

McKean caricature of the FitzHugh-Nagumo model: Traveling pulses in a discrete diffusive medium

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This paper investigates traveling wave solutions of the spatially discrete reaction-diffusion systems whose kinetics are modeled by the McKean caricature of the FitzHugh-Nagumo model. In the limit of a weak coupling strength, we construct the traveling wave solutions and obtain the critical coupling constant below which propagation failure occurs. We report the existence of two different pulse traveling waves with different propagation speeds. Analytical results on the wave speed are obtained. Earlier results on propagation in the bistable medium are found as a limiting regime of our analysis.

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I. INTRODUCTION

Reaction-diffusion equations are widely used in various fields from biology and image processing to material sciences. They model the activity of so-called active media and an extensive literature is available on this topic [1–3]. In most studies the underlying kinetics are bistable, i.e., the isolated system has two stable fixed points. However, many systems are excitable in the sense that the activity does not persist indefinitely but rather is transient in nature. A realistic description of excitable media needs the inclusion of a recovery process. A simple description of a one-dimensional excitable medium is given by the set of partial differential equations

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

where $v(x,t) \in \mathbb{R}$ is the activity at spatial point x at time t , $w(x,t) \in \mathbb{R}$ is a recovery variable, $d > 0$ is the coupling strength, and $b > 0$ monitors the time scale of the recovery. The reaction function f has a cubiclike shape (or S shape) which allows for a bistability regime when inhibition is blocked. System (1) has been introduced by FitzHugh [4] and Nagumo, Arimoto, and Yoshizawa [5] as a simplified description of the excitation and propagation of nerve impulses [28].

Recent studies have shown that spatially continuous models do not always adequately describe structures composed of discrete elements and differential-difference models are more appropriate if the coupling between cells is weak. Indeed, the space discreteness can lead to effects not present in continuum models. The most important example is the phenomenon of propagation failure (or pinning) which appears in the description of the myelinated axons of neurons [6], in chemical reactors coupled by mass exchange [7] or in mod-

els of species invasions [8]. A recent biological experiment has emphasized a direct observation of propagation block as the coupling is reduced [9]. In view of these and other applications, we study the infinite system of ordinary differential equations on the one-dimensional lattice Z ,

$$\begin{aligned} \frac{dv_n}{dt} &= d(v_{n+1} - 2v_n + v_{n-1}) + f(v_n) - w_n, \quad n \in Z, \\ \frac{dw_n}{dt} &= bv_n, \quad b > 0. \end{aligned} \quad (2)$$

The diffusion coefficient d plays a crucial role and in contrast to the continuum model (1), it is not possible to scale d to unity by rescaling x . Theoretical works on propagation and its failure in spatially discrete models have dealt mainly with the bistable medium, that is, when recovery is ignored [10–16] or does not allow a return to the low-activity state [17]. Keener [10] showed that there exists a critical coupling value below which wave front fails to propagate. This propagation failure is associated with the existence of nonuniform steady states. Zinner [12,11] demonstrated that there exists a stable traveling wave front for sufficiently large coupling. Erneux and Nicolis [13] carried out an asymptotic analysis to determine the behavior of the wave near the pinning transition. Excitable kinetics have retained less attention and analytical results are virtually nonexistent with the exception of the work of Booth and Erneux [18]. They investigated by asymptotic methods the role that the diffusion constant d plays in pulse propagation. Their mathematical analysis focused on the propagation failure for a limited chain of three excitable cells in the limit $b \rightarrow 0$.

In this paper, we study traveling pulse solutions of Eqs. (2) for f , the piecewise linear reaction function introduced by McKean [19,29],

$$f(v) = -v + h(v-a), \quad 0 < a < 1, \quad (3)$$

where a is a so-called detuning parameter and h is the Heaviside step function $h(x) = 1$ if $x > 0$ and 0 otherwise. The study of traveling pulses appears to be considerably more difficult than traveling fronts. As we will show, the use of the piecewise linear idealization (3) allows for a deeper under-

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standing of propagation and its failure in the spatially discrete system (2). For a coupling strength greater than a critical value, we report the existence of two traveling pulse solutions of Eqs. (2) and we give some analytical properties of these waves. At the same time, we investigate the effects of the recovery parameter b on propagation.

Our approach is based on an integral representation of traveling waves equivalent to the differential formulation of traveling wave solutions. However, beyond numerical simulations, the integral formulation does not lead to a tractable description of waves. In the limit of a weak coupling strength, traveling pulses are constructed. Based on these approximations, we obtain necessary conditions [30] for the existence of pulse waves and derive some scaling laws of the wave speeds.

The organization of the paper is as follows. In Sec. II, we derive the integral expression of traveling pulses. We restrict our attention to small diffusion coefficients and give analytical results on the existence, the shape, and the speed of pulse traveling waves. Next, we focus on particular values of b which allow explicit calculations. In Sec. III, we emphasize some links between single-pulse traveling waves and multiple-pulse traveling waves including periodic waves. Finally, we summarize and discuss the main results of our analysis.

