TRAVELING WAVE SOLUTIONS OF A NERVE CONDUCTION EQUATION

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ABSTRACT We consider a pair of differential equations whose solutions exhibit the qualitative properties of nerve conduction, yet which are simple enough to be solved exactly and explicitly. The equations are of the FitzHugh-Nagumo type, with a piecewise linear nonlinearity, and they contain two parameters. All the pulse and periodic solutions, and their propagation speeds, are found for these equations, and the stability of the solutions is analyzed. For certain parameter values, there are two different pulse-shaped waves with different propagation speeds. The slower pulse is shown to be unstable and the faster one to be stable, confirming conjectures which have been made before for other nerve conduction equations. Two periodic waves, representing trains of propagated impulses, are also found for each period greater than some minimum which depends on the parameters. The slower train is unstable and the faster one is usually stable, although in some cases both are unstable.

1. INTRODUCTION

The nonlinear partial differential equation proposed by Hodgkin and Huxley (10) is the most widely accepted mathematical description of the excitation and propagation of nerve impulses. The complexity of this equation led FitzHugh (6, 7) and Nagumo, Arimoto, and Yoshizawa (14) to introduce the simpler equation

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - f(v) - w$$

$$\frac{\partial w}{\partial t} = bv, \qquad b \geq 0. \tag{1}$$

While they set $f(v) = v(a - v)(1 - v)$, we follow McKean (13) and choose

$$f(v) = v - H(v - a), \quad 0 \leq a \leq \tfrac{1}{2}, \tag{2}$$

where H is the Heaviside step function. For this simplified FitzHugh-Nagumo equation we determine all the periodic and pulse traveling wave solutions and analyze their stability.

A traveling wave solution of Eq. 1 is a function $v(x, t) = v_c(z)$, where $z = x + ct$.

It follows that v_c satisfies the ordinary differential equation

$$v_c''' - cv_c'' - f'(v_c)v_c' - \frac{b}{c}v_c = 0, \qquad c \neq 0. \tag{3}$$

With f given by Eq. 2, we find v_c and its propagation speed c explicitly by solving a few transcendental equations. For each value of $b > 0$ and each a in the interval, $0 < a < a_v(b)$, we find two pulse solutions with different speeds of propagation. By a linear stability analysis we show that the slower wave is unstable. For this unstable pulse, we determine the growth rate of the unstable mode and find it to be a decreasing function of a. For $a = a_v(b)$ there is a unique pulse solution which is neutrally stable.

We also find two periodic solutions of Eq. 3 having different speeds, for each period larger than some minimum period $P_{\min}(a, b)$ provided that $0 < a < a_v(b)$. As the period becomes infinite, the periodic solutions tend to the pulse solutions. The linear stability analysis of these wave trains shows that for each a and b, all these solutions with speeds less than some speed $c_0(a, b)$ are unstable.

In the special case $b = 0$ and $w \equiv 0$ we find traveling change of state waveforms which are stable. We also find unstable standing waves of periodic and pulse type.

Our results for the pulse solutions support the numerical results of Huxley (11) and Cooley and Dodge (3). Their results suggest that, in addition to a solution which resembles the nerve impulse, there is a slower wave which satisfies the Hodgkin-Huxley equation. Similar calculations for the FitzHugh-Nagumo equation (see references 2, 7, and 14) indicate that there are two pulse solutions for $0 < a < a_v(b)$. Nagumo et al. (14) report observing only the faster pulse on their electronic line. These investigators all believe that the slower pulse is unstable. Our analysis has confirmed this belief for the simplified FitzHugh-Nagumo equation.

Infinite wave trains have been obtained numerically for the Hodgkin-Huxley (3) and FitzHugh-Nagumo (7) equations as solutions to appropriate initial boundary value problems. These evidently correspond to the faster wave trains which we have found for Eqs. 2 and 3. Casten, Cohen, and Lagerstrom (1) have obtained the faster wave trains and the faster pulse solution for the FitzHugh-Nagumo equation with $b \ll 1$ by using matched asymptotic expansions. Conley[1] has shown the existence of pulse and recurrent solutions for more general functions f and appropriate values of b and c. Offner, Weinberg, and Young (17) have also considered a nerve condition equation involving a piecewise constant coefficient.

2. SOLITARY TRAVELING PULSES

We shall now seek values of $c \neq 0$ for which Eq. 3 has a pulse-shaped solution. We may take $c > 0$ since, for each wave $v_c(z)$ with $c < 0$, which travels to the right,

[1] Conley, C. On the existence of bounded progressive wave solutions of the Nagumo equation. To be published.

there is a corresponding solution $v_{-c}(-z)$ with $-c > 0$, which represents a wave traveling to the left. Furthermore, because z does not appear in the equation explicitly, we can choose the origin $z = 0$ so that $v_c(0) = a$. We also assume that $v_c(z_1) = a$ for some $z_1 > 0$. Therefore, the solutions we seek are of the form illustrated in Fig. 1.

It follows from Eqs. 2 and 3 that these waves must satisfy the differential equation

$$v_c''' - cv_c'' - v_c' - \frac{b}{c}v_c = 0, \qquad b > 0, c > 0 \tag{4}$$

and the conditions

$$v_c''\Big[_{0^-}^{0^+} = -1, \qquad v_c''\Big]_{z_1^-}^{z_1^+} = 1, \tag{5 a}$$

$$v_c(0) = v_c(z_1) = a, \qquad z_1 > 0. \tag{5 b}$$

To represent pulses, they must also satisfy the condition

$$v_c(z) \to 0 \quad \text{as} \quad |z| \to \infty. \tag{6}$$

The jump conditions (5 a) result from the discontinuity in $f(v)$, which yields a delta function in $f'(v)$. From Eq. 1 and the requirement that w vanish at $z = -\infty$, we have

$$w_c(z) = \frac{b}{c}\int_{-\infty}^{z} v_c(\zeta)\, d\zeta. \tag{7}$$

In order that $w_c(+\infty) = 0$, the integral of v_c must vanish.

Solutions to Eq. 4 are linear combinations of the three exponentials exp $(\alpha_i z)$

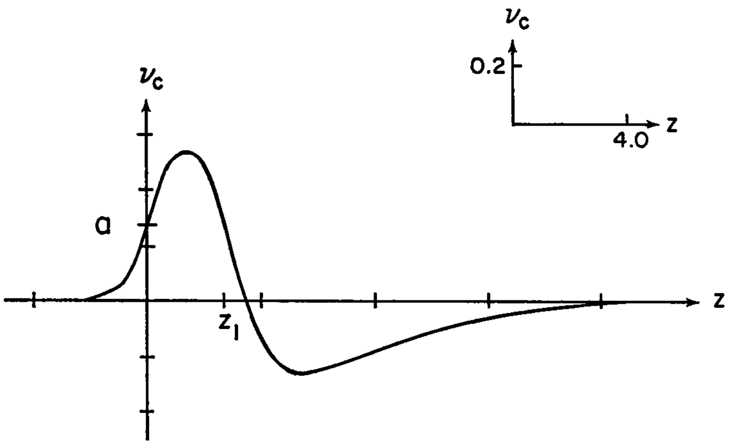

FIGURE 1 Solitary pulse traveling wave solution of Eqs. 1 and 2, $v_c(z)$, where $z = x + ct$, given by Eq. 11. The pulse illustrated here is for $a \approx 0.27$, $b = 0.2$, $c = 0.7$, and $z_1 \approx 2.7$.

$i = 1, 2, 3$, where the α_i are zeros of the cubic

$$p(\alpha) = \alpha^3 - c\alpha^2 - \alpha - \frac{b}{c}. \tag{8}$$

It follows from Eq. 8 that either:

$$\alpha_1 > 0, \qquad \alpha_3 < \alpha_2 < 0 \tag{9}$$

or

$$\alpha_1 > 0, \qquad \alpha_3 = \bar{\alpha}_2, \qquad Re\alpha_2 < 0 \tag{10}$$

according as $(1 - 4b)c^4 + 2(2 - 9b)c^2 - 27b^2$ is positive or nonpositive. We shall treat only the case in which the α_i are distinct. The special case $\alpha_2 = \alpha_3$ can be treated in a similar way, but it is not necessary to do so because the results for it can be obtained by continuity.

