Pinning and propagation in spatially discrete bistable systems

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Abstract

Pinning and propagation failure results for wave fronts in bistable spatially discrete FitzHugh-Nagumo systems are established by means of a weak comparison principle. This comparison principle relates the behavior of the wave front solutions of the full system to the behavior of reduced bistable equations. Additional pinning conditions are derived exploiting the asymptotic stability of stationary wave fronts, which are extended to more realistic models of Hodgkin-Huxley type for myelinated nerves. Extensions to variable diffusion and two dimensions are discussed.

Keywords: wave propagation, spatially discrete reaction-diffusion systems, propagation failure, myelinated nerves

1 Introduction

Discrete traveling waves describe propagation of impulses in a vast variety of biological and material systems: pulse propagation through myelinated nerves [2, 10] or cardiac cells [26], motion of dislocations [19], phase boundaries [37] or cracks [34] in crystalline materials, atoms adsorbed on a periodic substrate [12], motion of electric field domains and domain walls in semiconductor superlattices [3] and so on. Numerical evidence of the existence of discrete traveling waves is ubiquitous. Rigorous existence results are rare, and usually restricted to discrete equations rather than systems. We refer the reader to [5, 15, 28, 39, 21] for fronts in discrete bistable equations with applications in biology and [8, 20, 16] for fronts, solitons and wavetrains in conservative problems related to atomic chains or materials.

Let us consider as a model case the discrete FitzHugh-Nagumo (FHN) system, which is an elementary model for impulse propagation along myelinated nerves:

$$u_n' = D(u_{n+1} - 2u_n + u_{n-1}) + f(u_n) - w_n, \quad D > 0, \tag{1}$$

$$w_n' = \varepsilon(u_n - bw_n), \quad \varepsilon, b > 0, \tag{2}$$

for $n \in \mathbb{N}$. The nonlinear source $f(u)$ is 'cubic' function satisfying:

(C1) f and f' are continuous,

(C2) f has three consecutive zeros $f(z_1) = f(z_2) = f(z_3) = 0$, with $z_1 < z_2 < z_3$ and $f'(z_i) \neq 0$,

(C3) f is negative in (z_1, z_2) and positive in (z_2, z_3).

Condition (C3) implies that $f'(z_1)$ and $f'(z_3)$ are negative, whereas $f'(z_2)$ is positive. To simplify, we assume that f has no more zeros and set $z_1 = 0$, $z_2 = \alpha$, $z_3 = 1$.

System (1)-(2) has two possible behaviors: excitable and bistable. It is excitable when there is a unique stable constant solution $(0, 0)$. This happens when b is small enough. Traveling pulses rising temporally from the equilibrium state to an excited state are observed. The parameter ε is usually small enough for u_n and v_n to evolve in two different time scales: u_n is the fast (excitable) variable and v_n is the slow (recovery) variable. Asymptotic and numerical constructions of traveling pulses [7] show that pulses are formed joining a leading and a trailing front. Both fronts are solutions of system (1)-(2) for which w_n is almost constant. Pulses propagate only when the leading front is not pinned. Once the propagation of the leading front is ensured, the separation of scales allows to assemble the leading and trailing fronts in a stable way forming a traveling pulse. If ε is too large, pulses vanish without giving rise to a stable pattern.

Bistable behavior is observed when the system has three constant solutions, two stable and one unstable: $(u^{(1)}, w^{(1)}) = (0, 0)$, $(u^{(2)}, w^{(2)})$, $(u^{(3)}, w^{(3)})$.

In bistable systems, wave fronts joining the two stable constant states are generated. For a cubic function f satisfying (C1), (C2), (C3), system (1)-(2) has three constant solutions solving

$$f(u) = w, \quad \frac{u}{b} = w, \tag{3}$$

when we choose b larger than a critical value

$$b > b_c. \tag{4}$$

The relation $w_n \sim \frac{u_n}{b}$ for $|k|$ large implies that variations in w_n have small amplitude compared to variations in u_n. The leading and trailing fronts of FHN pulses in the excitable case are governed by bistable systems of this type. As we will see in Section 5, bistable systems with a similar structure describe the propagation of the leading edge of nerve impulses in models for nerve propagation along myelinated nerves. Nerve impulses only propagate when the leading front (which determines the speed) propagates successfully. Analytical studies yielding bounds for the propagation speed and characterizations of the parameter regimes for propagation provide information which may help to understand the mechanisms for propagation failure. They are a more focused alternative than costly numerical simulations.

Propagation of waves in continuous media has been the subject of intensive research, see for instance the classical review [32] or the books [27, 33] and references therein. Travelling pulses for continuous Hodgkin-Huxley (HH) and FitzHugh-Nagumo (FHN) model are constructed in [17, 30, 22, 25, 29, 31] by phase plane analysis, asymptotic expansions, or explicitly for simple nonlinearities. Travelling wave fronts for Nagumo equations have also been extensively studied [27, 32, 33]. However, continuous models fail to describe lack of propagation due to pinning [26, 11]. Waves propagating in atomic lattices are known to be pinned by the discrete spatial structure. They only propagate when the driving force surpases a threshold (the Peierls stress). The nerves of vertebrates are myelinated. They are partially covered by a substance called myelin with periodic uncovered sites, the Ranvier nodes. Impulses propagating along myelinated nerves may fail to propagate when the myelin sheath is damaged (multiple sclerosis). If we want to understand this phenomenon, we must use models able to describe it. This excludes classical continuous FHN, HH and Nagumo models unless singular modifications are included, becoming diffusion equations loaded with point sources [35]. On the contrary, spatially discrete versions of the HH and FHN models do account for propagation failure due to pinning [10]. More realistic models coupling a discrete system for the nodes with a continuum description of the myelin layer have been used to assess the influence of a wide variety of nerve parameters on propagation failure [11].

Few analytical results are available for traveling pulses and fronts in spatially discrete systems. In the excitable case, pulses are constructed asymptotically and numerically in [7, 9, 10] for discrete FHN and HH systems. Explicit constructions of pulses for discrete FHN systems with particular sources are presented in [14] and [36]. Existence and stability of travelling pulses for (1)-(2) is proved in [23, 24]. Earlier work in [13] gives an existence result for systems with a similar structure, but imposing additional hypotheses that exclude systems with FHN dynamics.

Existence of travelling wave fronts for discrete Nagumo equations was established studying the associated differential-difference equations by means of a Fredholm's alternative [28]. Fixed point methods are used in [21, 39] to prove an alternative: given cubic sources satisfying certain hypotheses either travelling or stationary wave fronts exist. Without additional hypotheses excluding pinning, all those fronts might be stationary. Complementary propagation and pinning results [26, 5] lead to existence of travelling waves and stationary waves for certain sources. Uniqueness, multiplicity and coexistence phenomena are discussed in [5, 40]. An explicit construction for piecewise linear sources is presented in [15]. The depinning transition from stationary to traveling wave fronts as control parameters vary is described in [6].

For spatially discrete bistable reaction-diffusion systems we are not aware of existence results for traveling fronts. In [1] pinning and propagation results are established using comparison principles for the whole system (1)-(2). Checking whether the resulting pinning and propagation conditions hold is quite hard in practice. We introduce here an alternative comparison principle involving solutions of bistable equations whose behavior is well known. This allows us to demonstrate a number of simpler pinning and propagation results, which are easier to exploit in a practical way, even in more complicated two dimensional or inhomogeneous frameworks. Simultaneously, we obtain some insight on the influence of the different parameters on propagation considering the full system as a perturbation of a bistable equation as b grows. For fixed f and D, wave front solutions of (1)-(2) show the same propagation behavior as the solutions of some reference bistable equations regardless the value of ε, provided b is not too small. For D small enough, depending on the symmetry of the source f, pinning is the dominant regime. As D grows, we approach the continuum limit and pinning is rarely observed. Extending these results to more realistic discrete systems with HH dynamics is not straightforward, due to the complicated nonlinear interaction between the variables. Instead, we use the existence of stationary wave fronts to prove propagation failure for particular classes of initial states.

The paper is organized as follows. Section 2 collects basic results on bistable equations. Section 3 states the comparison principle and establishes conditions for wave front pinning and propagation in discrete FitzHugh-Nagumo systems by comparison with discrete bistable equations. Section 4 studies the nonlinear dynamical stability of stationary wave fronts. In Section 5, we discuss the possibility of extending these results to more realistic Hodgkin-Huxley type models. Section 6 considers problems with variable diffusion and two dimensional systems. Finally, Section 7 contains our conclusions.

2 Stationary and travelling wave fronts for discrete bistable equations

Pinning and propagation results for (1)-(2) can be established comparing the solution u_n of equation (1) with stationary or travelling wave solutions of the bistable equation:

$$c_n' = D(c_{n+1} - 2c_n + c_{n-1}) + g(c_n) + F, \quad n \in \mathbb{Z} \tag{5}$$

for cubic functions g, satisfying (C1), (C2), (C3). Such fronts join the two stable zeros $z_1(F) < z_3(F)$ of the cubic source $g(u)+F$ for F small. If F is too large, the bistable structure is lost. We will work with two different choices of g: $g(u) = f(u)$ and $g(u) = f(u) - \frac{u}{b}$. If $b \geq b_c$ and $b \neq \frac{1}{f'(z_i)}$, $i = 1, 2, 3$, the source $f(u) - \frac{u}{b}$ satisfies (C1), (C2), (C3). For initial data $z_1(F) \leq u_n(0) \leq z_3(F)$, (5) has global and unique solutions satisfying $z_1(F) \leq u_n(t) \leq z_3(F)$ for all $n \in \mathbb{N}$ and $t > 0$ [26].