II. PULSE TRAVELING WAVE

By a traveling wave, with velocity $c > 0$, we mean a solution $\{v_n(t), w_n(t)\}_{n=-\infty}^{+\infty}$ of Eqs. (2) for which there exists (φ, ψ) such that

$$\begin{aligned} v_n(t) &= \varphi(n - ct), \\ w_n(t) &= \psi(n - ct), \end{aligned} \tag{4}$$

which satisfies the boundary conditions $\varphi(-\infty) = \varphi(\infty) = 0$ and $\psi(-\infty) = \psi(\infty) = 0$. Substituting the form of Eqs. (4) into Eqs. (2), we obtain the equations

$$\begin{aligned} -c\varphi'(\xi) &= d[\varphi(\xi + 1) - 2\varphi(\xi) + \varphi(\xi - 1)] + f(\varphi(\xi)) \\ &\quad - \psi(\xi), \\ -c\psi'(\xi) &= b\varphi(\xi), \end{aligned} \tag{5}$$

where $\xi = n - ct$ is the traveling wave coordinate. In the following, we focus our attention on the state variable v and hence on φ . Recall that v is the observable variable that can be obtained from experimental measurements, while w is an additional variable which mimics some recovery process. Alternatively to Eqs. (5), one may work with the equation

$$\begin{aligned} -c\varphi'(\xi) &= d[\varphi(\xi + 1) - 2\varphi(\xi) + \varphi(\xi - 1)] + f(\varphi(\xi)) \\ &\quad + \frac{b}{c} \int_{-\infty}^{\xi} \varphi(t) dt \end{aligned} \tag{6}$$

for the study of nonstanding waves, i.e., $c \neq 0$. By a pulse wave, we mean a solution of Eqs. (5), or equivalently of Eq.

(6), in $L^1(R)$, continuous and piecewise of class C^1 such that there exist two real numbers $\xi_0 > \xi_1$ that satisfy

$$(H): \begin{cases} \varphi(\xi_i) = a, & i = 0, 1 \\ \varphi(\xi) > a & \text{if } \xi \in]\xi_1, \xi_0[\\ \varphi(\xi) < a & \text{if } \xi \in]-\infty, \xi_1[\cup]\xi_0, +\infty[. \end{cases}$$

We are thus excluding any solutions which cross the value $\varphi(\xi) = a$ more than twice. Translation invariance of the traveling wave solution allows us to take $\xi_0 = 0$. Note that the boundary conditions

$$\varphi(-\infty) = \varphi(+\infty) = 0$$

are satisfied from the requirement $\varphi \in L^1(R)$. With the notations previously introduced, we have

$$f(\varphi(\xi)) = -\varphi(\xi) + h(-\xi) - h(\xi_1 - \xi). \tag{7}$$

Substituting Eq. (7) into Eqs. (5), the system now takes the form of the linear nonautonomous difference-differential equation

$$\begin{aligned} -c\varphi'(\xi) &= d[\varphi(\xi + 1) + \varphi(\xi - 1)] - (1 + 2d)\varphi(\xi) + h(-\xi) \\ &\quad - h(\xi_1 - \xi) - \psi(\xi), \\ -c\psi'(\xi) &= b\varphi(\xi), \end{aligned} \tag{8}$$

which can be solved with transform methods. Let us consider the Fourier transform of a function $\rho \in L^1(R)$,

$$\hat{\rho}(s) = \int_R e^{-2i\pi s x} \rho(x) dx.$$

Taking the Fourier transform of both sides of Eqs. (8) yields

$$\begin{aligned} -2i\pi c s \hat{\varphi}(s) &= d(e^{2i\pi s} + e^{-2i\pi s}) \hat{\varphi}(s) - (1 + 2d) \hat{\varphi}(s) \\ &\quad - \frac{1}{2i\pi s} (1 - e^{-2i\pi s \xi_1}) - \hat{\psi}(s), \\ -2i\pi c s \hat{\psi}(s) &= b \hat{\varphi}(s) \end{aligned}$$

for $s \neq 0$ and $\hat{\varphi}(0) = 0, \hat{\psi}(0) = -\xi_1$. We obtain

$$\begin{aligned} \hat{\varphi}(s) &= \frac{-c}{4\pi^2 c^2 s^2 - b + 2i\pi c s [1 + 4d \sin^2(\pi s)]} \\ &\quad \times (1 - e^{-2i\pi s \xi_1}). \end{aligned} \tag{9}$$

Clearly $\hat{\varphi}(s) \in L^1(R) \cap L^2(R)$ and so by the Fourier inversion theorem, we find that the pulse wave is given by

$$\varphi(\xi) = \eta(\xi) - \eta(\xi - \xi_1), \tag{10}$$

where

$$\eta(\xi) = \int_R e^{2i\pi\xi x} g(x) dx,$$

$$g(x) = \frac{-c}{4\pi^2 c^2 x^2 - b + 2i\pi c x [1 + 4d \sin^2(\pi x)]}. \quad (11)$$

We directly emphasize some basic properties of pulse waves.

Remark. From Eqs. (11), we have $g \in L^1(R)$ and using $\eta(\xi) = \hat{g}(-\xi)$ the function φ given by Eq. (10) satisfies

$$\varphi \in C^0(R) \quad \text{and} \quad \varphi(-\infty) = \varphi(+\infty) = 0.$$

Remark. From the above proof, we have $\hat{\varphi}(0) = 0$.

Remark. From Eq. (10) and $g(c,x) = -g(-c,-x)$ (where we explicitly report the c dependence), we obtain the symmetry property

$$\varphi(-\xi, -c) = \varphi(\xi, c)$$

for the solution $\varphi(\xi) = \varphi(\xi, c)$. In other words, the leftward and the rightward traveling waves coexist.