From conditions 9, 10, and 6, we see that, for $z \leq 0$, the pulse is given by $v_c(z) = a \exp(\alpha_1 z)$. Then, by using the continuity and jump conditions, we obtain v_c in the form:

$$\begin{aligned} v_c(z) &= a \cdot \exp(\alpha_1 z), \quad z \leq 0 \\ &= (a - 1/p_1') \exp(\alpha_1 z) - (p_2')^{-1} \exp(\alpha_2 z) - (p_3')^{-1} \exp(\alpha_3 z), \\ &\qquad\qquad 0 \leq z \leq z_1 \\ &= [(\exp(-\alpha_2 z_1) - 1)/p_2'] \exp(\alpha_2 z) + [(\exp(-\alpha_3 z_1) - 1)/p_3'] \exp(\alpha_3 z), \\ &\qquad\qquad z_1 \leq z. \end{aligned} \tag{11}$$

Here

$$p_i' = p'(\alpha_i), \quad i = 1, 2, 3. \tag{12}$$

The continuity of v_c' and the conditions of Eq. 5 lead to the following transcendental equation relating a, b, and c, previously given by McKean (13):

$$F(a, b, c) \equiv 2 - s + (p_1'/p_2')s^{-\alpha_2/\alpha_1} + (p_1'/p_3')s^{-\alpha_3/\alpha_1} = 0 \tag{13}$$

where

$$s = 1 - ap_1'. \tag{14}$$

The parameter z_1 is determined by the equation

$$1 - ap_1' = \exp(-\alpha_1 z_1). \tag{15}$$

Since $\alpha_1 z_1$ is positive, a value of s which satisfies Eqs. 13 and 14 must lie in the interval (0,1). As an equation for s, Eq. 13 does not depend on a. In terms of s, a is given by Eq. 14.

In the Appendix we prove the following theorem.

Theorem 1

For given positive values of b and c, a necessary and sufficient condition for Eq. 13 to have a root s, $0 < s < 1$, is that

$$c^2 > b(1 + 2b^{1/2})^{-1}. \tag{16}$$

The root s is unique.

To each such root s there corresponds a pulse solution v_c of Eqs. 4–6. Hence the following existence theorem is a direct consequence of Theorem 1.

Theorem 2

For given $b > 0$ and each value of the propagation speed $c > 0$ satisfying condition 16, the simplified FitzHugh-Nagumo Eqs. 1 and 2 have a unique nontrivial pulse-shaped traveling wave solution. The appropriate value of $a(b, c)$ is determined by Eq. 14 where s solves Eq. 13.

From the inequality 16 we see that there are pulses corresponding to every $c > c_{\min}(b)$ where

$$c_{\min}(b) = b^{1/2}(1 + 2b^{1/2})^{-1/2}. \tag{17}$$

From Eq. 17 $c_{\min} \sim (b/4)^{1/4}$ for $b \gg 1$ and $c_{\min} \sim b^{1/2}$ for $b \ll 1$. This behavior differs from that of the cubic FitzHugh-Nagumo equation for which there are no pulses with $c > 2^{-1/2}$ (2, 13).

Since $s > 0$, we have a bound on the value of a obtained from Eq. 14, namely $a < (p_1')^{-1}$. From Eq. 8 and the fact that $p(\alpha_1) = 0$, we obtain $p_1' = 2 + c\alpha_1 + 3b/c\alpha_1$. Then we can write the preceding inequality as

$$a < (2 + c\alpha_1 + 3b/c\alpha_1)^{-1} < (2 + b^{1/2})^{-1}, \tag{18}$$

where we get the last inequality from Eq. B.5 of Rinzel (16) and the neglect of the positive quantity $3b/c\alpha_1$. Hence, it follows that pulse solutions do not exist for $a > \frac{1}{2}$. Moreover, for given $b > 0$, condition 18 establishes a bound on the largest value of a for which pulses can exist.

We have solved Eq. 13 numerically with values of b and c which satisfy condition 16. The corresponding value of a for each pulse is obtained from Eq. 14. The results of these calculations are illustrated in the speed diagram, Fig. 2. It displays the various speed curves, c versus a for fixed $b > 0$. McKean (14) previously determined a portion of this diagram. Each speed curve has a clearly defined knee (a_r, c_r)

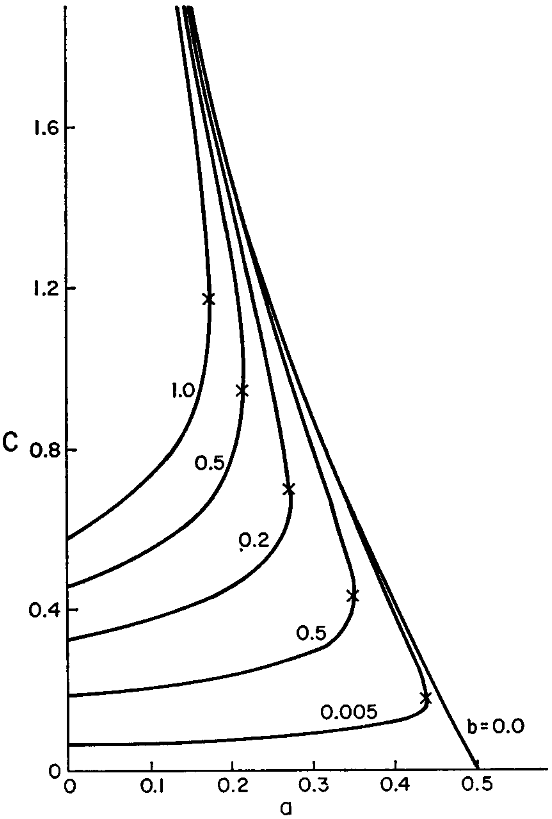

FIGURE 2 Propagation speed $c(a, b)$ of a pulse as a function of a for various positive values of b, determined numerically from Eqs. 13 and 14. The point a_v, c_v determined by Eq. 19 is indicated by x. As $a \to 0$, the upper branch $c_f(a, b) \to \infty$. For $b = 0$, C is the speed of a transition waveform and is given by Eq. 55.

characterized by

$$F(a_v, b, c_v) = 0, \qquad F_c(a_v, b, c_v) = 0. \tag{19}$$

For each value of $a < a_v$ we find two pulse solutions with speeds $c_f(a, b)$ and $c_s(a, b)$, with $c_f > c_s$.

We observe that $c_{\min}(b)$, the minimum value of c on each speed curve, occurs at $a = 0$. However, there are no pulse solutions with $a = 0$. Therefore $c_{\min}(b)$ is just the limit of $c_s(a, b)$ as a tends to zero:

$$c_{\min}(b) = \lim_{a \to 0} c_s(a, b). \tag{20}$$

We demonstrate this in Appendix C of Rinzel (16) by considering the behavior of $F(a, b, c)$ for $a \ll 1$.

We summarize our numerical and analytic results in the following statement.

Proposition 1

For given positive values of a and b where $a < a_v(b) < \frac{1}{2}$, the simplified FitzHugh-Nagumo Eqs. 1 and 2 have precisely two pulse-shaped traveling wave solutions. Their propagation speeds $c_f(a, b)$ and $c_s(a, b)$ satisfy $c_f > c_v(b) > c_s > c_{\min}(b)$. For $a = a_v$ there is a unique pulse which travels with speed c_v. There are no traveling pulses for $a > a_v(b)$ or for $a \leq 0$.

Figs. 3 and 4, respectively, are graphs of the pulse height $\sup_z v_c(z)$ and pulse width z_1 versus a for fixed values of b. They show that the slower pulses are low amplitude or subthreshhold waves. This is consistent with the numerical results for the Hodgkin-Huxley and FitzHugh-Nagumo equations. The curves for $b = 0$ correspond to solutions discussed in section 6. Fig. 5 shows curves of c versus b for a few values of a. The curve for $a = 0$ is just the graph of $c_{\min}(b)$.

In Fig. 2, the propagation speed is not shown for $c > 2$. To complete this speed diagram, we provide an asymptotic description of the fast branches of the speed curves for large c. Thus we find $a(b, c)$ for $c \gg 1$. In this region $s \ll 1$ since, from Fig. 4, z_1 becomes infinite and, from Appendix *A* of Rinzel (16), $\alpha_1 \sim c + c^{-1}$. Retaining only the dominant exponential in Eq. 13 and using the asymptotic expressions for α_i and p_1' from Appendix A (16), we find that s is exponentially small:

$$s \sim \left[\frac{2(1-4b)^{1/2}}{3+c^2}\right]^{2(c^2+1)[1-(1-4b)^{1/2}]^{-}}, \qquad c \gg 1. \tag{21}$$

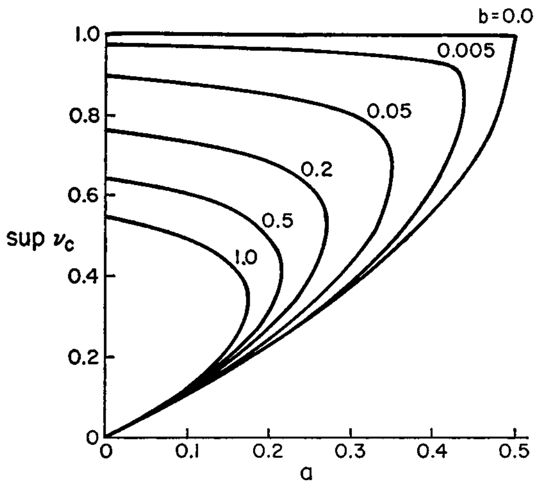

FIGURE 3 Pulse height $\sup_z v_c(z)$ versus a for various positive values of b, determined from Eq. 11 for $0 \leq z \leq z_1$. For $b = 0$, the upper branch corresponds to a transition waveform given by Eq. 54 for which $\sup v_c = v_c(\infty) = 1$. The lower branch for $b = 0$ corresponds to a standing pulse given by Eq. 56, for which $\sup_x v_c(x) = v_c(x_1/2)$.