The following comparison principle is a key tool in the study of (5) [26, 39]:

Lemma 1 (Comparison principle). *If $u_n(0) \leq v_n(0)$ for all n and*

$$u_{n,t} \leq h(u_{n+1}, u_n, u_{n-1}), \quad v_{n,t} \geq h(v_{n+1}, v_n, v_{n-1}), \qquad \forall n, t > 0,$$

for a continuously Lipzchitz function h satisfying a 'quasi monotonicity' condition:

$$h(u_{n+1}, u_n, u_{n-1}) \leq h(v_{n+1}, v_n, v_{n-1}), \quad \text{if} \quad u_k \leq v_k \ \forall k, \quad u_n = v_n,$$

then $u_n(t) \leq v_n(t)$ for all n and $t > 0$. In particular, for any solution u_n of $u_{n,t} = h(u_{n+1}, u_n, u_{n-1})$:

- *if $a_n = a$ and $b_n = b$ satisfy $h(a, a, a) = h(b, b, b) = 0$ and $a \leq u_n(0) \leq b$ for all n, then $a \leq u_n(t) \leq b$ for all n and $t > 0$,*
- *if $u_n(0) \leq u_{n+1}(0)$ for all n then $u_n(t) \leq u_{n+1}(t)$ for all n and $t > 0$.*

This comparison principle allows to order different solutions to (5). We are interested in wave front solutions. A time independent sequence c_n satisfying (5) is a stationary wave front when it increases (resp. decreases) monotonically from $z_1(F)$ at $-\infty$ to $z_3(F)$ at ∞ (resp. from $z_3(F)$ to $z_1(F)$). A solution $c_n(t)$ of (5) is a traveling wave front when $u_n(t) = u(n + ct)$ for a constant speed $c \neq 0$ and a regular wave profile $u(z)$ which increases (resp. decreases) monotonically from $z_1(F)$ at $-\infty$ to $z_3(F)$ at ∞ (resp. from $z_3(F)$ to $z_1(F)$).

Wave front like initial states $u_n(0)$ increasing from one equilibrium state to a different one generate solutions lying between both equilibrium states. Whether those initial wave fronts propagate or not depends on the controlling parameters: F (external drive) and D (diffusivity). The following pinning and propagation results hold, see [4, 26]. The first one ensures pinning whenever D is small enough compared to F. The second one ensures propagation if D is large enough.

Lemma 2 (Pinning). *Let us consider equation (5) with a source $f(u) + F$ satisfying (C1), (C2), (C3). Let us assume that there are numbers x_1,x_2,y_1, y_2 such that*

$$D(z_3(F) - x) + f(x) + F < 0, \quad z_1(F) < x_2 < x < x_1 < z_2(F), \tag{6}$$

$$D(z_1(F) - x) + f(x) + F > 0, \quad z_2(F) < y_1 < y < y_2 < z_3(F). \tag{7}$$

Let us assume that $z_1(F) \leq u_n(0) \leq z_3(F)$, for all n and that $u_n(0)$ grows with n. If $u_k(0) \in [z_1(F), x_1)$, then $u_n(t) \in [z_1(F), x_1)$ for all $t \geq 0$ and all $n \leq k$. If $u_k(0) \in (y_1, z_3(F)]$, then $u_n(t) \in (y_1, z_3(F)]$ for all $t \geq 0$ and all $n \geq k$. This is always the case when D is small enough (depending on f and

F).

Lemma 3 (Propagation). *Let us consider equation (5) with a source $f(u)+F$ satisfying (C1), (C2), (C3). If a travelling wave subsolution $l_n(t) = l(n+ct)$, such that*

$$l_{n,t} \leq D(l_{n+1} - 2l_n + l_{n-1}) + f(l_n) + F, \quad l_n(0) \leq u_n(0)$$

exists, then $l(n+ct) \leq u_n(t)$. The solution $u_n(t)$ of (5) with data $u_n(0)$ propagates to the left when $c > 0$ and l is increasing, or to the right when $c < 0$ and l is decreasing, at a speed equal or larger than $|c|$. If a travelling wave supersolution $s_n(t) = s(n-ct)$ such that

$$s_{n,t} \geq D(s_{n+1} - 2s_n + s_{n-1}) + f(s_n) + F, \quad s_n(0) \geq u_n(0)$$

exists, then $s(n-ct) \geq u_n(t)$. The solution $u_n(t)$ of (5) with data $u_n(0)$ propagates to the right when $c > 0$ and s is increasing, or to the right when $c < 0$ and s is decreasing, at a speed equal or larger than $|c|$.

For D large (depending on f and F), it is possible to find wave front subsolutions $l_n(t) = l(n+ct)$ and supersolutions $s_n(t) = s(n-ct)$ with profiles $l(z)$ and $s(z)$ satisfying

$$l(z) = \begin{cases} z_1(F), & z < z_1 \\ z, & z_1 < z < z_2 \\ A, & z > z_2 \end{cases}, \qquad s(z) = \begin{cases} A, & z < z_1 \\ z, & z_1 < z < z_2 \\ z_3(F), & z > z_2 \end{cases} \tag{8}$$

for $z_2 - z_1 < 1$. More precisely, if there is a value $A \in (z_2(F), z_3(F))$ such that

$$\begin{aligned} f(A) + F &\geq D(A - z_1(F)), & (9) \\ h(w; A, F) &= D(z_1(F) - w) + D(A - w) + f(w) + F \geq \eta > 0, & (10) \\ & \quad \text{when} \quad z_1(F) < w < A, \end{aligned}$$

then, there is a subsolution with profile $l(\xi)$ given by (8) propagating to the left at a speed c bounded from below by

$$(A - z_1(F))^{-1} \min_{z_1(F)<w<A} h(w; A, F).$$

Similarly, if there is a value $A \in (z_1(F), z_2(F))$ such that

$$\begin{aligned} f(A) + F &\leq D(A - z_3(F)), & (11) \\ h(w; A, F) &= D(z_3(F) - w) + D(A - w) + f(w) + F \leq -\eta < 0, & (12) \\ & \quad \text{when} \quad z_3(F) > w > A, \end{aligned}$$

then, there is a supersolution with profile $s(\xi)$ *given by (8) propagating to the right at a speed* c *bounded from below by*

$$(z_3(F)-A)^{-1}\mathrm{min}_{A<w<z_3(F)}|h(w;A,F)|.$$

Analogous constructions can be made for sub and supersolutions whose wave profiles $u(z)$ *and* $l(z)$ *decrease from* $z_3(F)$ *to* $z_1(F)$*.*

Solutions of (5) with wave front like initial data usually evolve into either stationary or travelling wave fronts, depending on the driving parameter F, which controls the symmetry of the source. When the source $g(u)$ is normalized in such a way that it is odd and $\int_{z_1}^{z_3} g(s)ds = 0$, three different regimes are separated by critical values $\pm F_c(D)$ [5, 6]:

- When $|F| \leq F_c(D)$, (5) has stationary wave front solutions. If D is small enough, $F_c(D) > 0$ and such fronts are intrinsically discrete. No strictly increasing regular functions such that $u_n = u(n)$ can be found [6]. There can be several stationary fronts with different profiles [5]. When $F_c(D) = 0$, fronts correspond to continous profiles: there is a uniparameter family of fronts depending on a continuous parameter [5]. It is believed that, generically, $F_c(D) > 0$.

- If $|F| > F_c(D)$, (5) has travelling wave fronts. When $F > F_c(D)$, increasing fronts travel to the left. If $F < -F_c(D)$, increasing fronts travel to the right. For decreasing fronts propagation is reversed.

- Travelling and stationary wave fronts cannot coexist for a given source [5]. Travelling fronts with different speeds cannot coexist either.

If $g(u)$ is not odd with respect to the intermediate zero, numerical studies show that the propagation and pinning regimes are defined by two unrelated thresholds [4]:

- If $F_{c_-}(D) \leq F \leq F_{c_+}(D)$, (5) has stationary wave front solutions.

- If $F > F_{c+}(D)$, (5) has increasing travelling wave front solutions travelling to the left. If $F < F_{c-}(D)$, such fronts travel to the right.

The partition in three regimes was established in [5], where a proof was given for sinusoidal sources. For general sources, the evidence of the presence of three contiguous regimes is mostly numerical.

Waves may propagate at arbitrarily low speeds. In the limit $|c| \to 0$, wave profiles generate steps and converge to a discontinuous profile, defined by the stationary wave fronts. This is shown numerically in [6]. For piecewise linear sources, this phenomenon can be analytically demonstrated by explicitly construction of the travelling wave fronts.