Rather than working with the difference-differential equation (5), we will make use of the integral representation of traveling wave solutions given by Eq. (10). Note that this expression is not completely explicit because of the two unknown values ξ_1 and c . More precisely, the existence of pulse waves is given by the existence of these two values which are obtained from the requirements $\varphi(0) = \varphi(\xi_1) = a$. Unfortunately, in the general case, we cannot derive tractable expressions since $\eta(\xi)$ cannot be expressed with known functions. We will consider the limit $d \rightarrow 0$ and then specialize our analysis on the onset of propagation. We will demonstrate that this limiting situation allows the capture and description of the propagation of waves.

A. Small diffusion coefficient

In this section, we investigate analytical results from the propagation of pulse waves and determine some scaling laws of the wave speed. Effects of parameters d , a , and b are analyzed by exploring the small d limit. We organize our analysis into three subsections. In Sec. II A, we obtain a first approximation of pulse traveling waves and derive a first condition for propagation: $d = O(a)$. In Sec. II A 2, we determine a more accurate estimate of a traveling pulse and give results on its existence and its velocity. To complete our analysis, we investigate the role of the recovery parameter studying the limit b small and $b \rightarrow 1/4$, which are the two bounds for the validity of our analysis.

1. Zero-order approximation of the wave

For small d , we write $g(x) = g_0(x) + O(d)$ and $\eta(\xi) = \eta_0(\xi) + O(d)$ and, from Eqs. (11), we have $g_0(x) = -c / (4\pi^2 c^2 x^2 - b + 2i\pi c x)$. Thus

$$\eta_0(\xi) = \frac{-1}{2\pi} \int_R \frac{e^{i\xi(x/c)}}{x^2 - b + ix} dx,$$

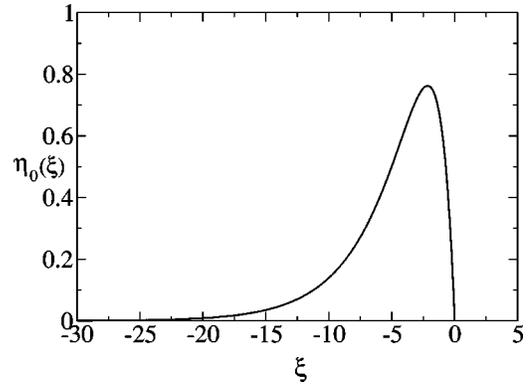


FIG. 1. Plot of the zero-order approximation of the superthreshold part of the traveling pulse $\eta_0(\xi)$ (for $b=0.2$). The speed acts as a scale parameter and we take $c=1$. The zero-order approximation of the traveling pulse is obtained from $\varphi(\xi) = \eta_0(\xi) - \eta_0(\xi - \xi_1) + O(d)$.

where we used the change of variable $x \rightarrow 2\pi c x$ in the integral. From Ref. [20], we have

$$\eta_0(\xi) = \frac{-2}{\sqrt{1-4b}} h(-\xi) e^{\xi/2c} \sinh \frac{\xi}{2c} \sqrt{1-4b}, \quad (12)$$

where $\sqrt{1-4b}$ varies in the complex plane [when b is greater than $1/4$, the hyperbolic function in Eq. (12) is rewritten as a trigonometric one]. From Eq. (10), the zero-order expansion of a pulse traveling wave is given by

$$\varphi(\xi) = \varphi_0(\xi) + O(d) = \eta_0(\xi) - \eta_0(\xi - \xi_1) + O(d). \quad (13)$$

This first approximation reveals the simple structure of traveling waves. Their amplitudes do not depend on c that only acts as a scale parameter [see Eq. (12)]. The zero-order approximation (13) describes the behavior of an isolated cell (i.e., $d=0$) in the traveling wave coordinate. It has been shown [21] that a self-oscillatory dynamics can be obtained when $b \geq 1/4$. Since we are interested on excitable kinetics, we restrict our attention to the case where $b < 1/4$. In this case, we show in Fig. 1 the shape of the function η_0 . The existence of a traveling pulse solution is related to the existence of c and ξ_1 such that

$$\begin{aligned} \varphi(0) &= a, \\ \varphi(\xi_1) &= a. \end{aligned} \quad (14)$$

From Eqs. (12) and (13), the first requirement yields the following necessary condition for propagation:

$$d = O(a), \quad (15)$$

similar to the result obtained in the bistable medium [13]. Expression (15) clearly shows that for small d a propagation is possible only if a is small enough, at least of the same order than d . Thus, we introduce the asymptotic expansion

$$d = d_1 a + O(a^2). \quad (16)$$

Note that the second requirement yields

$$e^{\xi_1/2c} \sinh \frac{\xi_1}{2c} \sqrt{1-4b} = O(a)$$

which gives a first approximation for ξ_1 :

$$\xi_1 = O(\ln a). \quad (17)$$

Not surprisingly, the zero-order expansion (13) does not provide a full description of the pulse traveling wave. In particular, it does not provide information on the wave speed. A more accurate description of pulse waves is thus desirable.