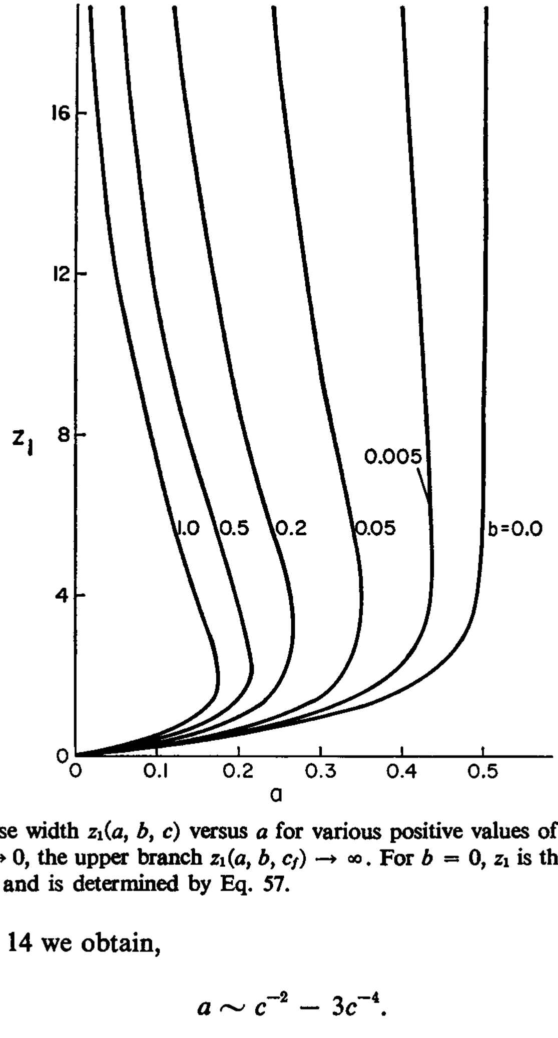

FIGURE 4 Pulse width $z_1(a, b, c)$ versus a for various positive values of b, determined by Eq. 15. As $a \to 0$, the upper branch $z_1(a, b, c_f) \to \infty$. For $b = 0$, z_1 is the width $x_1(a)$ of a standing pulse and is determined by Eq. 57.

Hence from Eq. 14 we obtain,

$$a \sim c^{-2} - 3c^{-4}. \tag{22}$$

To this order, $a(b, c)$ is independent of b.

By a similar argument we obtain an asymptotic description of the knee region of the speed curves in Fig. 2 for $b \ll 1$. From Eq. 17 we have $c = 0(b^{1/2})$ so that we use the expressions for α_i and p_i' from Appendix A (16) for $(b/c) \ll 1$, $c \ll 1$. Taking $s \ll 1$ leads to an asymptotic expression for s and, consequently, for a:

$$a \sim \left[1 - 2^{c/b}\left(2 + c + 3\frac{b}{c}\right)^{-c/b}\right]\left(2 + c + 3\frac{b}{c}\right)^{-1}. \tag{23}$$

From Eq. 23 we obtain an approximation to a_ν for $b \ll 1$:

$$a_\nu \sim 2^{-1}[1 + (3b)^{1/2}]^{-1}, b \ll 1. \tag{24}$$

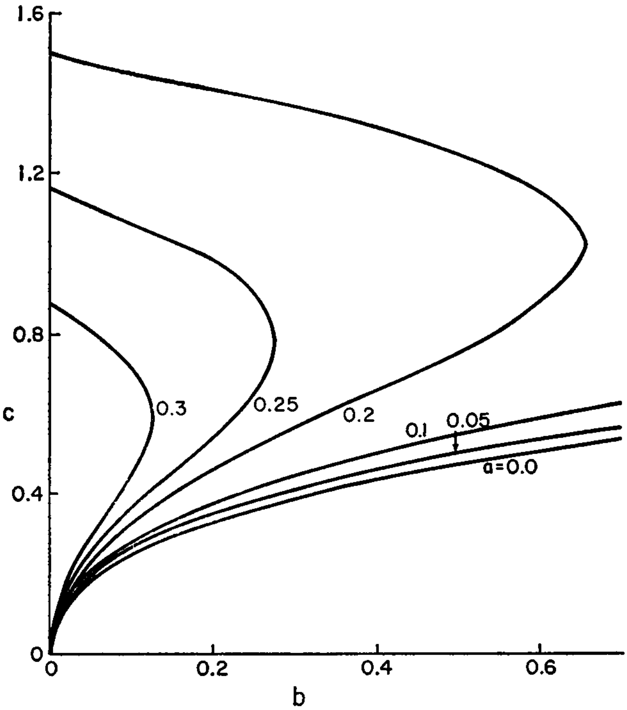

FIGURE 5 Propagation speed $c(a, b)$ of a pulse versus b for various values of a. Only portions of the double branched curves for $a = 0.05, 0.1$ can be shown with the limits of b and c chosen here. For $a = 0$, $c = c_{min}(b)$ and is given by Eq. 17.

These asymptotic results, along with similar results for $c = 0(1)$ and $b \ll 1$, provide excellent initial guesses for the numerical procedure to solve Eq. 13.

3. STABILITY ANALYSIS OF PULSES

We introduce the traveling coordinate frame (z, t) in which Eq. 1 takes the form

$$v_t = v_{zz} - cv_z - f(v) - w$$
$$w_t = bv - cw_z. \qquad (25)$$

The pulse v_c, w_c is a t-independent solution of this equation. To study its stability we consider the variational equation

$$\tilde{V}_t = \tilde{V}_{zz} - c\tilde{V}_z - f'(v_c)\tilde{V} - \tilde{W}$$
$$\tilde{W}_t = b\tilde{W} - c\tilde{W}_z \qquad (26)$$

where

$$f'(v_c) = 1 - \delta(v_c - a). \qquad (27)$$

Since $v_c(0) = a = v_c(z_1)$, the z-dependence of Eq. 27 is explicitly

$$f'(v_c) = 1 - \gamma_0^{-1}\delta(z) - \gamma_1^{-1}\delta(z - z_1) \tag{28}$$

where

$$\gamma_0 = v_c'(0) = a\alpha_1$$
$$\gamma_1 = -v_c'(z_1) = (\alpha_1/p_1') + (\alpha_2/p_2') \exp(\alpha_2 z_1) + (\alpha_3/p_3') \exp(\alpha_3 z_1). \tag{29}$$

We now look for solutions of Eq. 26 having the form

$$\tilde{V}(z, t) = e^{\lambda t}V(z), \tilde{W}(z, t) = e^{\lambda t}W(z). \tag{30}$$

It follows from Eqs. 26 and 30 that $\mathbf{V} = (V, V', W)$ must satisfy the ordinary differential equation

$$\begin{pmatrix} V \\ V' \\ W \end{pmatrix}' = \begin{pmatrix} 0 & 1 & 0 \\ \lambda + 1 & c & 1 \\ \dfrac{b}{c} & 0 & -\dfrac{\lambda}{c} \end{pmatrix} \begin{pmatrix} V \\ V' \\ W \end{pmatrix}, \qquad z \neq 0, z_1 \tag{31}$$

and the jump conditions

$$V']_{0-}^{0+} = -\gamma_0^{-1}V(0), \; V']_{z_1-}^{z_1+} = -\gamma_1^{-1}V(z_1). \tag{32}$$

The pulse v_c is unstable if Eqs. 31 and 32 have a bounded solution with $Re\lambda > 0$. This solution is an unstable mode with growth parameter $Re\lambda$. On the other hand, v_c is stable if Eqs. 31 and 32 have no bounded solutions with $Re\lambda > 0$. For $\lambda = 0$, there is always a solution of Eqs. 31 and 32: $\mathbf{V} = \mathbf{V}_c' = (v_c', v_c'', bv_c/c)$. This is because any translate of v_c is also a solution of Eq. 25.