3 Pinning and propagation of wave fronts for the bistable FHN system

Pinning and propagation conditions for wave front solutions of system (1)-(2) can be established exploiting the previous results on bistable equations, provided adequate comparison principles for the system are established. For b large, the recovery variable w_n is small (of order $\frac{u^{(3)}}{b}$ at maximum). This fact will be exploited to compare u_n with traveling or stationary wave fronts of (5) for $g = f$, and derive pinning and propagation results for the system.

The key result allowing to compare solutions of the FitzHugh-Nagumo system with solutions of bistable equations is the following.

Theorem 4. *Let u_n, w_n be a solution of system (1)-(2) with an initial wave front profile $u_n(0)$, $w_n(0)$ satisfying*

$$\begin{array}{l} u^{(1)} = 0 \leq u_n(0) \leq u_{n+1}(0) \leq u^{(3)}(b), \quad \forall n, \\ w^{(1)} = 0 \leq w_n(0) \leq w_{n+1}(0) \leq w^{(3)}(b), \end{array} \tag{13}$$

$$\begin{array}{lll} u_n(0) \to u^{(1)} = 0, & w_n(0) \to w^{(1)} = 0, & n \to -\infty, \\ u_n(0) \to u^{(3)}(b), & w_n(0) \to w^{(3)}(b), & n \to \infty, \end{array} \tag{14}$$

where $(0,0)$, $(u^{(3)}(b), w^{(3)}(b))$ are the two stable constant solutions of the system. Let us assume that the source f satisfies (C1), (C2), (C3) and

(C4) $\quad f''(s) > 0,\ s \leq u^{(1)} = 0, \quad f''(s) < 0,\ s \geq u^{(3)}(b).$

We set $m = m(b) = \min\{|f'(0)|, |f'(u^{(3)}(b))|\}$ and choose b large enough to ensure:

$$b\, m(b) > 1, \qquad b \neq \frac{1}{f'(z_i)}, i = 1,2,3, \qquad b > b_c + \eta,\ \eta > 0, \tag{15}$$

where b_c is defined in (4). The following bounds hold for all $n \in \mathbb{Z}$ and $t \geq 0$:

$$|w_n(t)| \leq w^{(3)}(b)(1 + \delta(b)), \tag{16}$$

$$w_n(t) \geq -\frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}, \tag{17}$$

$$l_n(t) < u_n(t) < s_n(t), \tag{18}$$

$$|u_n(t)| < u^{(3)}(b)(1+\delta(b)), \tag{19}$$

$$u_n(t) > -\frac{u^{(3)}(b)}{b|f'(0)|}(1+\delta(b)), \tag{20}$$

where $\delta = \delta(b) = \frac{1}{b\,m(b)-1} + \frac{1}{b\,|f'(u^{(3)}(b))|} + \frac{1}{b\,|f'(u^{(3)}(b))|(b\,m(b)-1)}$ *and*

- s_n *is a solution of the bistable equation (5) for* $g = f$ *with either* $F = w^{(3)}(b)(1+\delta(b))$ *or* $F = \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}$ *and wave front like initial data* $s_n(0) \in [u_n(0), z_3(F)]$,
- l_n *is a solution of the same equation with* $F = -w^{(3)}(b)(1+\delta(b))$ *and wave front like initial data* $l_n(0) \in [z_1(F), u_n(0)]$.

Hypothesis (C4) can be suppressed by further increasing b (as detailed in the proof).

Proof. Existence of a unique local solution for the initial value problem (1)-(2) with bounded data follows from the standard theory for ordinary differential equations in infinite dimensional Banach spaces [18, 38] (ℓ^∞ in this case). Global existence follows from the bounds (16)-(20), once they have been established.

The initial profile satisfies

$$|u_n(0)| \leq u^{(3)}(b), \quad |w_n(0)| \leq w^{(3)}(b) = \frac{u^{(3)}(b)}{b}, \quad \forall n.$$

Integrating (1), we have

$$\begin{aligned} |w_n(t)| \leq |w_n(0)|e^{-b\varepsilon t} + \varepsilon e^{-b\varepsilon t} \textstyle\int_0^t |u_n(s)| e^{b\varepsilon s} ds \leq \\ \max_{[0,T]} \tfrac{|u_n(t)|}{b} e^{-b\varepsilon t} + \max_{[0,T]} \tfrac{|u_n(t)|}{b}(1-e^{-b\varepsilon t}) = \max_{[0,T]} \tfrac{|u_n(t)|}{b}. \end{aligned} \tag{21}$$

Set $M(b,T) = \max_{[0,T]} \frac{|u_n(t)|}{b} \geq \frac{u^{(3)}(b)}{b} = w^{(3)}(b)$. Then, $|w_n(t)| \leq M(b,T)$ for all n and $t \leq T$. Thus, u_n is a subsolution or a supersolution of (5) for adequate choices of F :

$$u_n' \leq D(u_{n+1} - 2u_n + u_{n-1}) + f(u_n) + M(b,T), \tag{22}$$

$$u_n' \geq D(u_{n+1} - 2u_n + u_{n-1}) + f(u_n) - M(b,T), \tag{23}$$

when $t \le T$. Let $l_n(t)$ be a solution of (5) for $F = -M(b,T)$ with initial data $l_n(0) \le u_n(0)$ increasing from $z_1(-M(b,T))$ to $z_3(-M(b,T))$. The right hand side satisfies the quasi-monotonicity condition in Lemma 1, therefore:

$$u_n(t) \ge l_n(t) \ge z_1(-M(b,T))$$

if $t \le T$. The constants $z_1(-M(b,T))$ and $z_3(-M(b,T))$ are the smallest and largest roots of $f(u) = M(b,T)$, respectively. If $f''(0) > 0$, the tangent $f(0) + f'(0)u$ is below the graph of f near zero. Thus, $z_1(-M(b,T)) > -\frac{M(b,T)}{|f'(0)|}$, without restrictions on the size of b when $f''(u)$ does not vanish for $u < 0$. If $f''(u)$ vanishes for negative u, we select b large enough to ensure that the tangent is below the graph of f when $\frac{M(b,T)}{f'(0)} < u < 0$.

Similarly, let $s_n(t)$ be a solution of (5) for $F = M(b,T)$ with initial data $s_n(0) \ge u_n(0)$ increasing from $z_1(M(b,T))$ to $z_3(M(b,T))$ by Lemma 1:

$$u_n(t) \le s_n(t) \le z_3(M(b,T))$$

for $t \le T$. The constant $z_3(M(b,T))$ is the largest root of $f(u) = -M(b,T)$. If $f''(u^{(3)}(b)) < 0$, the tangent $f(u^{(3)}(b)) + f'(u^{(3)}(b))(u - u^{(3)}(b))$ is above the graph of f near $u^{(3)}(b)$. Thus, $z_3(M(b,T)) < \frac{M(b,T)}{|f'(u^{(3)}(b))|} + \left(1 + \frac{1}{b|f'(u^{(3)}(b))|}\right) u^{(3)}$ without restrictions on the size of b if $f''(u)$ does not vanish for $u > u^{(3)}(b)$. Otherwise, we take b large enough to ensure that the tangent is located below the graph of f if $\frac{M(b,T)}{|f'(u^{(3)}(b))|} + \left(1 + \frac{1}{b|f'(u^{(3)}(b))|}\right) u^{(3)}(b) > u > u^{(3)}(b)$.

Combining the upper and lower bounds, we find

$$-\frac{M(b,T)}{|f'(0)|} < u_n(t) < \frac{M(b,T)}{|f'(u^{(3)}(b))|} + \left(1 + \frac{1}{b|f'(u^{(3)}(b))|}\right) u^{(3)}(b). \qquad (24)$$

In particular,

$$-\left(1 + \frac{1}{b|f'(u^{(3)})|}\right) u^{(3)} - \frac{M(b,T)}{m} < u_n(t) < \frac{M(b,T)}{m} + \left(1 + \frac{1}{b|f'(u^{(3)})|}\right) u^{(3)},$$

where $m = m(b) = \min\{|f'(0)|, |f'(u^{(3)}(b))|\}$, that is,

$$\max_{[0,T]} |u_n(t)| < \frac{1}{b\, m(b)} \max_{[0,T]} |u_n(t)| + \left(1 + \frac{1}{b|f'(u^{(3)}(b))|}\right) u^{(3)}(b).$$

These inequalities imply

$$\max_{[0,T]} |u_n(t)| < u^{(3)}(b) \left(1 + \frac{1}{b\, m(b) - 1}\right) \left(1 + \frac{1}{b|f'(u^{(3)}(b))|}\right). \qquad (25)$$

We have chosen $b > b_c + \eta$, $\eta > 0$, so that $|f'(u^{(3)}(b))|$ is bounded away from zero. Therefore, $\frac{1}{m(b)}$ and $\frac{1}{|f'(u^{(3)}(b))|}$ are bounded from above by a constant depending on η, uniformly when $b > b_c + \eta$. Setting $\delta(b) = \frac{1}{b\,m(b)-1} + \frac{1}{b|f'(u^{(3)}(b))|} + + \frac{1}{b|f'(u^{(3)}(b))|(b\,m(b)-1)}$, inequality (19) follows for $t \leq T$. Combining (24) and (19), we find (20) for $t \leq T$:

$$\max_{\{t\in[0,T],u_n<0\}}|u_n(t)| < \frac{\max_{t\in[0,T]}|u_n(t)|}{b|f'(0)|} < \frac{u^{(3)}(b)}{b|f'(0)|}(1+\delta(b)). \qquad (26)$$