2. First-order approximation of the wave

We introduce the expansions $g(x) = g_0(x) + dg_1(x) + O(d^2)$ and $\eta(\xi) = \eta_0(\xi) + d\eta_1(\xi) + O(d^2)$. From Eqs. (11), we calculate $g_1(x) = 8i\pi x \sin^2(\pi x) g_0^2(x)$. Using $\eta_1(\xi) = \int_R e^{2i\pi\xi x} g_1(x) dx$, we find after some trivial manipulations

$$\eta_1(\xi) = \tilde{\eta}_1(\xi-1) - 2\tilde{\eta}_1(\xi) + \tilde{\eta}_1(\xi+1), \quad (18)$$

where

$$\tilde{\eta}_1(\xi) = \frac{-i}{2\pi} \int_R \frac{x e^{-i\xi(x/c)}}{(x^2 - b + ix)^2} dx.$$

From Ref. [20], we find

$$\tilde{\eta}_1(\xi) = \frac{2}{r^2} h(-\xi) e^{\xi/2c} \left(-\frac{1}{r} \sinh \frac{r\xi}{2c} + \frac{r\xi}{2c} \sinh \frac{r\xi}{2c} + \frac{\xi}{2c} \cosh \frac{r\xi}{2c} \right),$$

where $r = \sqrt{1-4b}$. The function η_1 stands for the coupling contribution to the isolated spike previously described by the function η_0 . More precisely, it gives the leading order correction, due to $d \neq 0$, to the expression of the pulse wave

$$\varphi(\xi) = \varphi_0(\xi) + d\varphi_1(\xi) + O(d^2), \quad (19)$$

where

$$\varphi_1(\xi) = \eta_1(\xi) - \eta_1(\xi - \xi_1).$$

Figure 2 shows the shape of η_1 . Expression (18) reflects the structure of the coupling between cells described by $d(v_{n-1} - 2v_n + v_{n+1})$ and gives a precise description of each cell contribution to the wave dynamics. In particular, the induction period of the wave, obtained for $\xi > 0$, is derived from the contribution of v_{n-1} which reads $\varphi(\xi) = d\tilde{\eta}_1(\xi - 1)$ for $\xi \geq 0$. Using Eqs. (19) and (16) and $\varphi_0(0) = 0$, the requirements at $\xi = 0$ and ξ_1 lead to

$$d_1 \varphi_1(0) = 1, \quad (20)$$

$$\varphi_0(\xi_1) + ad_1 \varphi_1(\xi_1) = a, \quad (21)$$

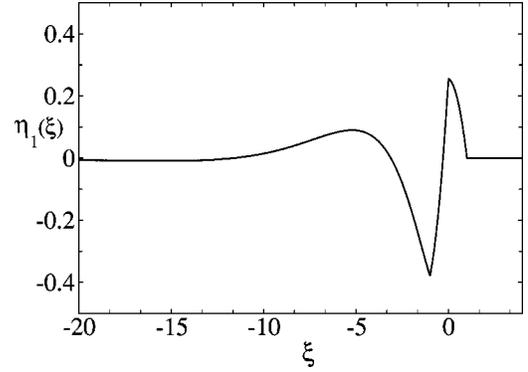


FIG. 2. Plot of the first-order correction $\eta_1(\xi)$ (for $b=0.2$), due to the coupling, of the traveling pulse. The speed acts as a scale parameter and we choose $c=1$. The first-order approximation of the traveling pulse is obtained adding $\eta_0(\xi)$, $d\eta_1(\xi)$, and expressions including subthreshold dynamics (terms express with respect to $\xi - \xi_1$).

respectively. The wave speed can be obtained from Eq. (20). Using $\varphi_1(0) = \tilde{\eta}_1(-1)$, we have to solve

$$s(x) = 2d_1 e^{-x} \left[\left(rx + \frac{1}{r} \right) \sinh rx - x \cosh rx \right] - r^2 = 0, \quad (22)$$

where we introduce for notational convenience $c = 1/2x$. If we assume that there exists a c satisfying Eq. (22), then to show the existence of a pulse wave, we have to show that the requirement (21) can be fulfilled for a suitable value of ξ_1 . Expression (21) yields $\eta_0(\xi_1) + ad_1[\eta_1(\xi_1) - \eta_1(0)] = a$. Using $d_1 \eta_1(0) = 1$ and Eq. (17), we obtain the following leading order approximation:

$$\eta_0(\xi_1) = 2a. \quad (23)$$

Using Eq. (12), we see that for a given c there exists a unique value of ξ_1 given by Eq. (23) that satisfies Eq. (17). Note that for a rigorous demonstration of the existence of pulse waves, one has to show that the requirement (14) can be fulfilled at any order.

Now, using Eq. (22), we show in Fig. 3 the critical value

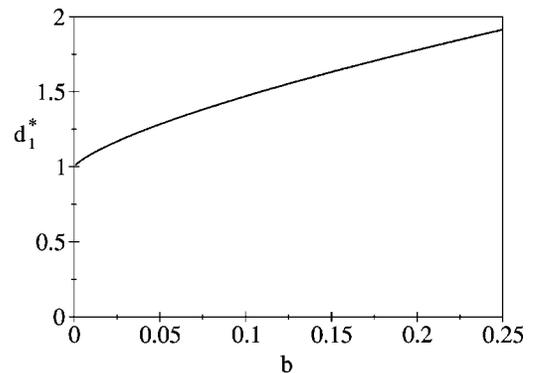


FIG. 3. Plot of the critical coupling strength $d_1^*(b)$ as a function of b such that there is no propagation for $d < ad_1^*$, in the limit $a \rightarrow 0$. For $d \geq ad_1^*$, pulse traveling waves exist.