Solutions of Eq. 31 are sums of the exponentials $\mathbf{X}_i \exp(\beta_i z)$, $i = 1, 2, 3$. The β_i are zeros of the cubic

$$Q(\beta, \lambda) \equiv \beta^3 + c^{-1}(\lambda - c^2)\beta^2 - (1 + 2\lambda)\beta - c^{-1}(\lambda^2 + \lambda + b), \tag{33}$$

and the vector $\mathbf{X}_i$ is given by

$$\mathbf{X}_i = (1, \beta_i, b(\lambda + c\beta_i)^{-1}), i = 1, 2, 3.$$

Since the slower pulses are expected to be unstable, we take $c = c_s(a, b)$ and consider λ real and non-negative. When $\lambda = 0$, Q reduces to p so that we may then take $\beta_i = \alpha_i$. For $\lambda > 0$, we conclude from Eq. 33 that the β_i can be indexed so that they are distributed in the same manner as the α_i in relations 9 and 10. By continuity, this is also true for $\lambda < 0$ in some interval containing $\lambda = 0$.

When the β_i are distributed in the above manner, we can determine a bounded solution to Eqs. 31 and 32 as follows. Using $V(0) = 1$ as a normalization condition, we must have $\mathbf{V} = \mathbf{X}_1 \exp(\alpha_1 z)$ for $z \leq 0$. We use the continuity of V and W and the jump condition 32 to continue the solution through the interval $0 \leq z \leq z_1$. In a similar way, we match across $z = z_1$ and then set the coefficient of $\mathbf{X}_1 \exp(\alpha_1 z)$ equal to zero to complete the definition of $\mathbf{V}$. Thus we are left with a transcendental equation for λ in terms of a, b, and c:

$$\tilde{F}(\lambda, a, b, c) = 0 \tag{34}$$

where a, b, and c satisfy Eqs. 13 and 14. Here $\tilde{F}$ is defined by

$$\begin{aligned}\tilde{F}(\lambda, a, b, c) = {} & [\gamma_0 - (\lambda + c\beta_1)(cQ_1')^{-1}][\gamma_1 - (\lambda + c\beta_1)(cQ_1')^{-1}] \\ & + \exp[(\beta_2 - \beta_1)z_1](\lambda + c\beta_2)(\lambda + c\beta_1)(c^2 Q_2' Q_1')^{-1} \\ & + \exp[(\beta_3 - \beta_1)z_1](\lambda + c\beta_3)(\lambda + c\beta_1)(c^2 Q_3' Q_1')^{-1}\end{aligned} \tag{35}$$

where

$$Q_i' = Q'(\beta_i, \lambda), \quad i = 1, 2, 3. \tag{36}$$

For each set of values a, b, $c = c_s(a, b)$ satisfying Eqs. 13 and 14, we solve Eq. 34 numerically for $\lambda > 0$. The growth curves $\lambda = \lambda(a, b, c_s)$ are illustrated in Fig. 6. The special case $b = 0$, $c = 0$ is treated in section 6. The positive branch ($\lambda > 0$) of each growth curve corresponds to the lower branch of the respective speed curve in Fig. 2. We notice that $\lambda \rightarrow 0$ as $a \rightarrow a_r$. Thus the knee of the speed curve corresponds to neutral stability. Moreover, we see that $\partial\lambda/\partial a < 0$, for $a < a_r$, with $\lambda \rightarrow \infty$ as $a \rightarrow 0$. Thus the instability, as measured by λ, becomes more severe as a gets further from a_r. These calculations indeed verify the instability conjecture, that the slow pulse is unstable, for the present nerve conduction model. In addition, we find, corresponding to some initial portion of the upper branch of each speed curve in Fig. 2, values of $\lambda = \lambda(a, b, c_f) < 0$ which satisfy Eq. 34. Thus the growth curves in Fig. 6 are continued below $\lambda = 0$. Each curve terminates at the point where the β_i are no longer distributed in a manner consistent with our assumption, in conditions 9 or 10. These curves could be continued by seeking a solution $\mathbf{V}$ to Eqs. 31 and 32 corresponding to some other distribution of the β_i.

We now proceed to demonstrate analytically that the pulse v_{c_r} corresponding to the speed curve knee, is neutrally stable. As we have pointed out, $\mathbf{V}_c'$ is a solution to Eqs. 31 and 32 with $\lambda = 0$. Correspondingly, $\lambda = 0$ is a root of Eq. 34. We observe further that if the transition from instability to stability on any particular speed curve is evidenced by λ passing from positive to negative values, then $\lambda = 0$ characterizes neutral stability. Consequently, $\lambda = 0$ should appear as a double root of $\tilde{F} = 0$. More precisely, if the knee is a point of neutral stability, under these

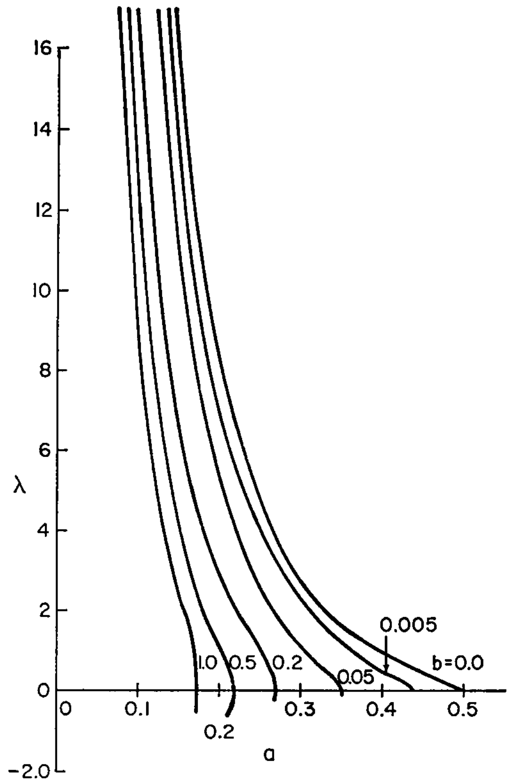

FIGURE 6 Growth rate $\lambda(a, b, c_s)$ of unstable mode for a slow pulse versus a for various positive values of b, determined numerically from Eqs. 34 and 35. As $a \rightarrow 0, \lambda(a, b, c_s) \rightarrow \infty$. For the neutrally stable pulse, $\lambda(a_\nu, b, c_\nu) = 0$. Negative values of λ correspond to a fast pulse. For $b = 0$, λ is determined numerically from Eq. 64.

hypotheses, then a_ν, c_ν must satisfy the pair of equations

$$\bar{F}_\lambda(0, a_\nu, b, c_\nu) = 0 \quad \text{and} \quad F(a_\nu, b, c_\nu) = 0. \tag{37}$$

With a great deal of algebra we have verified that Eq. 37 is equivalent to Eq. 19. and therefore that the knee is a point of neutral stability. This characterization of neutral stability obviously does not require the actual calculation of the growth rate of the unstable mode.

As a result of the above demonstration and numerical results, we state the following proposition.

Proposition 2

Each slow traveling pulse solution v_{c_s} of the simplified FitzHugh-Nagumo Eqs. 1 and 2 is unstable. The exponential growth rate $\lambda(a, b, c_s)$ of its unstable mode satisfies Eq. 34. The unique pulse v_{c_ν} is neutrally stable.

The preceding proof that v_{c_*} is neutrally stable depended on the fact that the growth rate λ satisfies a transcendental equation. To demonstrate this result for the cubic FitzHugh-Nagumo equation, as well as other nerve conduction models with double-branched speed curves, an alternate characterization of neutral stability is useful. It can be described as follows. We assume that at neutral stability the growth rate λ vanishes. However, except for a constant factor, v_c', w_c' is the unique solution of Eq. 26 having the form of Eq. 30 with $\lambda = 0$. Hence, for the neutrally stable pulse, there must be a nontrivial solution to the inhomogeneous equation obtained by replacing the left-hand side of Eq. 26 by v_c', w_c'. The solvability condition for this equation is

$$\int_{-\infty}^{\infty} (v_c' v^\dagger + w_c' w^\dagger)\, d\zeta = 0. \tag{38}$$

Here $v^\dagger$, $w^\dagger$ is the bounded solution to the homogeneous adjoint equation for the t-independent version of Eq. 26. This is the condition for neutral stability in the general case.

