluating $v_c(-z)$ in ref. 22. We have chosen the origin of the z -coordinate so that v_c takes the value a on the front of the wave at $z = 0$. Since z does not appear explicitly in Eq. 3, we are free to make this choice. On the back of the wave, we have $v_c(z_1) = a$ where z_1 depends on a, b , and c .

Let us now examine the spatial stability of these traveling wave solutions. First we introduce the traveling coordinate frame (z, x) . In this frame, Eqs. 1-2 become

$$\begin{aligned} -c(\partial v / \partial z) &= (\partial^2 v / \partial z^2) + 2(\partial^2 v / \partial z \partial x) + (\partial^2 v / \partial x^2) - f(v) - w, \\ -c(\partial w / \partial z) &= bv. \end{aligned} \quad (5)$$

We shall consider the region $x > 0$ and $-\infty < z < \infty$.

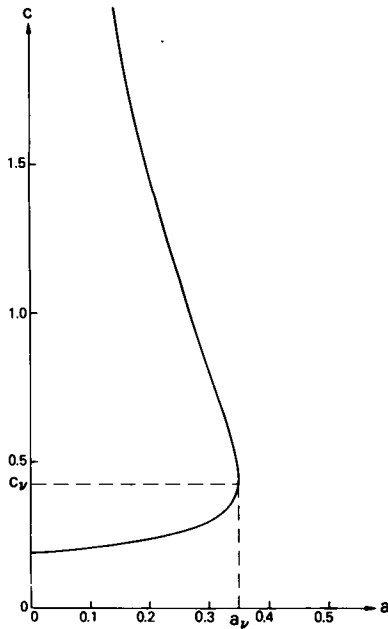


FIGURE 1

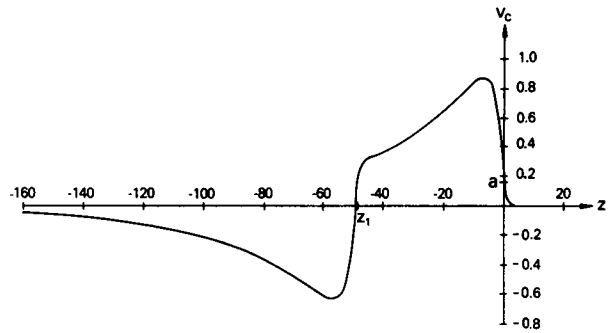


FIGURE 2

FIGURE 1 Propagation speed $c(a, b)$ of a pulse as a function of a for $b = 0.05$ as determined in ref. 22. As $a \rightarrow 0$, the upper branch $c(a, b) \rightarrow \infty$. The coordinates of the speed curve knee are a_v and c_v .

FIGURE 2 Solitary pulse traveling wave solution of Eqs. 1-2, $v_c(z)$ where $z = x - ct$. The fast pulse illustrated here is for $a = 0.15$, $b = 0.05$, $c \approx 1.95$, and $z_1 \approx -48.7$. The waveform and values of c, z_1 were determined in ref. 22.

A traveling wave v_c, w_c is an x -independent solution of Eq. 5. To study its stability we consider the linear variational equation

$$\begin{aligned} -c(\partial \tilde{V} / \partial z) &= (\partial^2 \tilde{V} / \partial z^2) + (\partial^2 \tilde{V} / \partial z \partial x) + (\partial^2 \tilde{V} / \partial x^2) - f'(v_c) \tilde{V} - \tilde{W}, \\ -c(\partial \tilde{W} / \partial z) &= b \tilde{V}, \end{aligned} \quad (6)$$

where, from Eq. 2,

$$f'(v_c) = 1 - \delta(v_c - a). \quad (7)$$

Here δ is the Dirac delta function. Since, for the pulse, $v_c = a$ at $z = 0$ and $z = z_1$, Eq. 7 can be written in terms of z as

$$f'(v_c) = 1 - \gamma_0^{-1} \delta(z) - \gamma_1^{-1} \delta(z - z_1), \quad (8)$$

where

$$\gamma_0 = -v'_c(0), \quad \gamma_1 = v'_c(z_1). \quad (9)$$

The quantities γ_0, γ_1 are expressed in terms of b, c , and z_1 by the right-hand sides of Eq. 29 in ref. 22. To evaluate those expressions, we replace z_l , which is negative here, by $-z_1$ and use Eqs. 8–10 and 12 of ref. 22.