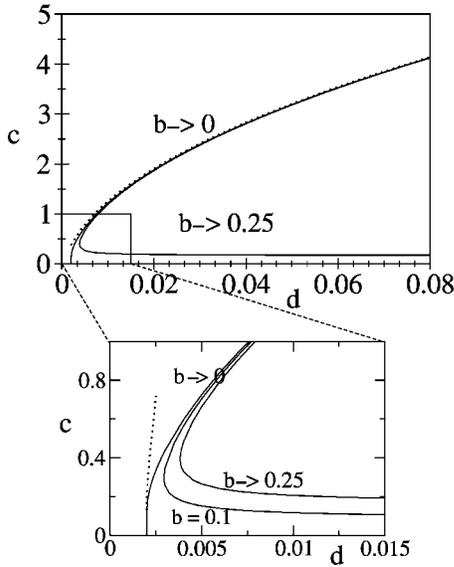


FIG. 4. Variation of the speed $c=c(d)$ of a traveling pulse as a function of the diffusion coupling d for the two limiting values of b : $b \rightarrow 0$ and $b \rightarrow 1/4$. We report $d=ad_1$ for $a=0.002$. The enlarged figure shows an additional curve obtained for $b=0.1$. The dotted curves are the approximations of the fast wave speed as $d \rightarrow \infty$ (top) and as $b \rightarrow 0, d \rightarrow d^*(0)$ (enlarged figure). The fast solution branch and the slow solution branch bifurcate at the point $d^*=ad_1^* + O(a^2)$ determined in Fig. 3. Note that the slow wave speed does not appear as $b \rightarrow 0$ (since $c_s \rightarrow 0$).

of the coupling constant $d_1^*(b)$ (as a function of b) above which propagation is possible. The d dependence of the wave speed for different values of b is shown in Fig. 4. The critical coupling constant $d^*=ad_1^* + O(a^2)$ is related to a wave speed c^* and is such that there is no propagation for $d < d^*$ and two traveling pulse solutions for $d > d^*$. In fact, using

$$\lim_{x \rightarrow +\infty} s(x) = s(0) = -r^2 < 0, \tag{24}$$

we see that traveling pulses appear in pair.¹ The knee point is given by solving the system

$$\begin{aligned} s(x^*, d_1^*) &= 0, \\ s_x(x^*, d_1^*) &= 0, \end{aligned} \tag{25}$$

where s_x stands for the derivative of s with respect to x . The stability analysis of the fast and slow solution branches displayed in Fig. 4 is left to future work but numerical simulations (not shown) reveal that the faster wave is stable while the slower is unstable. Note that the faster pulse can be regarded as the continuation of the traveling wave front states in the bistable medium for which a stability result is established [11]. In contrast to propagation failure in the discrete

bistable medium, the wave vanishes with a nonzero wave speed for a given value of $b > 0$. Note also that the wave speed leads to a direct evaluation of the corresponding wave shape, since the speed acts as a scale parameter stretching out a reference shape given, for example, for $c=c^*$. The fast wave is obtained from a dilatation and the slow wave from a contraction.

To complete the speed diagram (Fig. 4), we provide an asymptotic description of the speed curves for large d_1 . Let c_f and c_s denote the speed of the fast wave and the slow wave, respectively. For large d_1 , one may expect to obtain a large speed value for the faster wave. We seek an asymptotic expansion for large c_f ($x \ll 1$) and from Eq. (22) we obtain $s(x) = 2d_1 r^2 x^2 - r^2 + O(x^3)$. Using $c = (2x)^{-1}$, we find the following asymptotic behavior:

$$c_f \rightarrow \frac{1}{\sqrt{2}} \sqrt{d_1} \text{ as } d_1 \rightarrow \infty. \tag{26}$$

To this order, the fast wave speed does not depend on b . Note that a parabolic law has also been obtained for the wave front speed in the bistable medium [13,15]. Figure 4 emphasizes the outstanding quality of approximation (26) and shows that the fast wave speed is hardly affected by the recovery process.

The speed c_s of the slow wave is bounded as $d_1 \rightarrow \infty$ and hence, from Eq. (22), its first-order approximation satisfies $(rx + 1/r) \sinh rx - x \cosh rx = 0$ which is equivalent to (we have $x \neq 0$)

$$\tanh rx = \frac{rx}{1+r^2x}, \tag{27}$$

and using $0 < r < 1$, we find at least one strictly positive solution. Unfortunately, this solution cannot be expressed explicitly. However, expression (27) shows that, asymptotically, the speed of the slower wave does not depend on the coupling parameter but only on b (through parameter r). In the following section, we shall demonstrate more precise results for specific values of b .

3. Role of the recovery parameter b

We now study more closely the role of the recovery parameter b . There are two limits for which the functional form of $s(x)$ simplifies. These limits are related to the two limiting regimes of our analysis obtained as $b \rightarrow 0$ and $b \rightarrow 1/4$. As we have pointed out, our analytical expressions (η_0 and η_1) are obtained for $b < 1/4$. Recall that parameter b monitors the birth of oscillations for the space-clamped system [21] and our study does not concern propagation in the oscillatory medium.