For the simplified FitzHugh-Nagumo equation we have obtained $v^\dagger$, $w^\dagger$ in terms of a, b, and c which satisfy Eq. 13. The solvability condition 38 in this case reduces to a transcendental equation. Together with Eq. 13 it provides a pair of equations for the point of neutral stability on each speed curve. We have shown that this pair of equations is indeed equivalent to Eq. 19.

We now consider the FitzHugh-Nagumo equation with a general f which depends on a parameter a. We assume that $a(b, c)$ describes a double-valued speed curve. To demonstrate that v_{c_*} is neutrally stable we first substitute v_c, w_c into Eq. 25 and differentiate with respect to c. Next, we set $c = c_*$ and form the inner product with the $v^\dagger$, $w^\dagger$ corresponding to v_{c_*} to obtain a scalar equation. Since $\partial a/\partial c = 0$ at c_*, one term drops out of this equation. After performing an integration by parts and using the fact that $v^\dagger$ and $w^\dagger$ satisfy the homogeneous t-independent adjoint equation for Eq. 26, we see that v_{c_*} satisfies Eq. 38. Assuming that Eq. 38 determines neutral stability uniquely, we conclude that v_{c_*} is neutrally stable. Knight (unpublished) uses a similar argument to show that neutral stability occurs at the speed curve knee.

4. PERIODIC WAVE TRAINS

Repetitive firing behavior of many nerve fibers suggests that there should be periodic traveling wave solutions to nerve conduction equations. Cooley and Dodge (3) computed solutions to the Hodgkin-Huxley equation for an initial boundary value problem and found wave trains which appeared to become periodic as t increased. FitzHugh (7) calculated a periodic solution of his equation 3. Wave trains were also obtained asymptotically by Casten, Cohen, and Lagerstrom (1) for the FitzHugh-Nagumo equation 3 with $b \ll 1$.

For the simplified FitzHugh-Nagumo equation we seek a periodic traveling solution with period P and propagation speed c. The general form of such a wave over one period, $Z_{-1} \leq z \leq Z_1$ where $Z_{-1} < 0$ and $Z_1 > 0$, is illustrated in Fig. 7. Since w_c, a multiple of the integral of v_c, must also be periodic, v_c must be negative over some portion of its period so that its integral over a period is zero. We have again used the translation invariance of Eq. 3 to fix the origin $z = 0$, requiring $v_c(0) = a$. A solution having this form, with v_c and v_c' continuous, will satisfy Eq. 4 and the conditions

$$v_c''\big]_{0-}^{0+} = -1, \; v_c''(Z_{-1}^{+}) - v_c''(Z_1^{-}) = 1, \tag{39}$$

$$v_c(Z_{-1}) = v_c(0) = a, \tag{40}$$

$$v_c(Z) = v_c(Z + P), \tag{41}$$

$$P = Z_1 - Z_{-1}. \tag{42}$$

Thus v_c can be written as

$$v_c(z) = \sum_{i=1}^{3} A_i \exp(\alpha_i z), \qquad Z_{-1} \leq z \leq 0, \tag{43}$$

$$= \sum_{i=1}^{3} B_i \exp(\alpha_i z), \qquad 0 \leq z \leq Z_1.$$

Here

$$A_i = [1 - \exp(\alpha_i Z_1)](p_i')^{-1}[\exp(\alpha_i Z_{-1}) - \exp(\alpha_i Z_1)]^{-1}, \tag{44}$$

$$B_i = [1 - \exp(\alpha_i Z_{-1})](p_i')^{-1}[\exp(\alpha_i Z_{-1} - \exp(\alpha_i Z_1]^{-1}, \; i = 1, 2, 3,$$

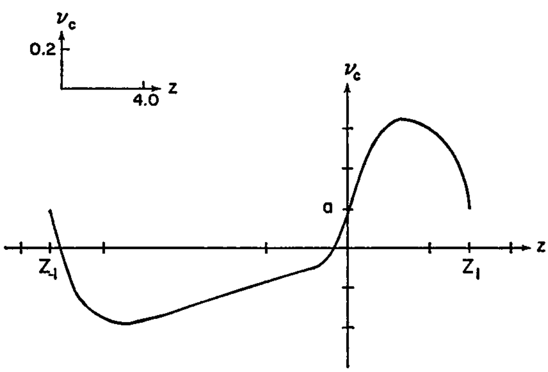

FIGURE 7 Periodic traveling wave solution of Eqs. 1 and 2, $v_c(z)$ with period P, given by Eqs. 43 and 44. Here $z = x + ct$ and $P = Z_1 - Z_{-1}$. The wave illustrated here is for $a = 0.2$, $b = 0.1$, $c = 0.75$, $Z_1 \approx 5.97$, $Z_{-1} \approx -14.5$, and $P \approx 20.5$.

where the α_i are the zeros of p given by Eq. 8 and the p_i' are defined by Eq. 12. The two conditions Eq. 40 yield the following transcendental equations for Z_{-1} and Z_i:

$$G_1(Z_{-1}, Z_1) = 0, \; G_2(Z_{-1}, Z_1) = 0. \tag{45}$$

Here

$$G_1(Z_{-1}, Z_1) = \frac{\exp(\alpha_1 Z_{-1}) - 1}{p_1' [\exp(-\alpha_1 P) - 1]} + \frac{\exp(\alpha_2 Z_1)[1 - \exp(-\alpha_2 Z_{-1})]}{p_2' [1 - \exp(\alpha_2 P)]} + \frac{\exp(\alpha_3 Z_1)[1 - \exp(-\alpha_3 Z_{-1})]}{p_3' [1 - \exp(\alpha_3 P)]} + a \tag{46}$$

$$G_2(Z_{-1}, Z_1) = \frac{[\exp(\alpha_1 Z_{-1}) - 1][1 - \exp(-\alpha_1 Z_1)]}{p_1' [\exp(-\alpha_1 P) - 1]} + \frac{[1 - \exp(-\alpha_2 Z_{-1})][\exp(\alpha_2 Z_1) - 1]}{p_2' [1 - \exp(\alpha_2 P)]} + \frac{[1 - \exp(-\alpha_3 Z_{-1})][\exp(\alpha_3 Z_1) - 1]}{p_3'[1 - \exp(\alpha_3 P)]}. \tag{47}$$

The period $P(a, b, c)$ as defined in Eq. 42 is determined by Eq. 45.

Since, with Z_1 fixed, Eq. 45 reduces to Eqs. 13 and 14 when $P \rightarrow \infty$, the solitary pulse is a limiting case of the periodic wave with infinite period. In Appendix D of Rinzel (16) this observation is used to obtain asymptotic expressions for parameters which describe large period waves in terms of those for the solitary pulses. These expressions provide initial guesses for the numerical procedure to solve Eq. 45.

We have solved Eq. 45 numerically for Z_{-1} and Z_1 for various values of a, b, and c. We find that for $0 < b \leq 0.1$ the region in the $a - b$ plane for which there are pulses is also the region in which there are wave trains. Fig. 8 represents a typical example of our results. It shows the propagation speed $c(a, b, P)$ of each wave train as a function of its period P for $b = 0.05$ and several values of a in the interval $0 \leq a < a_r(0.05) \approx 0.35$. Each curve is double valued. For $P > P_{\min}(a, b)$ there are two wave trains with speeds of propagation $c_f(a, b, P)$ and $c_s(a, b, P)$, $c_f > c_s$. The curves show that $\lim_{P\to\infty} c_f(a, b, P) = c_f(a, b)$ and $\lim_{P\to\infty} c_s(a, b, P) = c_s(a, b)$ consistent with the observations in the preceding paragraph. For some values of a, the wave train with minimum period travels slower than the pulse with speed $c_s(a, b)$. On the fast branch, the propagation speed increases with the period. In other words, densely packed wave trains travel more slowly. While this is intuitively expected, we have not seen it reported previously.

In Fig. 9 we display the amplitude max $v_c(z)$ of a wave train as a function of its period. The upper branch of each curve corresponds to the faster train in Fig. 8. Again we find that the slower waves have lower amplitudes.