The functions $\tilde{V}(z, 0), \tilde{W}(z, 0)$ correspond to infinitesimal perturbations of v_c, w_c which are imposed at $x = 0$. To determine if such perturbations grow with distance along the nerve we seek solutions to Eq. 6 of the form

$$\begin{aligned}\tilde{V}(z, x) &= e^{\lambda x} V(z), \\ \tilde{W}(z, x) &= e^{\lambda x} W(z).\end{aligned}\quad (10)$$

From Eqs. 6, 8, and 10 it follows that $\mathbf{V} = (V, V', W)$ must satisfy the ordinary differential equation

$$\begin{pmatrix} V \\ V' \\ W \end{pmatrix}' = \begin{pmatrix} 0 & 1 & 0 \\ 1 - \lambda^2 & -2\lambda - c & 1 \\ -b/c & 0 & 0 \end{pmatrix} \begin{pmatrix} V \\ V' \\ W \end{pmatrix}, \quad z \neq 0, z_1 \quad (11)$$

and the jump conditions

$$\left. V' \right|_{0^-}^{0^+} = -\gamma_0^{-1} V(0) \quad (12A)$$

$$\left. V' \right|_{z_1^-}^{z_1^+} = -\gamma_1^{-1} V(z_1). \quad (12B)$$

The solitary pulse v_c, w_c is spatially unstable if for any λ with $Re\lambda > 0$, Eqs. 11–12 have a bounded solution \mathbf{V} which belongs to an appropriate class C of admissible perturbations. This solution is an unstable mode with spatial growth rate $Re\lambda$. On the other hand, the pulse is spatially stable if there are no bounded solutions, \mathbf{V} belonging to C with $Re\lambda > 0$. Of course there is always one solution to Eqs. 11–12 with $\lambda = 0$; it is (v'_c, v''_c, w'_c) . This is because any translate of the traveling wave also satisfies Eq. 5. We note that the parameter λ appears nonlinearly in the eigenvalue problem 11–12, while in the case of *temporal* instability λ occurs linearly (see Eqs. 31–32 of ref. 22).

We now proceed to construct solutions to Eqs. 11–12. Since Eq. 11 has constant coefficients, its solutions are sums of the three exponentials $\mathbf{Y}_j \exp(\rho_j z)$, $j = 1, 2, 3$. The ρ_j are zeros of the cubic polynomial

$$R(\rho, \lambda) = \rho^3 + (2\lambda + c)\rho^2 + (\lambda^2 - 1)\rho + b/c, \quad (13)$$

and the vectors Y_j are given by

$$Y_j = (1, \rho_j, -b(c\rho_j)^{-1}), \quad j = 1, 2, 3. \quad (14)$$

For $-1 < \lambda < 1$, it follows from Eq. 13 that the ρ_j satisfy either:

$$\rho_1 < 0 < \rho_2 < \rho_3 \quad (15)$$

or

$$\rho_1 < 0, \rho_2 = \bar{\rho}_3, \operatorname{Re} \rho_2 > 0. \quad (16)$$

Under the assumption that either condition 15 or 16 holds, a bounded solution of Eqs. 11–12 which satisfies the normalization condition, $V(0) = 1$, is given by $V(z) = Y_1 \exp(\rho_1 z)$ for $z > 0$. We extend V to the interval $z_1 < z < 0$ by imposing the jump condition 12 A and the continuity of V and W at $z = 0$. In the same way we extend V to $z < z_1$. To insure that V remains bounded as $z \rightarrow -\infty$, we equate to zero the coefficient of $Y_1 \exp(\rho_1 z)$ in the region $z < z_1$. This yields a transcendental equation for λ in terms of the parameters a and b and the pulse speed c :

$$\mathfrak{F}(\lambda, a, b, c) = 0. \quad (17)$$

Note, here a , b , and c are related according to the pulse speed curve.