Notice that the bounds in (25)-(26) do not depend on T, and are bounded from above as b grows. From (21) we obtain (16) for $t \leq T$. We substitute $M(b,T)$ by $w^{(3)}(b)(1+\delta(b))$ in (22)-(23) and find (18). The lower bound on $w_n(t)$ can be improved using (20) to get (17) for $t \leq T$:

$$w_n(t) = w_n(0)e^{-b\varepsilon t} + \varepsilon e^{-b\varepsilon t}\int_0^t u_n(s)e^{b\varepsilon s}ds \geq -\frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}.$$

We have to extend the bounds to all $T > 0$. When $f''(0) \leq 0$, we take $b = b(T)$ large for $M(b,T)$ to be small enough to ensure that $f(u) = M(b,T)$ has a root close to the root 0 of $f(u) = 0$, say $|z_1(-M(b,T))| < \varepsilon$. When $f''(u^{(3)}) \geq 0$, we take $b = b(T)$ large for $M(b,T)$ to be small enough to ensure that $f(u) = -M(b,T)$ has a root close to the root $u^{(3)}$ of $f(u) = 0$, say $|z_3(M(b,T)) - u^{(3)}| < \varepsilon$. Then, (25) holds for $b \geq \max\{b_c, b(T), \frac{1}{m(b)}\}$. As b grows, the bound on $M(b,T)$ provided by (25) remains bounded. We deduce that $b(T)$ does not increase with time but is bounded from above by a constant b_0. Once this is clear, we may reproduce all the steps above for all any $T > 0$ and (16)-(20) follow.

Let us see now how to use this comparison principle to analyze pinning and propagation of fronts in our system. Given a large enough value of $b \geq b_c$, we set $F^-(b) = -w^{(3)}(b)(1+\delta(b))$ and $F^+(b) = \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}$. As $b \to \infty$, $u^{(3)}(b) \to z_3(0)$, $w^{(3)}(b) \to 0$, $m(b) \to \min\{|f'(0)|, |f'(z_3(0))|\}$ and $\delta(b) \to 0$. Therefore, $F^-(b) \to 0$ and $F^+(b) \to 0$ as b grows.

Let us assume that the thresholds introduced in Section 2 for (5) satisfy $F_{c-}(D) < 0 < F_{c+}(D)$. Then, for small F, equation (5) has stationary wave fronts. Instead, if $0 > F_{c+}(D)$ fronts travel to the left for small F. When $F_{c-}(D) > 0$, fronts travel to the right for F small. Wave front solutions of (1)-(2) inherit this behavior thanks to inequality (18) and the behavior of

$F^+(b)$ and $F^-(b)$ for large b. This idea is made precise in the following results.

Corollary 5. *Let u_n, w_n be a solution of (1)-(2) with a wave front profile satisfying (13)-(14). Let us assume that the hypotheses of Theorem 4 hold, and keep the same notations. The estimates below follow for $t \geq 0$ and $n \in \mathbb{Z}$*

$$-\frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|} \leq w_n(t) \leq w^{(3)}(b)(1+\delta(b)), \tag{27}$$

$$l_{n+n_1}(t) < u_n(t) < s_{n+n_2}(t), \tag{28}$$

for adequate choices of n_1 and n_2, where $s_n(t)$ and $l_n(t)$ are wave front solutions of (5) for $g = f$ with $F = \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}$ and $F = -w^{(3)}(b)(1+\delta(b))$, respectively. Let $F_{c^+}(D)$ and $F_{c^-}(D)$ be the thresholds separating different propagation regimes for equation (5) introduced in Section 2. Then,

- *If $F_{c-}(D) < -w^{(3)}(b)(1+\delta(b)) < \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|} < F_{c+}(D)$, u_n and w_n are pinned,*
- *If $0 > -w^{(3)}(b)(1+\delta(b)) > F_{c+}(D)$, u_n and w_n travel to the left,*
- *If $F_{c-}(D) > \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|} > 0$, u_n and w_n travel to the right.*

The sign of the thresholds $F_{c-}(D)$, $F_{c+}(D)$ for the bistable equation (5) indicates whether propagation succeeds or fails in the system (1)-(2) for large enough b:

- *If $F_{c-}(D) < 0 < F_{c+}(D)$, u_n and w_n are pinned,*
- *If $0 > F_{c+}(D)$, u_n and w_n travel to the left,*
- *If $F_{c-}(D) > 0$, u_n and w_n travel to the right.*

Proof. Set $F^+ = \frac{w^{(3)}(1+\delta)}{b|f'(0)|}$ and $F^- = -w^{(3)}(1+\delta)$. Then, (27) follows applying Theorem 4.

Let $l_n(t)$ be a wave front solution of (5) for $g = f$ and $F = F^-$. We select n_1 such that $u_n(0) \geq l_{n+n_1}(0)$. This is possible thanks to (13)-(14) because $l_n(0)$ tends to $z_1(F^-) < u^{(1)} = 0$ at $-\infty$ and to $z_3(F^-) \leq u^{(3)}$ at ∞. Similarly, let $s_n(t)$ be a wave front solution (5) for $g = f$ and $F = F^+$. We select n_2 such that $u_n(0) \leq s_{n+n_2}(0)$. This is possible because $s_n(0)$ tends to $z_1(F^+) > u^{(1)} = 0$ at $-\infty$ and to $z_3(F^+) \geq u^{(3)}$ at ∞. Then, (28) follows applying Lemma 1 to $u_n(t)$, $l_{n+n_1}(t)$ and $s_{n+n_2}(t)$. The three regimes are found choosing b large enough to ensure that $F_{c^-}(D) < F^-(b) < 0 < F^+(b) < F_{c+}(D)$ (l_n, s_n pinned), $0 > F^-(b) > F_{c^+}(D)$ (l_n travels to the left) or $F_{c-}(D) > F^+(b) > 0$ (s_n travels to the right), respectively. As $b \to \infty$, $F^+(b)$ and $F^-(b)$ tend to zero and this yields the propagation behavior of the system for b large.

Let us illustrate how to use this Corollary to predict the dynamics of fronts in the system.

Figure 1 shows the thresholds $F_{c-}(D)$ and $F_{c+}(D)$ when $f(u) = u(2-u)(u-a)$ for several choices of $a \in (0,2)$ varying the symmetry of f. Figure 1(a) corresponds to small $a = 0.1$. The positive half of $f(u)$ is much larger than the negative part. Both $F_{c-}(D)$ and $F_{c+}(D)$ are negative, and lie always below $F^+(a,b) = \frac{w^{(3)}(a,b)(1+\delta(a,b))}{b|f'(0)|}$. For $b \geq 8$, the curve $F^-(a,b) = -w^{(3)}(a,b)(1+\delta(b))$ increases from -1 to 0 as b grows. For each D, there is a value $b(D)$ such that $0 > F^-(a,b) > F_{c^+}(D)$ for $b \geq b(D)$, and wave fronts propagate to the left. For $D > 1$, $F_{c^+}(D) \sim -0.54$ and $b(D) \sim 9$. By marking the value $F^-(0.1, 10)$ (dotted line) in Figure 1(a) we identify the interval $(D(10), \infty)$ in which the criteria holds and wave fronts propagate to the left. $D(b)$ is the abscissa of the intersection with $F^{c+}(D)$. For each fixed b propagation occurs if D is large enough.

Figure 1(c) corresponds to large $a = 1.8$. The negative half of $f(u)$ is much larger than the positive part. Both $F_{c-}(D)$ and $F_{c+}(D)$ are positive, and lie always above $F^-(1.8, b)$. Unlike previous cases, b must be very large to ensure bistable behavior, $b \geq 100$. The curve $F^+(1.8, b)$ decreases from 6×10^{-5} to 0 as b grows. For $D > 0.01$, $0 < F^+(a,b) < F_{c^-}(D)$ and fronts propagate to the right.