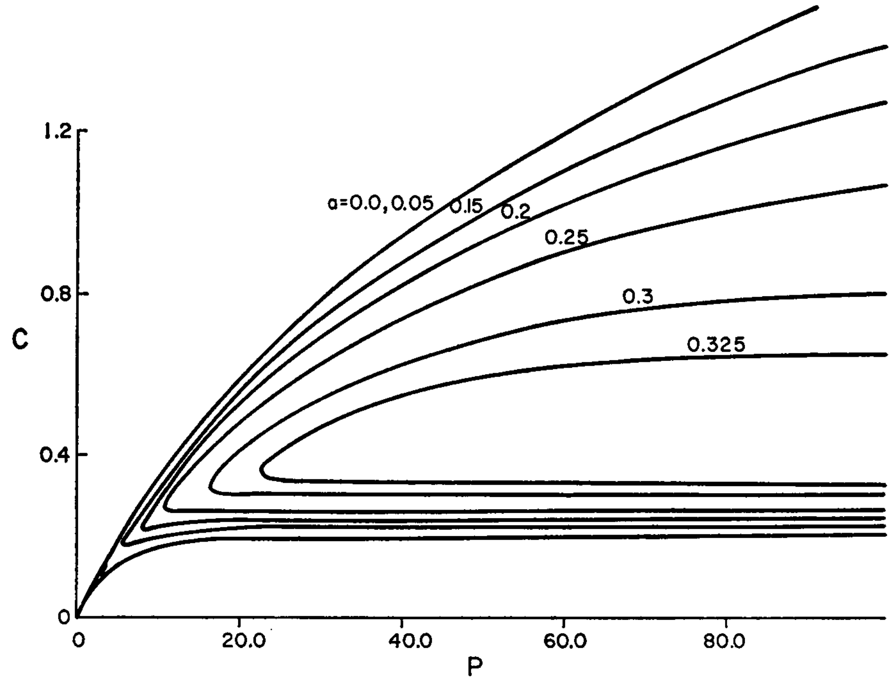

FIGURE 8 Propagation speed $c(a, b, P)$ of a periodic wave train as a function of its period P for $b = 0.05$ and various positive values of a, determined numerically from Eqs. 42 and 45–47. As $P \rightarrow \infty$, $c_f(a, b, P) \rightarrow c_f(a, b)$ and $c_s(a, b, P) \rightarrow c_s(a, b)$. For $a = 0$, $c_f(0, b, P)$ and $c_s(0, b, P)$ are determined numerically from E.2 and E.9 of Rinzel (16).

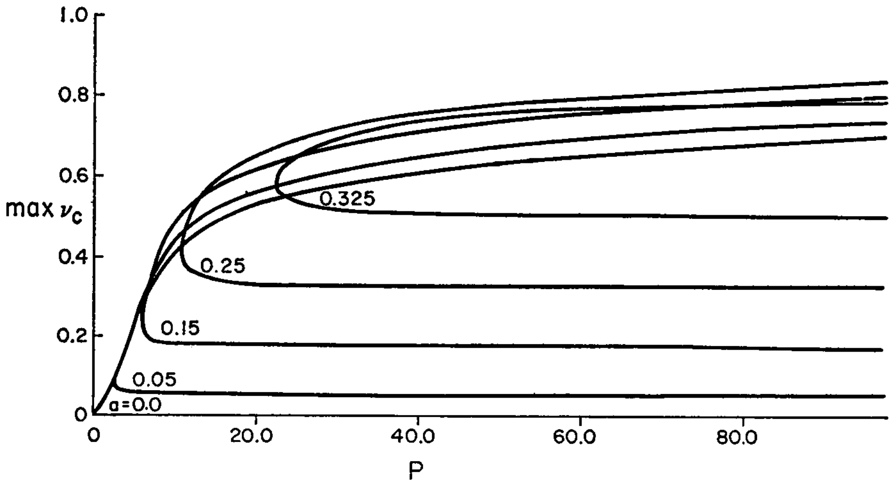

FIGURE 9 Amplitude max $v_c(a)$ of a periodic wave train as a function of its period P for $b = 0.05$ and various values of a. The amplitude is determined from Eqs. 43 and 44 for $a > 0$, and from Eq. 59, for $a = 0$.

Figs. 8 and 9 show certain results for $a = 0$. In this case $P(0, b, c)$ can be determined by solving a single transcendental equation. As in the case of pulses, there are no slow trains for $a = 0$ so that $P(0, b, c_s)$ is obtained by taking the limit as a tends to zero, $P(0, b, c_s) = \lim_{a\to 0} P(a, b, c_s)$. These results for $a = 0$ are presented in greater detail in Appendix E of Rinzel (16).

For each wave train, the firing frequency $\omega = cP^{-1}$ is the frequency of oscillation with respect to t. For given a and b we calculate the maximum possible firing frequency,

$$\omega_{\max}(a, b) = \max_{c_f, c_s} [\sup_{P > P_{\min}} \omega].$$

In Fig. 10 we illustrate, for $b = 0.05$, $\omega_{\max}$ as a function of a, $0 \leq a \leq a_\nu(0.05) \approx 0.35$. We also show the propagation speed corresponding to $\omega_{\max}$.

To illustrate clearly the range of parameter values a, b, and c for which there are wave train solutions of Eqs. 1 and 2 we define

$$C_{\min}(a, b) = \min_P c(a, b, P). \tag{48}$$

We can now state the results of our numerical calculations as follows.

Proposition 3

For given $b > 0$ and a in the interval $0 < a < a_\nu(b)$, the simplified FitzHugh-Nagumo Eqs. 1 and 2 have periodic traveling wave solutions for each c in the

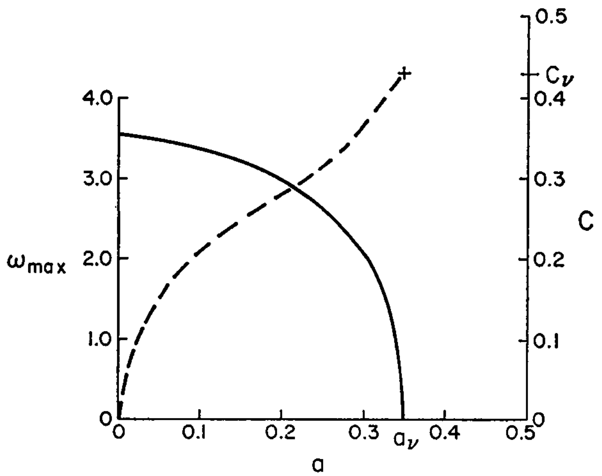

FIGURE 10 Maximum frequency, $\omega_{\max}(a, b) = \max_{c_f, c_s} [\sup_{P > P_{\min}} (cP^{-1})]$, of periodic wave trains shown solid as a function of a, for $b = 0.05$. Propagation speed of the wave with $\omega_{\max}(a, b)$ plotted (dashed) versus a for $b = 0.05$.

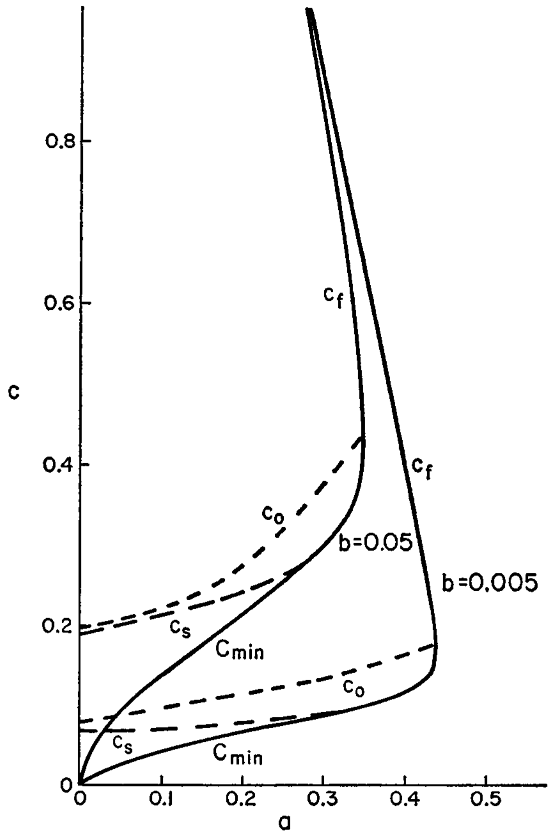

FIGURE 11 Various critical propagation speeds of periodic wave trains as functions of a for $b = 0.005$ and 0.05. The speeds $c_f(a, b)$ of the fastest train and $C_{min}(a, b)$ of the slowest train are shown solid. The speed $c_s(a, b)$ of the unstable pulse is shown dashed. A lower bound $c_0(a, b)$ for the speed of the neutrally stable train is shown dotted.

interval

$$C_{min}(a, b) \leq c \leq c_f(a, b). \tag{49}$$

The period of each wave train $P(a, b, c)$ is determined by Eqs. 42 and 45. For $b > 0.1$ there may be other periodic solutions with $c > c_f(a, b)$.

The interval 49 is indicated by double-branched curves in Fig. 11 for two values of b. The dashed curves correspond to the propagation speed of the slower pulse $c_s(a, b)$ and are reproduced from Fig. 2. The region in the a-c plane bounded by $c = c_s$, $c = C_{min}$, and $a = 0$ corresponds to parameter values for which Eqs. 2 and 3 have two periodic solutions. For $c > c_s$ there is only one periodic solution.