The function \mathfrak{F} is defined by:

$$\begin{aligned} \mathfrak{F}(\lambda, a, b, c) = & (\gamma_0 - \rho_1/R'_1)(\gamma_1 - \rho_1/R'_1) + \exp[(\rho_2 - \rho_1)z_1]\rho_1\rho_2(R'_1R'_2)^{-1} \\ & + \exp[(\rho_3 - \rho_1)z_1]\rho_1\rho_3(R'_1R'_3)^{-1}, \end{aligned} \quad (18)$$

where

$$R'_j = \partial R(\rho_j, \lambda)/\partial \rho, \quad j = 1, 2, 3. \quad (19)$$

For any real solution $\lambda = \lambda(a, b, c)$ of Eq. 17 which satisfies $-1 < \lambda < 1$, or more generally for which condition 15 or 16 holds, the above construction yields a bounded solution V of Eqs. 11–12. By construction, this solution decays exponentially to zero as $|z| \rightarrow \infty$. We refer to the value of λ as a point eigenvalue of the ordinary differential operator in Eqs. 11–12.

We have solved Eq. 17 numerically for λ with specified sets of values of b and c ; for each set, the corresponding value of a lies on the pulse speed curve. Fig. 3 shows the results for the case $b = 0.05$ and a range of values of c . For each value of λ shown either condition 15 or 16 applies, and therefore a bounded solution of Eqs. 11–12 exists. From Fig. 3 we see that $\lambda > 0$ for $\hat{c} \leq c < c_*$, and $\lambda < 0$ for $c > c_*$. Therefore we conclude that slow pulses, $\hat{c} \leq c < c_*$, are spatially unstable and the fast ones, $c > c_*$, are spatially stable. Since these conclusions are based on numerical calculations

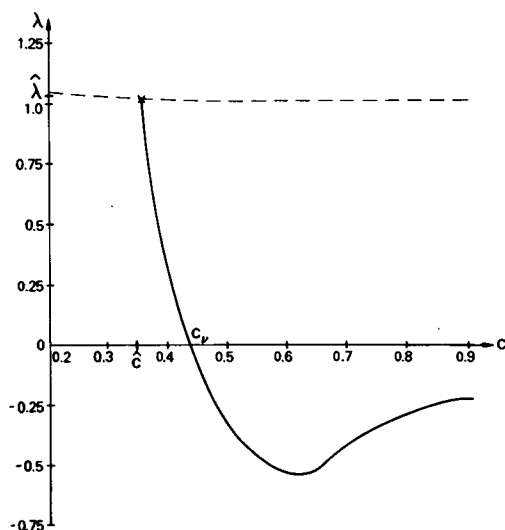


FIGURE 3

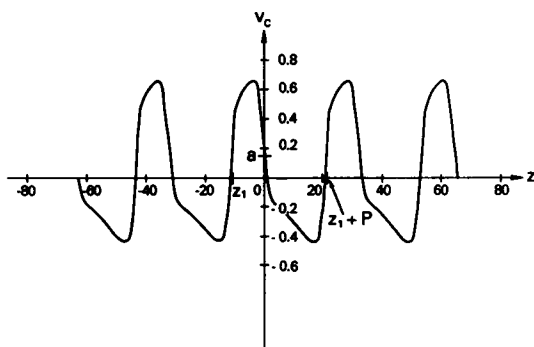


FIGURE 4

FIGURE 3 Growth rate $\lambda(a, b, c)$ of spatially unstable mode for a slow pulse versus c , $\hat{c} < c < c_p$, for $b = 0.05$, determined numerically from Eqs. 17 and 18. For the spatially neutrally stable pulse, $\lambda(a_p, b, c_p) = 0$. Negative values of λ correspond to a fast pulse.

FIGURE 4 Four pulses from a periodic traveling wave solution of Eqs. 11–12, $v_c(z)$ with wavelength P , where $z = x - ct$. For this wave train $a = 0.15$, $b = 0.05$, $c = 0.75$, $P \approx 31.2$, and $z_1 \approx -10.7$. The waveform and values of P , z_1 were determined in ref. 22.

they are strictly valid only for those values of b and c for which the calculations were performed. However it seems that the calculations could be performed for any value of $c > \hat{c}$ with the result indicated above and in Fig. 3. We also conclude, since $\lambda = 0$ for $c = c_p$, that the pulse with speed c_p has neutral spatial stability. This result can be demonstrated analytically and it applies to a general class of nerve conduction equations where a is a typical parameter (25).