Results are summarized in the two following propositions.

Proposition 1. In the limit $b \rightarrow \frac{1}{4}$, we obtain the critical values

$$d_1^* \rightarrow \frac{e^{3-\sqrt{3}}}{4(2\sqrt{3}-3)} \sim 1.914,$$

¹In the limit $a \rightarrow 0$ the assumptions (H) are still not fulfilled by the slow wave. In this case, we expect that the slow wave is related to sliding solutions and a precise statement is left to future works.

$$c^* \rightarrow \frac{1}{2(3-\sqrt{3})} \sim 0.394$$

and we have the following asymptotic behavior as $d_1 \rightarrow \infty$:

$$c_f \rightarrow \frac{1}{\sqrt{2}} \sqrt{d_1},$$

$$c_s \rightarrow \frac{1}{6}.$$

We shall sketch the proof of this property. From Eq. (22), we calculate the expansion as $b \rightarrow 1/4$, (or equivalently $r \rightarrow 0$) $s(x) = s_2(x)r^2 + O(r^3)$ where $s_2(x) = 2d_1 e^{-x} x^2 (1 - x/3) - 1$. The function s_2 has a global maximum at $3 - \sqrt{3}$. This implies that a traveling wave exists if $s_2(3 - \sqrt{3}) \geq 0$. It follows the critical value of the diffusion coefficient given in the proposition. At the limit point (d^*, c^*) , the fast and the slow wave branches coalesce. Near this point, the asymptotic behavior is derived from the maximum of s_2 . For large values of d_1 , we have to distinguish between the stable and the unstable branches. The fast wave speed c_f has an asymptotic behavior given by Eq. (26). The slow wave speed is obtained taking $r \ll 1$ in Eq. (27). This leads to $xr - x^3 r^3/3 + O(r^4) = xr - x^2 r^3$ and thus we obtain the leading approximation $x = 3$ which gives the asymptotic behavior of c_s as $d_1 \rightarrow \infty$.

Proposition 2. In the limit $b \rightarrow 0$, we have

$$d_1^* \rightarrow 1$$

and $\forall d_1 > 1$

$$c_f \rightarrow -\frac{1}{1 + W_{-1}\left(\frac{1-d_1}{ed_1}\right)}, \tag{28}$$

$$c_s \rightarrow \frac{b}{\varsigma},$$

where $\varsigma = 1 - W_0(e/d_1)$, W_0 is the principal branch of the Lambert W function and W_{-1} the branch corresponding to -1 [22].

The proposition above describes traveling pulses in the limit of the singularly perturbed system obtained as $b \rightarrow 0$ or equivalently $r \rightarrow 1$. Keeping x fixed, the asymptotic expansion of Eq. (22) as $r \rightarrow 1$ is given by

$$s(x) = d_1 [1 - e^{-2x}(1+2x)] - 1 + O(r-1). \tag{29}$$

The leading approximation is an increasing function of x and we easily find the critical value of the diffusion coefficient $d_1^*(b) \rightarrow 1$ as $b \rightarrow 0$. For $d > 1$, the approximation of the fast wave speed is obtained from $d_1 [1 - e^{-2x}(1+2x)] - 1 = 0$. We rearrange this into $-(1+2x)e^{-(1+2x)} = (1-d_1)/(ed_1)$. We have to keep the solution which satisfies $c_f \rightarrow 0^+$ ($x \rightarrow +\infty$) as $d_1 \rightarrow 1$. Such a solution is expressed with the Lambert function W_{-1} [22] which gives the approximation of the

faster wave $\forall d_1 > 1$, $c_f \rightarrow -1/[1 + W_{-1}((1-d_1)/(ed_1))]$. In the limit $b \rightarrow 0$, we have lost, in the leading order expansion (29), the solution corresponding to the slow wave speed. In fact, the expansion (29) becomes nonuniform if $x(1-r)$ remains a nonzero constant as $r \rightarrow 1$. Equivalently, the expansion (29) is no longer valid if $x \rightarrow \infty$ as $r \rightarrow 1$. In this critical situation, we obtain from Eq. (22) the new expansion $d_1 [x(r-1)e^{(r-1)x} + e^{(r-1)x}] - 1 = 0$ or equivalently $[x(r-1)+1]e^{x(r-1)+1} = e/d_1$. It follows that $x(r-1) = W_0(e/d_1) - 1$ and using $r-1 = -2b + O(b^2)$, we find the asymptotic behavior given by Proposition 2.

Using Proposition 2, we now emphasize some properties of the pulse waves as $b \rightarrow 0$. We have already mentioned that the speed shapes the corresponding wave. Since $c_s \rightarrow 0$ as $b \rightarrow 0$, the slower pulse wave becomes more and more tight and vanishes in the bistable medium.

For d_1 large and using Eq. (28), we derive a more precise approximation than already obtained,

$$c_f \rightarrow \frac{1}{\sqrt{2}} \sqrt{d_1} - \frac{1}{3},$$

which shows that the speed curve is below its asymptote.