5. STABILITY ANALYSIS OF PERIODIC WAVE TRAINS

Because the slow pulse waves are unstable, we expect that the slower periodic traveling waves are likewise unstable. Therefore we consider the linear variational equation 27, where now 29 is replaced by

$$f'(v_c) = 1 - \gamma_0^{-1} \sum_{n=-\infty}^{\infty} \delta(nP) - \gamma_1^{-1} \sum_{n=-\infty}^{\infty} \delta(Z_1 + nP). \tag{50}$$

Here $\gamma_0 = v_c'(0)$, $\gamma_1 = -v_c(Z_1)$. Considering solutions of Eq. 27 having the exponential form of Eq. 31 leads to 32 which is a third order system of ordinary differential equations with periodic coefficients. An unstable mode V, W is a bounded solution of Eq. 32, with $Re\lambda > 0$, which is continuous for all z and which satisfies

$$V']_{(nP)^-}^{(nP)^+} = -\gamma_0^{-1}V(nP), \qquad V']_{(Z_1+nP)^-}^{(Z_1+nP)^+} = -\gamma_1{}^{-1}V(Z_1 + nP), \tag{51}$$

$$n = 0, \pm 1, \pm 2, \cdots$$

A bounded solution is associated with a Floquet multiplier, i.e. eigenvalue of the Floquet matrix, of absolute value one. Since the differential equation has piecewise constant coefficients, the Floquet matrix can be obtained explicitly in terms of exponential solutions. We have examined the Floquet multipliers as functions of λ for the wave trains corresponding to regions near $C_{\min}$ on the c versus P curves in Fig. 8. We find typically two or three unstable modes with different values of $\lambda > 0$. Moreover, the multiplier associated with the largest growth rate is equal to one, so that this unstable mode is periodic with period P.

The calculations described above led us to consider periodic solutions of Eqs. 32 and 51. Such a solution can be written as a sum of exponentials $X_i \exp(\beta_i z)$, $i = 1, 2, 3$, for $Z_{-1} \leq z \leq 0$ and a different sum for $0 \leq z \leq Z_1$, where the β_i are zeros of the cubic Eq. 33. The coefficients are determined by the continuity and jump conditions along with the normalization condition $V(0) = 1$. This last requirement results in a transcendental equation which relates λ to the parameters a, b, c, and P. This complicated equation, which we omit, can be written as

$$\tilde{G}(\lambda, a, b, c, P) \equiv \tilde{F}(\lambda, a, b, c) + \tilde{E}(\lambda, a, b, c, P) = 0, \tag{52}$$

where $\tilde{F}$ is given by Eq. 35 and $\tilde{E} = 0$ for $P = \infty$. Thus as $P \to \infty$, this equation reduces to Eq. 34 which determines the growth rate of the unstable modes for the slower pulses.

We have solved Eq. 52 numerically for various values of a and $b \leq 0.1$ and have obtained the growth rates of periodic unstable modes for all trains with speeds less than a certain speed $c_0(a, b)$. Thus we have found instability for c in the interval $C_{\min}(a, b) \leq c \leq c_0(a, b)$. The results of these calculations are illustrated in Fig. 12 for the particular case $b = 0.05$, which corresponds to Fig. 8. For several values of a, $0 \leq a < a_r(b)$, the value of λ is shown versus propagation speed. We find that $c_0(a, b) > c_s(a, b)$. Consequently, whenever two periodic solutions exist with the same speed $c \leq c_s(a, b)$, they are both unstable. This explains why some of the

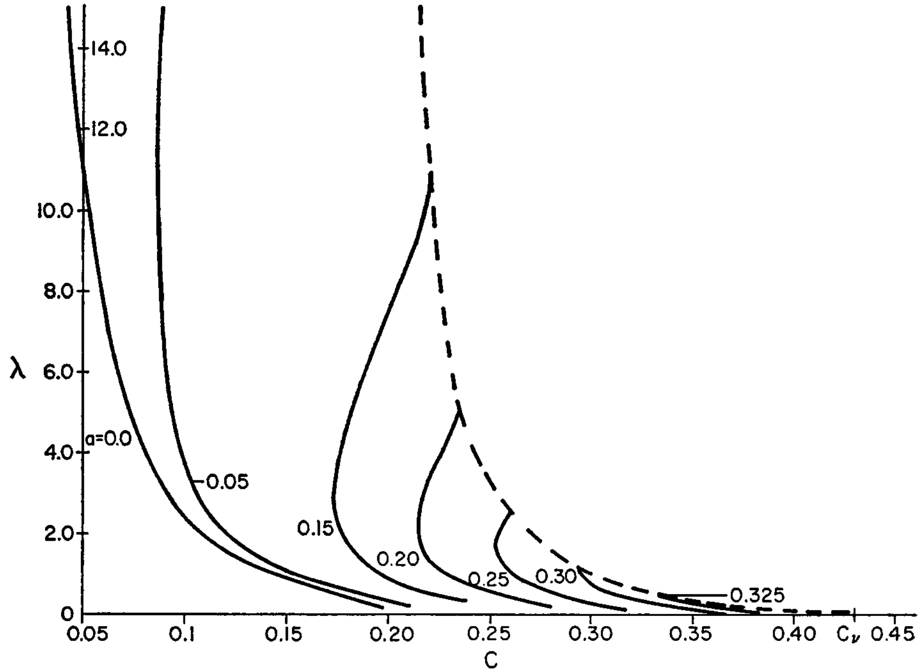

FIGURE 12 Growth rate $\lambda[a, b, c, P(a, b, c)]$ of a periodic unstable mode for a periodic wave train versus c for $b = 0.05$ and various values of a, determined numerically from Eq. 52. The growth rate $\lambda(a, b, c_s)$ of the slow pulse for $b = 0.05$, obtained from Figs. 6 and 2, is shown dashed.

growth rate curves are double valued. Furthermore, it follows that for some values of the parameters a, b, and P, both the fast and the slow trains are unstable.

The dashed curve in Fig. 12 corresponds to the unstable pulses. It is obtained from Figs. 2 and 6. Because of the limiting form of Eq. 52 as $P \to \infty$, each curve for constant a terminates at the dashed curve when $c = c_s(a, b)$. The other end of the growth curve, $c = c_0(a, b)$, seems to be characterized by the coalescence of the two largest roots for λ of Eq. 52. Since $\lambda(a, b, c_0) \neq 0$, c_0 does not correspond to neutral stability. However, since $\lambda(a, b, c_0)$ is close to zero, c_0 provides a good lower bound for the propagation speed of the neutrally stable wave train. We have shown $c_0(a, b)$ versus a for $b = 0.05, 0.005$, as dotted curves in Fig. 11. The instability properties of the trains with $c > c_0$ can be found by using the Floquet theory outlined above. In this case, there will be no Floquet multiplier with absolute value one for $\lambda > 0$. Hence an unstable mode will have λ complex with $Re\lambda > 0$.

We summarize our stability analysis of the periodic wave trains in the following proposition.

Proposition 4

For positive values of $b \leq 0.1$ and $a < a_\nu(b)$, each nontrivial periodic traveling wave solution of the simplified FitzHugh-Nagumo Eqs. 1 and 2 with speed

$c < c_0(a, b)$ is unstable. The exponential growth rate $\lambda(a, b, c, P)$ of its periodic unstable mode satisfies Eq. 52.

6. WAVES AND THEIR STABILITY FOR $b = 0$ AND $w \equiv 0$

The Waveforms

Wave solutions of the following types have been found (1, 2, 7, 12, and 15) for the cubic FitzHugh-Nagumo equation: a traveling change of state waveform (the Huxley solution), a family of periodic standing waves, and a solitary standing pulse. McKean (13) found similar solutions for the simplified Eqs. 1 and 2 with $b = 0$ and $w \equiv 0$, which is

$$v_t = v_{xx} - v + H(v - a), 0 \leq a \leq \tfrac{1}{2}. \tag{53}$$

The transition waveform for Eq. 53 is given by

$$\begin{aligned} v_c(z) &= a \exp\,[zc/2 + z(1 + c^2/4)^{1/2}],\ z \leq 0 \\ &= 1 + (a - 1) \exp\,[zc/2 - z(1 + c^2/4)^{1/2}],\ 0 \leq z \end{aligned} \tag{54}$$

with

$$c = (1 - 2a)[a(1 - a)]^{-1/2}. \tag{55}$$

The graph of $c(a)$ is the $b = 0$ speed curve in Fig. 2. We notice that $c \to \infty$ as $a \to 0$ which is to be expected since for $a = 0$ and $v \geq 0$, Eq. 53 is a linear parabolic equation. The waveform Eq. 54 is a limiting case of the fast pulse solution found in section 2. To see this we let z_1 tend to infinity in Eqs. 15 and 11 which then reduce to Eqs. 55 and 54.