The preceding calculation demonstrates instability for each slow pulse with speed c satisfying $\hat{c} < c < c_p$. Here $\hat{c} > c_{\min}$, where c_{\min} is the limit of the slow pulse speed as a tends to zero for fixed b ; for $b = 0.05$, $c_{\min} \approx 0.186$ (see Fig. 1). For $c_{\min} < c < \hat{c}$, the calculation does not yield a growing mode because then conditions 15 and 16 are both violated. However, in the Appendix, we develop an argument to show that each slow pulse for $c_{\min} < c < \hat{c}$ is spatially unstable. The growth rate $Re\lambda_{\max}$ of its fastest growing unstable mode satisfies $Re\lambda_{\max} \geq 1$. This argument along with our numerical calculations confirm the conjecture that each slow pulse is spatially unstable. We summarize our results in the following statement.

Proposition 1

Each slow traveling pulse solution of the simplified FitzHugh-Nagumo Eq. 1–2 is spatially unstable. For $\hat{c} \leq c < c_p$, the exponential growth rate $\lambda(a, b, c)$ of its un-

stable mode satisfies Eq. 17. For $c < \hat{c}$, the growth rate $Re\lambda_{\max}$ of the fastest growing unstable mode satisfies $Re\lambda_{\max} \geq 1$. The unique pulse v_c has spatial neutral stability.

SPATIAL STABILITY ANALYSIS OF PERIODIC WAVE TRAINS

Rinzel and Keller (22) obtained a one parameter family of periodic traveling wave solutions of Eqs. 1–2 for values of a and b which satisfy $0 < b \leq 0.1$ and $a < a_*(b)$; subsequently, we determined the solutions for $b = 0(1)$. These periodic solutions correspond to repetitive firing behavior of a nerve. Four pulses from one such rightward traveling wave train are illustrated in Fig. 4. We have characterized a periodic wave train by its propagation speed c and its wavelength P , the distance along the nerve from one pulse front to the next. Curves of $c(a, b, P)$ vs. P are shown in Fig. 8 of ref. 22 for $b = 0.05$ and several values of a . We note that corresponding curves for $b = 0(1)$ are not necessarily monotonic on their fast branches. In addition, for some values of a and b , there are isolated closed curves of c vs. P .

For the present analysis, it is useful to describe a periodic solution by its temporal frequency ω and wavelength P . In terms of propagation speed and period, the temporal or firing frequency ω is given by $\omega = cP^{-1}$. The dispersion relationship $\omega = \omega(a, b, P^{-1})$ is illustrated in Fig. 5 for $b = 0.05$ and two values of a . The maximum frequency on the dispersion curve is denoted by $\omega_{\max}(a, b)$. In the remaining discussion we will take $b = 0.05$. In that case, there are no other local maxima on the dispersion curve, although in general this may not be true. For a given frequency ω with $0 < \omega < \omega_{\max}$, there are two wave trains with different wavelengths $P_1 > P_2$. In Fig. 5 $P_1(P_2)$ corresponds to the left (right) branch of the dispersion curve. Since $c = \omega P$, we note that for given ω the left branch corresponds to the faster wave train. As P^{-1} tends to zero, the slope of the left (right) branch of the dispersion curve tends

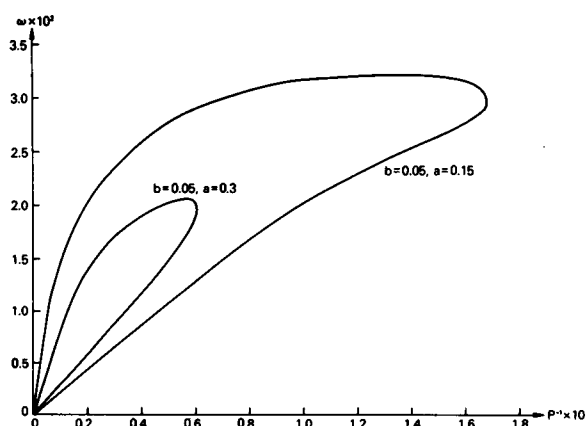


FIGURE 5 Temporal frequency ω of a periodic wave train as a function of P^{-1} for $b = 0.05$ and $a = 0.15, 0.3$ as determined in ref. 22. The unique maximum on each dispersion curve is $\omega = \omega_{\max}$. For each ω with $0 < \omega < \omega_{\max}$, the left branch corresponds to the faster wave train.

to the speed of the fast (slow) solitary pulse solution. Correspondingly, the solitary pulse is a limiting case of the periodic wave with infinite period.