Figure 1(b) corresponds to intermediate $a = 1$. The source $f(u)$ is symmetric. The thresholds $F_{c-}(D) < 0$ and $F_{c+}(D) > 0$. The curve $F^+(1,b)$ decreases from 0.1 to 0 as $b > 4$ grows. $F^-(1,b)$ increases from -0.7 to 0. For $b > 10$, both thresholds lie between $F_{c-}(D) < 0$ and $F_{c+}(D) > 0$ if $D \leq 0.1$. Fronts do not propagate. As D grows, we must increase b to ensure this fact. We can always find a value $b(D)$ such that propagation fails if $b \geq b(D)$. This situation is quite exceptional. For intermediate values of $a \neq 1$, it is only encountered for $D \leq D(a)$. As D grows both $F_{c-}(D)$ and $F_{c+}(D)$ become either positive or negative as in the previous two cases and

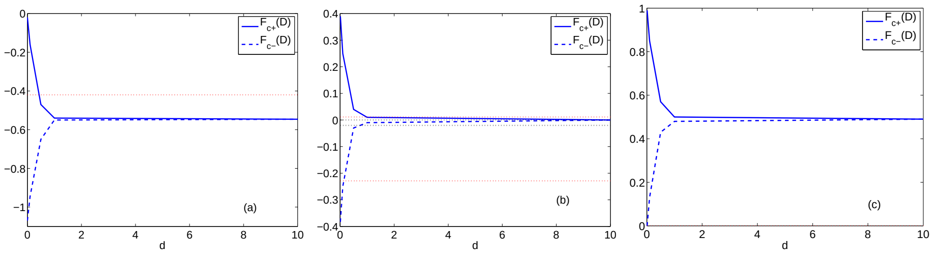

Figure 1: Thresholds separating the different propagation regimes for the equation (5) for $f(u) = u(2-u)(u-a)$ selecting different values of a: (a) $a = 0.1$, (b) $a = 1$, (c) $a = 1.8$.

propagation prevails. By marking the values $F^+(1, 10)$ and $F^-(1, 10)$ (higher and lower dotted lines) we find the interval $(0, D(10))$ in which propagation fails. $D(10)$ is the smallest of the abscissas of the intersections with $F_{c-}(D)$ and $F_{c+}(D)$, respectively. Marking the values $F^+(1, 100)$ and $F^-(1, 100)$ (intermediate dotted lines) we find the interval $(0, D(100))$. As b grows, $D(b)$ tends to infinity, and propagation fails for a larger range of D.

The speeds for wavefront propagation in the system are bounded from below by the propagation speeds for (5). Since the bistable equation admits wave front solutions propagating at arbitrarily small speeds, we expect the system to reproduce this behavior.

The previous results are based on the previous knowledge of the thresholds $F_{c^-}(D)$ and $F_{c^+}(D)$ of the wave front solutions of (5). Without that knowledge, we can establish pinning and propagation results for system (1)-(2) directly related to the properties of g. However, the conditions are usually much more restrictive. Corollary 6 contains the conditions for pinning, whereas Corollary 7 gives conditions for propagation.

Corollary 6. *Let u_n, w_n be a solution of (1)-(2) with wave front initial data satisfying (13)-(14). We assume that the hypotheses of Theorem 4 hold, and set $F^-(b) = -w^{(3)}(b)(1+\delta(b))$, $F^+(b) = \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}$, keeping the same notations. If D is large enough to find x_1,x_2, y_1,y_2 such that*

$$D(z_3(F^+(b)) - x) + f(x) + F^+(b) < 0, \qquad (29)$$
$$\text{if} \quad 0 = z_1(0) < z_1(F^+(b)) < x_2 < x < x_1 < z_2(F^+(b)),$$
$$D(z_1(F^-(b)) - x) + f(x) + F^-(b) > 0, \qquad (30)$$

$$\text{if} \quad z_2(F^-(b)) < y_1 < x < y_2 < z_3(F^-(b)) < z_3(0) = 1,$$

then,

$$u_n(0) \leq x_1, \quad n \leq n_1, \qquad u_n(0) \geq y_1, \quad n \geq n_2,$$

implies

$$u_n(t) \leq x_1, \quad n \leq n_1, \tag{31}$$

$$u_n(t) \geq y_1, \quad n \geq n_2, \tag{32}$$

for all $t \geq 0$*. The initial wave front does not propagate for the dynamics (1)-(2).*

Proof. Integers n_1 and n_2 exist because $u_n(0)$ grows from $u^{(1)} = 0$ to $u^{(3)}(b) > z_3(F^-(b))$ (since $f(u^{(3)}(b)) + F^-(b) = -w^{(3)}(b)\delta(b) < 0$).

Let $l_n(t)$ be a wave front solution of (5) with source $f(u)+F^-$ and initial data $l_n(0) \leq u_n(0)$ such that $l_n(0) = z_3(F^-)$ for $n \geq n_2$. By Lemma 2, $l_n(t) \geq y_1$ for $n \geq n_2$. Let $s_n(t)$ be a wave front solution of (5) with source $f(u)+F^+$ and initial data $s_n(0) \geq u_n(0)$ such that $s_n(0) = z_1(F^+)$ for $n \leq n_1$. By Lemma 2, $s_n(t) \leq x_1$ for $n \leq n_1$. Theorem 4 implies $u_n(t) \geq l_n(t)$ and $u_n(t) \leq s_n(t)$ for all n and $t > 0$. Thus, $u_n(t) \geq y_1$ for $n \geq n_2$ and $u_n(t) \leq x_1$ for $n \leq n_1$.

Figure 2 visualizes this result. Conditions (29)-(30) always hold for b large ($F^+(b)$ and $F^-(b)$ tend to zero) and D small because $f(x)$ is a cubic function satisfying (C1), (C2) and (C3). However, when the source is strongly asymmetric, one of the two conditions only holds for small enough D tending to zero as b tends to infinity. For larger D it is possible to find complementary conditions ensuring propagation.

(30) forbids propagation to the right of increasing wave fronts, whereas (29) blocks propagation to the left. For motion to be possible either (29) or (30) must fail. The following result ensures propagation when only (29) or (30) holds provided an additional condition is satisfied.

Corollary 7. *Let u_n, w_n be a solution of (1)-(2) with wave front like initial data satisfying (13)-(14). We assume that the hypotheses of Theorem 4 hold, and set $F^-(b) = -w^{(3)}(b)(1+\delta(b))$, $F^+(b) = \frac{w^{(3)}(b)(1+\delta(b))}{b|f'(0)|}$, keeping the same notations.*

If there is a value $A \in (z_2(F^-), z_3(F^-))$ such that

$$D(z_1(F^-) - A) + f(A) + F^- \quad \geq \quad 0, \tag{33}$$

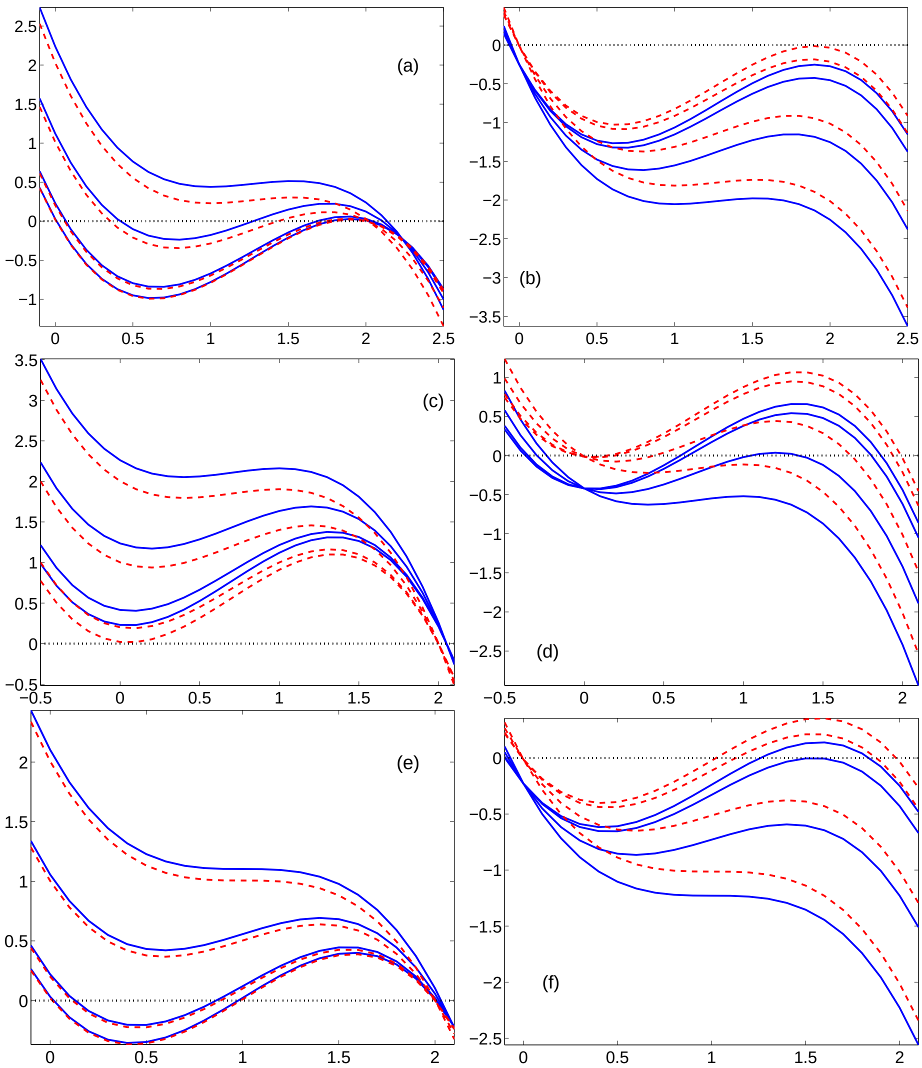

Figure 2: Curves defining conditions (29) and (30) for $f(u) = u(2-u)(u-a)$ selecting different values of a: (a), (b) $a = 0.1$, (c), (d) $a = 1.8$, (e), (f) $a = 1$. Solid lines correspond to $b = 10$ and dashed lines to $b = 150$. (29) is illustrated in (a), (c), (e), whereas (b), (d), (f) represent (30). We have superimposed curves corresponding to different values of $D : 0.01, 0.1, 1, 10$. As D grows, they increase in (a), (c), (e) and decrease in (b), (d), (f). For $a = 0.1$, (29) always holds for D moderately small (the curves are negative near the smallest zero), but (30) always fails unless we further reduce the value of D depending on b. This situation is reversed if $a = 1.8$. When $a = 1$, both conditions hold for D moderately small.

$$h(v;A,F^-) = D(z_1(F^-)-v)+D(A-v)+f(v)+F^- \geq \eta>0, \quad \text{when} \quad z_1(F^-)<v<A, \tag{34}$$

then, the solution u_n, w_n propagates to the left at a speed c bounded from below by $(A-z_1(F^-))^{-1}\min_{z_1(F^-)<v<A}h(v;A,F^-)$.