The standing pulse for Eq. 53 with $v_0(0) = a = v_0(x_1)$ is given by

$$\begin{aligned} v_0(x) &= ae^x,\ x \leq 0 \\ &= 1 + (a - \tfrac{1}{2})e^x - \tfrac{1}{2}e^{-x},\ 0 \leq x \leq x_1 \\ &= ae^{x_1 - x},\ x_1 \leq x \end{aligned} \tag{56}$$

with

$$e^{-x_1} = 1 - 2a. \tag{57}$$

From Eq. 57 $x_1 \to \infty$ as $a \to \tfrac{1}{2}$ and the coefficients in Eq. 56 tend to those in Eq. 54. Thus the pulse solution tends to the transition wave as $a \to \tfrac{1}{2}$. The pulse (Eq. 56) is obtained from the slow pulse (Eq. 11) by taking the limit as b tends to zero with z_1 finite. In this case Eq. 15 tends to Eq. 57.

There is a one parameter family of periodic standing waves $v_{0,\sigma}$ with $a/2 < \sigma < a$.

The period $P_\sigma = X_1 - X_{-1}$ is determined by the two equations

$$\exp(X_1) = (a-1)(2\sigma-1)^{-1} - (2\sigma-1)^{-1}[a^2 - 4\sigma(a-\sigma)]^{1/2}$$
$$\exp(X_{-1}) = a/2\sigma - (2\sigma)^{-1}[a^2 - 4\sigma(a-\sigma)]^{1/2}. \tag{58}$$

The waveform is given by

$$v_{0,\sigma}(x) = \sigma e^x + (a-\sigma)e^{-x}, \quad X_{-1} \le x \le 0$$
$$= (\sigma - \tfrac{1}{2})e^x + (a - \sigma - \tfrac{1}{2})e^{-x} + 1, \quad 0 \le x \le X_1 \tag{59}$$

From Eqs. 58 and 57, $X_{-1} \to \infty$ and $X_1 \to x_1$ as $\sigma \to a$, while the coefficients in Eq. 59 tend to those in 56. In this sense, the solitary pulse (Eq. 56) is the limit of the periodic waveform as $P_\sigma \to \infty$.

Stability

We first demonstrate that the transition waveform is linearly stable. We consider the variational equation

$$\tilde{v}_t = \tilde{v}_{zz} - c\tilde{v}_z - [1 - \gamma^{-1}\delta(z)]\tilde{v} \tag{60}$$

where

$$\gamma = v_c'(0) = a[c/2 + (1 + c^2/4)^{1/2}]. \tag{61}$$

With $\tilde{v}(z,t) = e^{\lambda t}V(z)$ we find that the only solution with V bounded and $Re\,\lambda \ge 0$ is $V = v_c'$ corresponding to $\lambda = 0$. Thus there are no unstable modes.

To demonstrate the decay of initial perturbations we solve the initial value problem for Eq. 60 with $\tilde{v}(z,0) = \phi(z)$ by Laplace transforms. From a residue calculation we obtain the t-independent solution

$$\lim_{t\to\infty} \tilde{v}(z,t) = Av_c'(z).$$

where

$$A = \int_{-\infty}^{\infty} v_c'(-z)\phi(z)\,dz \left(\int_{-\infty}^{\infty} [v_c'(z)]^2\,dz\right)^{-1}.$$

Here $v_c'(-z)$ satisfies the homogeneous t-independent adjoint equation for Eq. 60. For bounded ϕ which satisfies

$$\int_{-\infty}^{\infty} |\phi(z)\exp(-cz/2)|\,dz < \infty$$

we can show that

$$|\tilde{v}(z,t) - Av_c'(z)| < C\exp(-\lambda^* t).$$

Here C is a constant depending upon a and ϕ, and λ^* can be chosen in the interval $0 < \lambda^* < 1$ independently of a. Thus we conclude that the transition waveform is linearly stable.

The stability of the standing pulse (Eq. 56) can be analyzed in a manner similar to that used by Lindgren and Buratti (12). The linear variational equation is

$$\tilde{v}_t = \tilde{v}_{xx} - [1 - a^{-1}\delta(x) - a^{-1}\delta(x - x_1)]\tilde{v} \tag{62}$$

We assume a solution of the form $\tilde{v}(x, t) = e^{\lambda t}V(x)$ and seek bounded V which satisfies

$$V'' - [\lambda + \psi(x)]V = 0, \quad -\infty < x < \infty. \tag{63}$$

Here

$$\psi(x) = 1 - a^{-1}\delta(x) - a^{-1}\delta(x - x_1).$$

Since v_0' is a solution of Eq. 63 with $\lambda = 0$ and v_0' has one node, there must be another solution of Eq. 63 with $\lambda > 0$.

To find the growth rate λ we let $\omega = (1 + \lambda)^{1/2}$. Then the unstable mode can be written in terms of the two exponentials, exp $(\pm\omega x)$, where ω satisfies

$$\omega 2a - 1 = (1 - 2a)^{\omega}. \tag{64}$$

The solution $\lambda = \lambda(a)$ of this equation was obtained numerically and is illustrated in Fig. 6. Because $(1 - 2a)^{\omega}$ must be positive, we obtain the following lower bound on λ

$$\lambda > \frac{1}{4a^2} - 1. \tag{65}$$

From Eq. 65 we see that $\lambda \rightarrow \infty$ as $a \rightarrow 0$ and from Eq. 64 that $\lambda \rightarrow 0$ as $a \rightarrow \frac{1}{2}$. This is consistent with our instability analysis of the slower pulses for $b > 0$.

To analyze the stability of the periodic waves we consider Eq. 63 on the finite interval $X_{-1} \leq x \leq X_1$ with $\psi(x) = 1 - (2\sigma - a)^{-1}\delta(x) - (2\sigma - a)^{-1}\delta(x - X_1)$. We look for $V(x)$ which is periodic. Since $v_{0,\sigma}'$ has one node, we conclude as above that there is an unstable mode with $\lambda > 0$. Hence the periodic waveforms are unstable.

APPENDIX

Proof of Theorem 1

For fixed positive values of b and c, we consider the function

$$h(s) = 2 - s + (p_1'/p_2')s^{-\alpha_2/\alpha_1} + (p_1'/p_3')s^{-\alpha_3/\alpha_1}, \quad 0 \leq s \leq 1. \tag{66}$$

We obtain necessary and sufficient conditions for the equation $h(s) = 0$ to have a root s in the interval (0, 1). Using the polynomial identities from Appendix A of Rinzel (16), we evaluate h and its derivatives:

$$h(0) = 2, \quad h(1) = 0, \quad h'(1) = 0 \tag{67}$$

and

$$h''(1) = \alpha_1^{-2} p_1' - 2. \tag{68}$$

We observe that the equation $h''(s^*) = 0$ has a unique root $s^* > 0$,

$$s^* = \left[-\frac{(\alpha_3 + \alpha_1)\alpha_3 p_2'}{(\alpha_2 + \alpha_1)\alpha_2 p_3'} \right]^{\alpha_1/(\alpha_3 - \alpha_2)}. \tag{69}$$

In the case $\alpha_3 = \bar{\alpha}_2$, the unique determination of s^* requires choosing a branch of the logarithm function. From Eq. 67 and the uniqueness of s^* it follows that $h(s)$ can have at most one zero in the interval (0, 1).

An obvious sufficient condition for $h(s) = 0$ to have a root s, $0 < s < 1$, is that h have a local maximum at $s = 1$, i.e. $h''(1) < 0$. On the other hand, if such an s exists with $h''(1) \geq 0$, then we reach a contradiction to the uniqueness of s^*. Therefore the condition $h''(1) < 0$ is also necessary.

Evaluating Eq. 68 in terms of α_1 and using $p(\alpha_1) = 0$, we see that our necessary and sufficient condition can be expressed as

$$c^{-1} b^{1/2} < \alpha_1. \tag{70}$$

Since $c^{-1}b^{1/2} > 0$, the condition $c^{-1}b^{1/2} < \alpha_1$ is equivalent to $p(c^{-1}b^{1/2}) < 0$. Evaluating the cubic we finally obtain the necessary and sufficient condition

$$c^2 > b(1 + 2b^{1/2})^{-1} \tag{71}$$

as stated in Theorem 1.

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