To analyze the spatial stability of these periodic wave train solutions we consider the variational equation 6 where now Eq. 8 is replaced by

$$f'(v_c) = 1 - \gamma_0^{-1} \sum_{n=-\infty}^{\infty} \delta(nP) - \gamma_1^{-1} \sum_{n=-\infty}^{\infty} \delta(z_1 + nP). \quad (20)$$

Here $\gamma_0 = -v'_c(0)$ and $\gamma_1 = v'_c(z_1)$. As Fig. 4 indicates, we have chosen $z = 0$ so that $v_c = a$ on the front of the wave at $z = 0$; and, therefore we have $v_c(z_1) = a = v_c(z_1 + P)$. The quantities z_1 and $z_1 + P$ are negatives of the quantities Z_1 and Z_{-1} associated with a leftward traveling wave of ref. 22. These latter quantities satisfy Eqs. 45–47 of ref. 22. We now seek solutions to Eq. 6 of the exponential form of Eq. 10. It follows that $V = (V, V', W)$ satisfies the ordinary differential equation 11 and the jump conditions

$$\left. \begin{matrix} V' \\ (nP)^+ \\ (nP)^- \end{matrix} \right] = -\gamma_0^{-1} V(nP) \quad (21 A)$$

$$\left. \begin{matrix} V' \\ (z_1 + nP)^+ \\ (z_1 + nP)^- \end{matrix} \right] = -\gamma_1^{-1} V(z_1 + nP) \quad (21 B)$$

for $n = 0, \pm 1, \pm 2, \dots$. The wave train is spatially unstable if for any λ with $Re\lambda > 0$, Eqs. 11 and 21 have a bounded solution V belonging to the admissible class of perturbations. The solution V is an unstable mode with growth parameter $Re\lambda$.

As in the temporal stability analysis (22) of the wave train solutions, we consider periodic solutions of Eqs. 11 and 21 for real values of λ . We construct such a solution by patching sums of exponentials $Y_j \exp(\rho_j z)$ over the intervals $z_1 < z < 0$ and $0 < z < z_1 + P$. By imposing the normalization condition $V(0) = 1$ we are led to a transcendental equation which relates λ to the parameters a, b, ω , and P . This equation for λ is quite complicated and we will not display it here. Rather, we point out that it can be written as

$$\mathcal{G}(\lambda, a, b, \omega, P^{-1}) \equiv \mathcal{F}(\lambda, a, b, c) + \mathcal{E}(\lambda, a, b, \omega, P^{-1}) = 0, \quad (22)$$

where \mathcal{F} is given by Eq. 18 and $c = \omega P$. If the ρ_j satisfy inequalities 15 or 16, we have that $\mathcal{E} = 0$ for $P = \infty$. Thus as $P \rightarrow \infty$, this equation reduces to Eq. 17 which determines the growth and decay rates of unstable and stable modes for solitary pulses.

We have solved Eq. 22 numerically for λ with various specified values of a and b . Fig. 6 illustrates our results for the two cases $b = 0.05, a = 0.15, 0.3$ which correspond to Fig. 5. For those values of ω , $\omega_0 \leq \omega < \omega_{\max}$, and P^{-1} on the slow (right) branch of the dispersion curve we find a solution $\lambda > 0$ to Eq. 22. This is the growth