From Eq. (28), the asymptotic behavior in the ‘‘pinning limit’’ is given by

$$c_f \rightarrow \frac{-1}{\ln(d_1-1)} \quad \text{as } d_1 \rightarrow 1,$$

i.e., the speed c vanishes logarithmically near the critical point. This result has been obtained for the wave front speed in the bistable medium [14]. As noted by Fàth [14], this logarithmic transition is not due to the jump of discontinuity of the function f . We will demonstrate that it is the result of a linear evolution during the onset of propagation. We will show this property using a similar asymptotic analysis to the one introduced in Ref. [13]. The time evolution of the cells shows the existence of a critical time $t = t_n = (n-1)t_c$ such that $v_n(t)$ reaches the threshold value a . At this critical time, we assume that $v_n(t)$ quickly jumps from a $O(a)$ value to $v_n \sim 1$. Let $t = t_{n-1}$ be the origin of time. We seek a solution of the form

$$v_n(t) = av_{n,1}(t) + a^2 v_{n,2}(t) + \dots \tag{30}$$

Introducing Eq. (30) into Eqs. (2), we equate to zero the coefficients of each power of a . We may choose b sufficiently small such that (i) the excited period (time during which $v_{n-1} \sim 1$) is greater than t_c (the induction period) and (ii) the recovery process can be neglected. From the $O(a)$ problem, we obtain the following linear differential equation for $v_{n,1}$:

$$\frac{dv_{n,1}}{dt} = d_1 - v_{n,1} \tag{31}$$

with the initial condition $v_{n,1}(0) = 0$. Equation (31) is valid up to the moment of the threshold crossing, i.e., $t \leq t_c$. We find

$$v_{n,1}(t) = d_1(1 - e^{-t}). \tag{32}$$

The time t_c is defined by $v_{n,1}(t_c) = 1$ which gives the propagation speed $c = (t_c)^{-1}$ and we obtain

$$c = \frac{-1}{\ln(1 - d_1^{-1})}. \tag{33}$$

As we emphasized, the calculations are valid if the jump transition (from the threshold a to the saturation value 1) is instantaneous compared with the induction period (from 0 to the threshold a). Using Eq. (32), expression (33) is valid only in the limit $d_1 \rightarrow 1^+$ (then $t_c \rightarrow +\infty$) and we find the result previously obtained.

III. MULTIPLE-PULSE TRAVELING WAVES AND PERIODIC WAVES

In this section, we investigate the relation between traveling pulses and multiple-pulse waves. Our study is formal and does not concern the existence of multiple-pulse waves. We define an n -pulse wave, $\varphi(n, \xi)$, as a solution of Eq. (6) for which there exists $\xi_0, \xi_1, \dots, \xi_{2n-1}$ such that

$$\begin{aligned} \varphi(n, \xi_i) &= a, \quad i = 0, \dots, 2n-1, \\ \varphi(n, \xi) &> a, \quad \text{if } \xi \in \cup_{k=0}^{n-1}]\xi_{2k+1}, \xi_{2k}[, \\ \varphi(n, \xi) &< a, \quad \text{if } \xi \in \{ \cup_{k=0}^{n-2}]\xi_{2k+2}, \xi_{2k+1}[\cup \} \\ &-\infty, \xi_{2n-1}[\cup]\xi_0, +\infty[. \end{aligned} \tag{34}$$

Then, the nonlinearity of Eqs. (5) is rewritten as

$$f(\varphi(\xi)) = -\varphi(\xi) + \sum_{k=0}^{n-1} h(\xi_{2k} - \xi) - h(\xi_{2k+1} - \xi).$$

The technique is mathematically similar to the technique of Sec. II and we find that the n -pulse wave resembles a superposition of n solitary pulse waves in the sense that

$$\varphi(n, \xi) = \sum_{p=0}^{2n-1} (-1)^p \eta(\xi - \xi_p), \tag{35}$$

where η is given by Eqs. (11).

For an infinite number of pulses, one expects to find periodic waves. To clarify this intuition, we shall describe periodic waves. A periodic wave is a periodic solution of Eq. (6). We seek for a solution in the space $L^2_p(0, T)$ where T is the period of the wave. We consider periodic waves $\varphi_\gamma(\xi)$ that present a single pulse on one period and we note τ the real number such that $0 < \tau < T/2$, and $\varphi_\gamma(\xi) > a$, on $]-\tau, \tau[$. Then we have

$$h[\varphi_\gamma(\xi) - a] = H(\xi),$$

where $H(\xi)$ is the T -periodic function such that $H(\xi) = 1$ if $\xi \in]-\tau, \tau[$ and $H(\xi) = 0$ if $\xi \in]-T/2, -\tau[\cup]\tau, T/2[$. It follows that Eqs. (5) take the form

$$\begin{aligned} -c\varphi'_\gamma(\xi) &= -\varphi_\gamma(\xi) + d[\varphi_\gamma(\xi+1) - 2\varphi_\gamma(\xi) + \varphi_\gamma(\xi-1)] \\ &+ H(\xi) - \psi_\gamma(\xi), \\ -c\psi'_\gamma(\xi) &= b\varphi_\gamma(\xi). \end{aligned} \tag{36}$$

Introducing the Fourier series

$$\begin{aligned} \varphi_\gamma(\xi) &= \sum_n \varphi_n e^{2i\pi n(\xi/T)}, \\ \psi_\gamma(\xi) &= \sum_n \psi_n e^{2i\pi n(\xi/T)}, \end{aligned}$$

$$H(\xi) = \frac{2\tau}{T} + \sum_{n \neq 0} \frac{1}{\pi n} \sin \frac{2\pi n \tau}{T},$$