If there is a value $A \in (z_1(F^+), z_2(F^+))$ such that

$$D(z_3(F^+)-A)+f(A)+F^+ \leq 0, \tag{35}$$

$$h(v;A,F^+) = D(z_3(F^+)-v)+D(A-v)+f(v)+F^+ \leq -\eta<0, \quad \text{when} \quad z_3(F^+)>v>A, \tag{36}$$

then, the solution u_n, w_n propagates to the right at a speed c bounded from below by $(z_3(F^+)-A)^{-1}\min_{A<v<z_3(F^+)}|h(v;A,F^+)|$.

Proof. If (33)-(34) hold, Lemma 3 ensures that equation (5) with source $f(u)+F^-$ has wave front subsolutions $l_n(t) = l(n+ct)$ propagating to the left and gives a bound for the speed. The wave profile $l(\xi)$ grows from $z_1(F^-)$ for $\xi<\xi_1$ to A for $\xi>\xi_2$, with $0<\xi_2-\xi_1<1$. The speed c is bounded by $(A-z_1(F^-))^{-1}\min_{z_1(F^-)<v<A}h(v;A,F^-)$. Shifting this profile, if necessary, to guarantee that $u_n(0) \geq l_{n+n_1}(0)$, Theorem 4 implies that $u_n(t) \geq l_{n+n_1}(t)$ for all n and $t>0$. Equation (2) has $u_n(t)$ as source term, thus $w_n(t)$ and $u_n(t)$ propagates at a speed equal or larger.

When (35)-(36) hold, the proof is similar, but using wave front supersolutions of the form $s_n(t) = s(n-ct)$ travelling to the right.

For (34) or (36) to hold, D cannot be too small. The term $D(A-v)$ must compensate the wrong sign of the rest of the expression near the zeros. The conditions stated in Corollaries 6 and 7 are more restrictive than those stated in Corollary 5. They give no information for very large values of D.

Basically, all the pinning and propagation conditions stated in this section have the same physical meaning. Propagation fails whenever the source is not asymmetric enough depending on the value of the diffusion or when the diffusion is very small for a fixed source. Propagation succeeds when the source is asymmetric enough for the value of the diffusion or the diffusion is large enough for a fixed source.

4 Stability of stationary wave fronts

Once we have established conditions for pinning of the tails of initial patterns with a wave front structure we may obtain existence results for stationary wave fronts. It was observed in [1] that stationary solutions of (1)-(2) satisfy:

$$0 = D(u_{n+1} - 2u_n + u_{n-1}) + f(u_n) - w_n, \quad w_n = \frac{u_n}{b}.$$

Therefore, they are stationary solutions of the bistable equation:

$$u_{n,t} = D(u_{n+1} - 2u_n + u_{n-1}) + f(u_n) - \frac{u_n}{b}. \tag{37}$$

The source $g(s) = f(s) - \frac{s}{b}$ is a 'cubic' function satisfying (C1), (C2), (C3) if $b \geq b_c$. We denote by $z_1 < z_2 < z_3$ the three consecutive zeroes.

In [21], the following alternative for equations of the form (37) is proved: either travelling or stationary wave front solutions exist, generated as long time limits of initial value problems with initial data $u_n(0) = z_1$ for $n \leq 0$ and $u_n(0) = z_3$ for $n > 0$. Conditions for the existence of stationary wave front solutions of the discrete FitzHugh-Nagumo system follow then from the pinning results in Section 2, as stated in the following theorem.

Theorem 8. *The spatially discrete FitzHugh-Nagumo system (1)-(2) has stationary wave front solutions u_n, w_n provided the bistable equation (5) with $g(u) = f(u) - \frac{u}{b}$ and $F = 0$ satisfies one of the following conditions:*

- *A) there are stationary sub and supersolutions with wave front structure blocking propagation,*
- *B) the propagation thresholds for (5) with $g = f(u) - \frac{u}{b}$ satisfy $F_{c-}(D) < 0 < F_{c+}(D)$,*
- *C) the pinning conditions stated in Lemma 2 hold.*

Generically, no smooth functions $u(\xi)$ and $w(\xi)$ can be found such that $u_n = u(n)$ and $w_n = w(n)$.

Under the conditions A), B) or C), propagation of wave front like initial patterns is excluded. Thus, stationary wave front solutions exist. The last claim follows from the known fact that no such functions exist for static wave fronts in discrete bistable equations [6].

We can improve Theorem 8 ensuring uniform proximity of the solutions of initial value problems of (1)-(2) to stationary wave front solutions for all times (nonlinear stability of stationary solutions). This implies that certain patterns cannot propagate for the system dynamics. The first result in that direction holds for D small.

Theorem 9. *Let (a_n, c_n) be a stationary wave front solution of (1)-(2). We take D small enough to ensure that none of the values a_n enters the region in which the derivative of f is positive. Let (u_n, w_n) be a solution of (1)-(2) with initial data satisfying*

$$\sum_n |u_n(0) - a_n|^2 < \delta^2, \quad \sum_n |w_n(0) - c_n|^2 < \delta^2,$$

with δ small enough (detailed in the proof). Then, for all $t > 0$

$$\sum_n |u_n(t) - a_n|^2 + \frac{1}{\varepsilon} \sum_n |w_n(t) - c_n|^2 < \sum_n |u_n(0) - a_n|^2 + \frac{1}{\varepsilon} \sum_n |w_n(0) - c_n|^2.$$

Solutions generated by such initial data cannot propagate.

Proof. By assumption, $|u_n(0) - a_n| < \delta < \delta(1 + \frac{1}{\varepsilon})^{\frac{1}{2}} = \eta$. For D small the values of a_n are concentrated near z_1 and z_3, and do not enter the region where $f' > 0$. We select η in such a way that $f'(u_n(0) \pm \eta) < -\lambda$ for some $\lambda > 0$. Then, $f'(u_n(t)) < -\lambda$ holds up to a time T. Let T be the first time at which $|u_n(T) - a_n| = \eta$.

Set $x_n = u_n - a_n$ and $y_n = w_n - c_n$. We substract the equations satisfied by u_n and a_n, w_n and c_n to find equations for x_n and y_n. Then, we multiply the first equation by x_n, the second one by y_n and add with respect to n to get

$$\begin{aligned} \frac{1}{2}\frac{d}{dt}\sum |x_n|^2 &= -D\sum_n |x_{n+1} - x_n|^2 + \sum_n (f(u_n) - f(a_n))x_n - \sum_n y_n x_n, \\ \frac{1}{2\varepsilon}\frac{d}{dt}\sum |y_n|^2 &= \sum_n x_n y_n - b\sum_n y_n^2. \end{aligned}$$

Adding up both identities and taking into account that $f(u_n(t)) - f(a_n) = f'(\xi_n(t))x_n$, $\xi_n(t) \in (u_n(t), a_n)$ with $f'(\xi_n(t)) \leq -\lambda$ for $t \leq T$, we get

$$\frac{1}{2}\frac{d}{dt}\sum |x_n|^2 + \frac{1}{2\varepsilon}\frac{d}{dt}\sum |y_n|^2 \leq \sum_n (f(u_n) - f(a_n))x_n - b\sum_n y_n^2, \quad (38)$$

$$\leq \quad -\lambda \sum_n x_n^2 - b \sum_n y_n^2 < 0,$$

for $t \leq T$.

Inequality (38) implies $\sum_n |u_n(t) - a_n|^2 < \delta^2(1 + \frac{1}{\varepsilon})$ for $t \leq T$ and $|u_n(T) - a_n| < \eta$, obtaining a contradiction. Thus, $|u_n(t) - a_n| < \eta$ for all $t > 0$ and (38) holds for all $t > 0$.