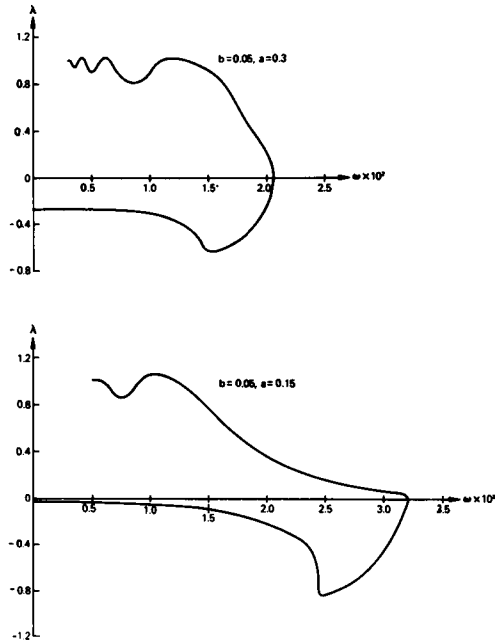


FIGURE 6 Growth rate $\lambda(a, b, \omega, P^{-1})$ of a periodic spatially unstable mode for a slow periodic wave train versus ω for $b = 0.05$, $a = 0.15, 0.3$, determined numerically from Eq. 29. The range of ω here is $\omega_0(a, b) \leq \omega < \omega_{\max}$. For the maximum frequency wave train, $\lambda(a, b, \omega_{\max}, P^{-1}) = 0$. Negative values of λ correspond to a fast wave train.

rate of an unstable periodic mode. For values of ω and P on the fast (left) branch of the dispersion curve we find a solution $\lambda < 0$ to Eq. 22. Hence we conclude that the slow wave trains, for $\omega_0 \leq \omega < \omega_{\max}$, are spatially unstable while the fast wave trains are spatially stable. For $\omega = \omega_{\max}$ the solution λ to Eq. 22 passes through zero demonstrating that the maximum frequency wave has neutral spatial stability.

For a slow wave train, with $0 < \omega < \omega_0$, we did not obtain an unstable periodic mode by the above calculation. Numerically we found that for small values of ω , the dependence of λ on ω appears to be oscillatory and complicated by a multiplicity of roots to Eq. 22. It is not surprising that we encounter numerical uncertainty in the limit, $\omega \rightarrow 0$, because for the slow solitary pulse Eq. 17 may not have a solution $\lambda > 0$. We have no doubt however that the slow speed, long wavelength trains are spatially unstable; the precise nature of their instability is not entirely clear to us. On the other hand, for a fast wave train, with ω small, we found a solution, $\lambda < 0$, to Eq. 22. As ω tends to zero, this solution tends to the negative solution of Eq. 17 which corresponds to the fast solitary pulse.

In addition to the periodic solution of Eqs. 11 and 21 for λ obtained from Eq. 22, and the periodic solution $V = (v'_c, v''_c, w'_c)$ for $\lambda = 0$, we discovered some nonperiodic solutions to Eqs. 11 and 21 for other values of λ . We determined such solutions, for sets of values a, b, ω , and P , by applying the Floquet theory for linear ordinary differ-

ential equations with periodic coefficients. For many wave trains we found a non-periodic solution with $\lambda = O(1)$. We found such solutions even for fast wave trains which we concluded above were spatially stable. For such cases, we argue, analogous to the development in the Appendix, that these nonperiodic solutions are spurious to our stability analysis. We summarize our spatial stability analysis of the periodic wave trains and numerical example for $b = 0.05$ in the following statement.

Proposition 2

For $b = 0.05$, and positive values of $a < a_*(b)$, and for each $\omega < \omega_{\max}(a, b)$, there are two periodic wave train solutions to Eqs. 1–2 with different propagation speeds. The slow wave train is spatially unstable. For ω satisfying $\omega_b(a, b) \leq \omega < \omega_{\max}$ the growth rate $\lambda(a, b, \omega, P^{-1})$ of its periodic unstable mode satisfies Eq. 22. The unique wave train of maximum frequency has spatial neutral stability.

We conclude with the following remark. The fact that neutral spatial stability corresponds to a point on the dispersion curve where $d\omega/d(P^{-1}) = 0$ can be demonstrated analytically; its proof may be found in ref. 25. We emphasize that this qualitative feature of our spatial stability analysis appears not to be common to a temporal stability analysis. Indeed, *temporal* stability analysis (22) of the wave train solutions to Eqs. 1–2 for $b = 0.005$ shows that waves of maximum frequency as well as some fast wave trains are temporally unstable.

APPENDIX

Here we indicate the instability of a slow pulse whose speed c satisfies $c_{\min} < c < \hat{c}$. The argument is based on certain spectral properties of the ordinary differential operator in Eqs. 11–12. We will now describe the relevant properties.