Eqs. (36) transform into

$$\begin{aligned} -\frac{2i\pi n c}{T} \varphi_n &= -\varphi_n + d\varphi_n(e^{2in\pi/T} - 2 + e^{-2in\pi/T}) \\ &+ \frac{1}{\pi n} \sin \frac{2\pi n \tau}{T} - \psi_n, \\ -\frac{2i\pi n c}{T} \psi_n &= b\varphi_n \end{aligned}$$

and $\varphi_0 = 0$. One finds after some algebra

$$\begin{aligned} \frac{4\pi^2 n^2 c^2}{T} \varphi_n &= -2i\pi n c \varphi_n \left(1 + 4d \sin^2 \frac{n\pi}{T} \right) \\ &+ 2ic \sin \frac{2\pi n \tau}{T} + bT\varphi_n, \end{aligned}$$

which yields the expression of periodic waves,

$$\varphi_\gamma(\xi) = \sum_n \varphi_n e^{2i\pi n(\xi/T)}, \tag{37}$$

where

$$\varphi_n = \frac{2iTc \sin\left(\frac{2\pi n \tau}{T}\right)}{4c^2 n^2 \pi^2 - bT^2 + 2i\pi c T n \left[1 + 4d \sin^2\left(\frac{\pi n}{T}\right) \right]}. \tag{38}$$

Note that the existence of periodic waves is related to the existence of (c, T, τ) such that

$$\varphi_\gamma(\tau) = \varphi_\gamma(-\tau) = a.$$

The periodic wave is obtained from the n -pulse traveling wave in the sense of the following.

Proposition 3. Let $\varphi(n, \xi)$ be the n -pulse wave defined by Eq. (35). For regular interspike intervals, we have the convergence in the space of tempered distribution S' ,

$$\lim_{n \rightarrow +\infty} \varphi(n, \xi) = \varphi_\gamma(\xi),$$

where φ_γ is the periodic wave given by Eq. (37).

We shall demonstrate this result using the expressions previously obtained. Translating the argument ξ , we recast Eq. (35) as the symmetric summation

$$\varphi(n, \xi) = \sum_{p=-n}^n \eta(\xi - \xi_{2p}) - \hat{g}(\xi - \xi_{2p+1}). \quad (39)$$

For regular interspike intervals, there exists (τ, T) such that $\xi_{2p} = pT - \tau$ and $\xi_{2p+1} = pT + \tau$. Using $\eta(\xi) = \hat{g}(-\xi)$, the Poisson formula applied to Eq. (39) yields

$$\lim_{n \rightarrow \infty} \varphi(n, \xi) = \frac{1}{T} \sum_{p \in \mathbb{Z}} -g\left(\frac{p}{T}\right) 2i \sin\left(2\pi p \frac{\tau}{T}\right) e^{2i\pi p(\xi/T)}$$

in the space of tempered distribution S' . Using Eqs. (11), (37), and (38), we obtain the stated result.

IV. DISCUSSION

The study of traveling wave solutions of the discrete reaction-diffusion equation is of great interest to various fields but the analysis appears to be difficult and results are scarce even in one dimension. One approach is to consider nonlinearities that are amenable to explicit calculations [23–25]. Previous works mainly focus on the bistable medium and little was done for traveling waves in the

monostable case. In this paper, we have studied traveling pulses in coupled systems of discrete monostable cells whose kinetics are modeled by McKean's caricature of the FitzHugh-Nagumo model.

Our analysis is based on an integral representation of traveling waves from which we derived some asymptotic expressions in the limit of a weak coupling strength. The combination of these expressions and some matching conditions provide an analytical description of pulse waves. As for the space-continuous reaction-diffusion system (1)–(3) [26], there exist two pulse waves with different shapes and different propagation speeds. However, an important qualitative difference with the continuum is the phenomenon of propagation failure that occurs at a critical value of the coupling parameter. We studied how the propagation and its failure are affected by the recovery process. In particular, we show that in the limit of a slow recovery process, the faster pulse wave shares some properties of the traveling front previously described in the bistable medium. Moreover, we showed that the logarithmic law of the speed close to the pinning transition is related to the linear evolution of the excitation in the initiation of the wave.

Using a particular nonlinearity gives rise to the issue of whether it is representative of a more general function. Continuation of traveling wave solutions while parameters of the nonlinearity are varied can provide insight into this problem. As it has been shown for the continuum [27], one expects that the main features of the dynamics are preserved. However, some limiting situations (for example, as $c \rightarrow 0$) reveal a distinct behavior and provide the definition of different class of models.

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- [28] The complete FitzHugh-Nagumo model has an additional term in the recovery equation $w_t = b(v - \gamma w)$ but, since we focus our analysis on the excitable regime, we consider $\gamma = 0$.
- [29] Our study includes the more general function; $f(v) = -v/\tau + \mu h(v - a)$ where $0 < a < \mu\tau$, since the change of variables

$(t, v_n, w_n, d, a, b) \rightarrow (\tau t, \mu\tau v_n, \mu w_n, \tau d, a\mu\tau, b/\tau^2)$ allows us to consider $\tau = \mu = 1$.

- [30] Our work is not a rigorous demonstration of the existence of pulse waves and we will not show that these conditions are sufficient.