The previous result is a simple case of a more general statement for arbitrary D:

Theorem 10. *Let (a_n, c_n) be a stationary wave front solution of (1)-(2). Let us assume that either*

$$\lambda = \mathrm{Inf} \frac{D\sum_n |k_{n+1} - k_n|^2 - \sum_n f'(a_n)|k_n|^2 + (1-\varepsilon)\sum h_n k_n + \varepsilon b \sum_n |h_n|^2}{\sum_n |k_n|^2 + \sum_n |h_n|^2} > 0, \quad (39)$$

or

$$\lambda = \mathrm{Inf} \frac{D\sum_n |k_{n+1} - k_n|^2 - \sum_n f'(a_n)|k_n|^2 + b\sum_n |h_n|^2}{\sum_n |k_n|^2 + \sum_n |h_n|^2} > 0, \quad (40)$$

where the infimums are taken over real sequences satisfying $\sum_n |k_n|^2 + \sum_n |h_n|^2$. Let (u_n, w_n) be a solution of (1)-(2) with initial data satisfying:

$$\sum_n |u_n(0) - a_n|^2 < \delta^2, \quad \sum_n |w_n(0) - c_n|^2 < \delta^2,$$

for δ small enough (detailed in the proof), then

$$\sum_n |u_n(t) - a_n|^2 + r\sum_n |w_n(t) - c_n|^2 < \sum_n |u_n(0) - a_n|^2 + r\sum_n |w_n(0) - c_n|^2, \quad (41)$$

for all $t > 0$, where $r = 1$ if (39) holds and $r = \frac{1}{\varepsilon}$ if (40) holds. Wave fronts generated by such initial data cannot propagate.

Proof. Set $x_n = u_n - a_n$ and $y_n = w_n - c_n$. Initially, $|x_n(0)| = |u_n(0) - a_n| < \delta\sqrt{1+r}$. Let us assume this inequality remains true up to a time T at which $|u_n(T) - a_n| = \delta\sqrt{1+r}$. Proceeding as in Theorem 9, we find

$$\frac{1}{2}\frac{d}{dt}\sum |x_n|^2 = -D\sum_n |x_{n+1} - x_n|^2 + \sum_n (f(u_n) - f(a_n))x_n - \sum_n y_n x_n,$$

$$\frac{1}{2}\frac{d}{dt}\sum |y_n|^2 = \varepsilon \sum_n x_n y_n - \varepsilon b \sum_n y_n^2.$$

Set $M = \max|f''|$. Adding up both identities and using (39) we have:

$$\begin{aligned}\frac{1}{2}\frac{d}{dt}\sum |x_n|^2 + \frac{1}{2}\frac{d}{dt}\sum |y_n|^2 &\leq -\lambda\sum_n x_n^2 - \lambda\sum_n y_n^2 + \sum_n \frac{f''(\xi_n)}{2}x_n^3 \\ &\leq (-\lambda + \delta M\sqrt{1+r})\sum_n x_n^2 - \lambda\sum_n y_n^2,\end{aligned}$$

provided $|x_n| = |u_n - a_n| \leq \delta\sqrt{1+r}$ for $t \leq T$. If $\delta < \frac{\lambda}{M\sqrt{1+r}}$, (41) follows for $t \leq T$. This implies that $|x_n(T)| = |u_n(T) - a_n| < \delta\sqrt{1+r}$. Thus, $|u_n(t) - a_n| < \delta\sqrt{1+r}$ remains true for all $t > 0$ and (41) holds for all $t > 0$.

Adding up both identities again and using (40) we have:

$$\frac{1}{2}\frac{d}{dt}\sum |x_n|^2 + \frac{1}{2\varepsilon}\frac{d}{dt}\sum |y_n|^2 \leq -\lambda\sum_n x_n^2 - \lambda\sum_n y_n^2 + \sum_n f''(\xi_n)x_n^3,$$

and we conclude as before.

Condition (39) for stability is related to the physical idea of linear stability of the stationary solution. A static wave front is linearly stable if when looking for solutions of the form $a_n + e^{-\mu t}k_n$, $c_n + e^{-\mu t}h_n$, the resulting eigenvalue problem

$$-\mu k_n = D(k_{n+1} - 2k_n + k_{n-1}) + f'(a_n)k_n - h_n, \tag{42}$$
$$-\mu h_n = \varepsilon(k_n - bh_n),$$
$$|h_n|, |k_n| \to 0 \quad n \to \infty, \tag{43}$$

admits non vanishing solutions only if $\mathrm{Re}\,\mu > 0$. Multiplying the first equation by $\overline{k}_n$ and the second one by $\overline{h}_n$ we find

$$\mu = \frac{D\sum_n |k_{n+1} - k_n|^2 - \sum_n f'(a_n)|k_n|^2 + (1-\varepsilon)\sum \overline{h}_n k_n + \varepsilon b\sum_n |h_n|^2}{\sum_n |k_n|^2 + \sum_n |h_n|^2}. \tag{44}$$

When $\varepsilon = 1$, both components of system (1)-(2) evolve in the same time scale. Expression (44) for the eigenvalues is real, and bounded uniformly from below when $h_n \in l^2(\mathbb{C})$ and $k_n \in l^2(\mathbb{C})$. The smallest eigenvalue λ_1 is then the minimum of the quotients (44) when $h_n \in l^2(\mathbb{R})$ and $k_n \in l^2(\mathbb{R})$. In this case, linear stability implies that Theorem 10 applies. Wave fronts initially close to the static wave front remain close to it for all times and cannot propagate.

On the other hand, condition (40) extends Theorem 9 to arbitrarily large values of D. Quotient (40) reduces to the expression defining the eigenvalues of the linearized problem for (37) when $h_n = k_n$.

5 The discrete Hodgkin-Huxley model

FitzHugh-Nagumo models were introduced as a simplification of more realistic Hodgkin-Huxley models for nerve propagation [32]. They provide qualitative understanding about pinning and propagation, together with some insight on the role of the controlling parameters. For quantitative information, we must resort to more elaborated models. For instance, the dimensionless discrete Hodgkin-Huxley model takes the form:

$$\frac{dv_k}{dt} + I_{ion}(v_k, m_k, n_k, h_k) = D_d\left(v_{k+1} - 2v_k + v_{k-1}\right), \tag{45}$$

$$\begin{aligned} \frac{dm_k}{dt} &= \lambda_m \Lambda_m(v_k)(m_\infty(v_k) - m_k), \\ \frac{dn_k}{dt} &= \varepsilon \lambda_k \Lambda_k(v_k)(n_\infty(v_k) - n_k), \\ \frac{dh_k}{dt} &= \varepsilon \lambda_h \Lambda_h(v_k)(h_\infty(v_k) - h_k). \end{aligned} \tag{46}$$

The variable v_k represents the deviation from rest of the membrane voltage. m_k, n_k and h_k govern the activation and inactivation of sodium and potassium ion channels. The ion current is given by the classic Hodgkin-Huxley relation [22]:

$$I_{ion}(v, m, n, h) = g_{Na} m^3 h(v - 1) + g_L(v - V_L) + g_K n^4 (v - V_K). \tag{47}$$

Typical values for the parameters and usual expressions for the nonlinear rate and equilibrium profiles are given in [32, 10]. For toads and frogs, $D_d \sim 10^{-1}$ and $\lambda_k, \lambda_h \sim 10^{-2}$ are small parameters.

For such experimental values, (45)-(46) has a unique constant solution (v^*, m^*, n^*, h^*), which is stable. The asymptotic study performed in [10] shows that the two slow variables, n_k and h_k, remain almost constant in the leading fronts of the nerve impulses. The two fast variables, n_k and h_k, form a travelling wave front governed by the reduced equations:

$$\frac{dv_k}{dt} + I_{ion}(v_k, m_k, n^*, h^*) = D_d(v_{k+1} - 2v_k + v_{k-1}), \tag{48}$$

$$\frac{dm_k}{dt} = \lambda_m \Lambda_m(v_k)(m_\infty(v_k) - m_k), \tag{49}$$

which form a system of bistable nature: it admits three constant stationary solutions, two of which are stable. This system differs qualitatively from the bistable FitzHugh-Nagumo systems we have studied so far because m_k is not small. It typically varies between 0 and 1, and its variations have larger amplitude than the variations of v_k. The techniques developed in Sections 3 do not seem to apply in this case. On the contrary, stationary wave fronts can be constructed and pinning results established following the ideas in Section 4.

Theorem 11. *The reduced discrete Hodgkin-Huxley model (48)-(49) has stationary wave front solutions v_k, m_k increasing from (v^*, m^*) to (V, M) provided the bistable equation (5) with $g(u) = -I_{ion}(u, m_\infty(u), n^*, h^*)$ and $F = 0$ verifies one of the following conditions:*

A) there are stationary sub and supersolutions with wave front structure blocking propagation,

B) the propagation thresholds for (5) with $g(u) = -I_{ion}(u, m_\infty(u), n^*, h^*)$ satisfy $F_{c-} < 0 < F_{c+}$,

C) the pinning conditions stated in Lemma 2 hold.

Proof. It is straightforward using the same arguments to establish Theorem 8. v_k is a stationary wave front for the discrete bistable equation (5) with $g(u) = -I_{ion}(u, m_\infty(u), n^*, h^*)$ and $F = 0$. Then, $m_k = m_\infty(v_k)$.

Once we have established an existence result for stationary wave fronts, we must link it with propagation failure. It is expected that propagation of wave front patterns will fail within the ranges of parameters for which wave fronts exist.