For a given set of values a , b , and c , the growth parameter calculated in the section on Spatial Stability Analysis of Solitary Pulses as a solution to Eq. 17 corresponds to a solution $V(z)$ of Eqs. 11–12 which satisfies

$$V(z) \rightarrow 0 \text{ as } |z| \rightarrow \infty.$$

In addition to this decaying solution and the decaying solution (v'_c, v''_c, w'_c) for $\lambda = 0$, there is a one parameter family of bounded solutions, $V(z, \lambda)$ with $\lambda = \lambda(a, b, c, k)$ and $-\infty < k < \infty$, which oscillate sinusoidally as $|z| \rightarrow \infty$. These oscillatory solutions correspond to the continuous spectrum of the ordinary differential operator in Eqs. 11–12.

We can construct such an oscillatory solution if $\text{Re} \rho_j = 0$ for at least one value of j . Suppose for example that for some complex value of λ we have

$$\text{Re} \rho_1 < \text{Re} \rho_2 < 0 = \text{Re} \rho_3. \quad (23)$$

Then an oscillatory solution to Eqs. 11–12 is constructed in the following way. Let $V(z, \lambda) = Y_3 \exp(\rho_3 z)$ for $z < z_1$. Now match across $z = z_1$ by using the continuity of V and W and the jump condition (12 B) to define $V(z, \lambda)$ in the interval $z_1 < z < 0$. Continue the solution for $z > 0$ by matching at $z = 0$. The solution $V(z, \lambda)$ will be bounded for $z > 0$ since $\text{Re} \rho_j \leq 0$ for $j = 1, 2, 3$. Solutions can be constructed in a similar manner if $\text{Re} \rho_j = 0$ for $j = 1, 2$.

We now demonstrate how values of λ may be generated which insure $\text{Re} \rho_j = 0$ for at least one

value of j . With $\rho = ik$, $-\infty < k < \infty$, $i = \sqrt{-1}$, and the cubic polynomial R defined by Eq. 13, the equation

$$R(ik, \lambda) = 0 \quad (24)$$

is a quadratic equation for $\lambda(k)$ (here, for convenience, we drop the arguments a , b , c). From Eq. 24, it follows that

$$\lambda = \lambda(k) = -ik \pm [1 + i(b - c^2 k^2)(ck)^{-1}]^{1/2}, \quad k \neq 0. \quad (25)$$

In Eq. 25 we choose the branch of $u(\sigma) = \sqrt{\sigma}$ which satisfies $-\pi/2 \leq \arg u < \pi/2$. With λ given by Eq. 25, the other two zeros of the cubic $R(\rho, \lambda)$ can be determined and thus $V(z, \lambda)$ can be constructed as above.

Since $\lambda(-k) = \bar{\lambda}(k)$, we can describe the behavior of $\lambda(k)$ by assuming that k is positive. According to the sign (\pm) chosen in Eq. 25 we have

$$\pm \operatorname{Re} \lambda \geq 1, \quad (26)$$

$$\lambda \sim -ik \pm (ck/2)^{1/2}(1 + i) \text{ for } k \gg 1, \quad (27)$$

and

$$\lambda \sim \pm (2ck/b)^{-1/2}(1 + i) \text{ for } 0 < k \ll 1. \quad (28)$$

Because k can be taken as positive or negative and the sign of the square root can be taken as plus or minus there are actually four branches to the continuous spectrum. The two branches associated with the minus square root lie in the left half plane $\operatorname{Re} \lambda \leq -1$ and correspond to solutions of Eqs. 6-7 which remain bounded as $x \rightarrow \infty$. We denote these two branches by Λ^- . The two branches associated with the plus square root lie in the right half plane $\operatorname{Re} \lambda \geq 1$ and correspond to solutions of Eqs. 6-7 which grow with increasing distance x . These two branches are denoted by Λ^+ . The two branches of Λ^+ intersect on the axis, $\operatorname{Im} \lambda = 0$, at the point $\lambda = \lambda^*$. By equating to zero the real and imaginary parts of Eq. 24, we find that λ^* is the unique positive root of

$$\lambda^3 + (c/2)\lambda^2 - \lambda - (b + c^2)(2c)^{-1} = 0. \quad (29)$$

The dashed curve in Fig. 3 represents λ^* as a function of c for $b = 0.05$. For the parameters $b = 0.05$, $a \approx 0.345$, and the slow pulse speed $c = 0.375$, Fig. 7 illustrates the four branches of $\lambda(k)$. The point eigenvalue $\lambda \approx 0.565$ which satisfies Eq. 17 is indicated in Fig. 7 by x on the axis, $\operatorname{Im} \lambda = 0$.

We now develop the crux of our argument. Suppose, for each pulse that the oscillatory solutions with $\lambda \in \Lambda^+$ are relevant to our stability analysis. That is, suppose they belong to the admissible class C of perturbations. Then, because $\operatorname{Re} \lambda > 0$ for $\lambda \in \Lambda^+$, we would be led to conclude that each solitary pulse is spatially unstable. Rather, we maintain, for given $b > 0$ and speed curve coordinates a , c with $c > \hat{c}$, that the solutions $V(z, \lambda)$, $\lambda \in \Lambda^+$ are irrelevant to our stability analysis. The portion Λ^+ of the continuous spectrum is spurious in this case of, $c > \hat{c}$. The spatial linear stability of the pulse is determined by Λ^- and any point eigenvalues λ which satisfy Eq. 17.

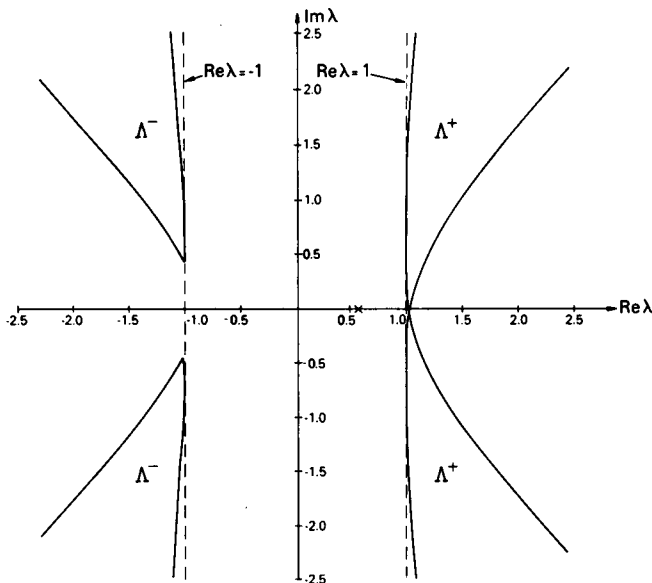


FIGURE 7 Values of λ for which Eqs. 11–12 have a bounded oscillatory solution for the slow pulse with $a \approx 0.35$, $b = 0.05$, and $c = 0.375$. Here, $\lambda = \lambda(k)$ and is given by Eq. 22. The values of $\lambda(k)$ with $\text{Re} \lambda > 0$ belong to Λ^+ and those with $\text{Re} \lambda < 0$ belong to Λ^- . The solution $\lambda \approx 0.565$ of Eq. 17 for $a \approx 0.345$, $b = 0.05$, $c = 0.375$ is denoted by x on the axis $\text{Im} \lambda = 0$.

For each fast pulse, $c > c_*$, and each slow pulse, $c_* > c > \hat{c}$, Λ^+ is spurious. For the pulse with $c = \hat{c}$, we find numerically that the limit $\hat{\lambda}$ of the point eigenvalue, as $c \rightarrow \hat{c}$ from above, coincides with λ^* , the intersection of Λ^+ and $\text{Im} \lambda = 0$; see Fig. 3. Consequently, the limit, as $c \rightarrow \hat{c}$ from above, of the decaying solution associated with the point eigenvalue is in general oscillatory. For pulses with $c < \hat{c}$ we hypothesize that some subset Λ_c of Λ^+ which includes λ^* must be considered as relevant to our stability analysis. Correspondingly, the oscillatory solutions $V(z, \lambda)$, $\lambda \in \Lambda_c$, must be included in the admissible class C of perturbations. We let λ_{\max} be a value of λ which satisfies $\text{Re} \lambda_{\max} = \max[\text{Re} \lambda]$ for $\lambda \in \Lambda_c$. Since $\text{Re} \lambda \geq 1$ for $\lambda \in \Lambda^+$, we have that $\text{Re} \lambda_{\max} \geq 1$. Hence we conclude that v_c for $c < \hat{c}$ is spatially unstable.

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