Let us define the following auxiliary matrices:

$$M_K = \begin{pmatrix} A_K & B_K \\ C_K & D_K \end{pmatrix}, \tag{50}$$

where B_K, C_K, D_K are diagonal matrices

$$B_K \;=\; \text{diag}\Big(\frac{\partial I_{ion}}{\partial m}(v_{-K}, m_{-K}, n_{-K}, h_{-K}), ..., \frac{\partial I_{ion}}{\partial m}(v_k, m_k, n_k, h_k),$$

$$
\begin{aligned}
& \quad ..., \frac{\partial I_{ion}}{\partial m}(v_K, m_K, n_K, h_K)\Big), \\
C_K &= \operatorname{diag}\Big(-\lambda_m \Lambda(v_{-K}) m'_\infty(v_{-K}), \\
& \quad ..., -\lambda_m \Lambda(v_k) m'_\infty(v_k), \\
& \quad ..., -\lambda_m \Lambda(v_K) m'_\infty(v_K)\Big), \\
D_K &= \operatorname{diag}\Big(\lambda_m \Lambda(v_{-K}), ..., \lambda_m \Lambda(v_k), ..., \lambda_m \Lambda(v_K)\Big),
\end{aligned}
$$

and A is a tridiagonal matrix:

$$
A_K = \begin{pmatrix} \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & -D_d & 2D_d + \frac{\partial I_{ion}}{\partial v}(v_k, m_k, n_k, h_k), & -D_d & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \end{pmatrix}. \tag{51}
$$

M_K is applied to vectors of the form $z_K = (x_{-K}, ..., x_0, ..., x_K, y_{-K}, ..., y_0, ..., y_K)$. Letting $K \to \infty$ we obtain infinite matrices and sequences A, B, C, D, M and $z = (x, y)$. We define:

$$
\lambda = Min_{z=(x,y),\, x,y \in \ell^2(I\!R)} \frac{z^t M z}{z^t z}. \tag{52}
$$

Theorem 12. *Let (a_k, c_k) be a stationary wave front solution of (48)-(49). If λ given by (52) is positive and the initial state satisfies:*

$$
\sum_k |v_k(0) - a_k|^2 < \delta^2, \quad \sum_k |m_k(0) - c_k|^2 < \delta^2,
$$

for δ small enough, then

$$
\sum_k |v_k(t) - a_k|^2 + \sum_k |m_k(t) - c_k|^2 < \sum_k |v_k(0) - a_k|^2 + \sum_k |m_k(0) - c_k|^2, \tag{53}
$$

for $t > 0$.

Proof. Set $x_k = v_k - a_k$ and $y_k = m_k - c_k$. Subtracting the equations satisfied by v_k and a_k, m_k and c_k, we find equations for x_k and y_k. Multiplying the first one by x_k, the second one by y_k and adding with respect to k, we get:

$$
\frac{1}{2}\frac{d}{dt}\sum |x_k|^2 = -D_d \sum_k |x_{n+1} - x_k|^2
$$

$$
\begin{aligned}
& -\sum_k (I(v_k, m_k, n^*, h^*) - I(a_k, c_k, n^*, h^*))x_k, \\
\frac{1}{2}\frac{d}{dt}\sum |y_k|^2 \quad = \quad & \sum_k (\Lambda(v_k)m_\infty(v_k) - \Lambda(a_k)m_\infty(a_k))y_k \\
& -\sum_k (\Lambda(v_k)m_k - \Lambda(a_k)c_k)y_k.
\end{aligned}
$$

Combining both identities, linearizing about (a_k, c_k) and using (52) we get:

$$
\begin{aligned}
\frac{1}{2}\frac{d}{dt}\left(\sum|x_k|^2+\sum|y_k|^2\right) < \quad & -\lambda \textstyle\sum_k x_n^2 - \lambda \sum_k y_k^2 \\
& +\sqrt{2}\delta \textstyle\sum_k \mathrm{Max}_{\xi,\eta}|D^2 I(\xi, \eta, n^*, h^*)|(x_k^2 + 2|x_k y_k| + y_k^2) \\
& + \sqrt{2}\delta \textstyle\sum_k \mathrm{Max}_{\xi}|D^2(\Lambda(\xi)m_\infty(\xi))|x_k^2 \\
& +\sqrt{2}\delta \textstyle\sum_k \mathrm{Max}_{\xi,\eta}|D^2(\Lambda(\xi)\eta)|(x_k^2 + 2|x_x y_k| + y_k^2),
\end{aligned}
$$

as long as $|x_k|$, $|y_k|$ are bounded by $\sqrt{2}\delta$. This is true for short times. $|D^2 r(\xi, \eta)|$ denotes the maximum of the components of the hessian matrix. Set $S = \max_{\xi\in(v^*,V),\eta\in(0,1)}(|D^2 I(\xi, \eta, n^*, h^*)|, |D^2(\Lambda(\xi)m_\infty(\xi))|, |D^2(\Lambda(\xi)\eta)|)$.

Choosing $\delta < \frac{\lambda}{5\sqrt{2}S}$, (53) follows as long as $|x_k|$, $|y_k|$ are bounded by $\sqrt{2}\delta$. Now, (53) implies that neither of them can reach the value $\sqrt{2}\delta$, therefore (53) holds for all $t > 0$.

Now, we have to justify the hypothesis on λ. We expect it to hold at least when $D_d << 1$, for the typical experimental values. In fact, for the small values of D_d corresponding to vertebrates, the wave fronts show the following structure: Two constant tails

$$v_k = v^*, m_k = m^* = m_\infty(v^*), \quad k < 0, \tag{54}$$

$$v_k = V, m_k = M = m_\infty(V), \quad k > 0, \tag{55}$$

joined by an intermediate value (v_0, m_0), $m_0 = m_\infty(v_0)$. The stability of the fronts reduces to the stability of (v_0, m_0) for the reduced dynamics:

$$\tfrac{dv}{dt} + I_{ion}(v, m, n^*, h^*) = D_d\left(V - 2v + v^*\right), \tag{56}$$

$$\tfrac{dm}{dt} = \lambda_m \Lambda_m(v)(m_\infty(v) - m). \tag{57}$$

Looking for solutions of the form $v = v_0 + e^{-\mu t}a$, $m = m_0 + e^{-\mu t}b$, we see that μ must be an eigenvalue of the matrix:

$$M_0 = \begin{pmatrix} 2D_d + \frac{\partial I_{ion}}{\partial v}(v_0, m_0, n^*, h^*) & \frac{\partial I_{ion}}{\partial m}(v_0, m_0, n^*, h^*) \\ -\lambda_m \Lambda_m(v_0)m'_\infty(v_0) & \lambda_m \Lambda_m(v_0) \end{pmatrix}, \tag{58}$$

where $\frac{\partial I_{ion}}{\partial v}(v_0,m_0,n^*,h^*) = g_{Na}m_0^3h^* + g_L + g_K(n^*)^4 > 0$ and $\frac{\partial I_{ion}}{\partial m}(v_0,m_0,n^*,h^*) = 3g_{Na}m_0^2h^*(v_0-1) < 0$. Typical values of the dimensionless conductivities g_{Na}, g_L, g_K are positive. The variables m, n, h takes values between 0 and 1. In the dimensionless model, $|v|$ also ranges from 0 to 1. The product $\lambda_m\Lambda_m(v_0) > 0$ and $m'_\infty(v_0) > 0$ for any v_0. The eigenvalues of (58) are real. Both are positive whenever

$$\left(2D_d + g_{Na}m_0^3h^* + g_L + g_K(n^*)^4\right) > -3g_{Na}m_0^2h^*(v_0-1)m'_\infty(v_0) > 0, \quad (59)$$

that is,

$$2D_d + g_{Na}m_0^2h^*(m_0 + 3(v_0-1)m'_\infty(v_0)) + g_L + g_K(n^*)^4 > 0. \quad (60)$$

This is true for typical parameter values as long as D_d is small enough. In this case,

$$\lambda_0 = Min_{z=(x,y),\, x,y\in R}\frac{z^tM_0z}{z^tz} > 0. \quad (61)$$

This may be seen as a reduction to finite dimension of the original stability problem for D_d small and suggests Theorem 12 should hold at least for D_d small. In general, M_K are the matrices corresponding to linear stability problems reduced to finite dimension $2K+1$.

6 Variable diffusion and extensions to two dimensions

In this section, we discuss the implications of the previous results in problems with variable diffusion or in several dimensions.

Let us first consider problems with variable diffusion. Theorem 4 still holds if we replace the first equation in (1)-(2) by:

$$u'_n = D_n(u_{n+1} - 2u_n + u_{n-1}) + f(u_n) - w_n, \quad 0 < D_n < D, \quad (62)$$

or

$$u'_n = D_1(u_n)(u_{n+1} - u_n) + D_2(u_n)(u_{n-1} - u_n) + f(u_n) - w_n, \quad (63)$$

with $0 < D_1, D_2 < D$ keeping the same hypotheses on f, and assuming D_1, D_2 are smooth enough. These equations admit constant solutions and satisfy the comparison principle stated in Lemma 1. These are the only requirements for Theorem 4 to hold.

Corollary 5 holds provided pinning and propagation results similar to the ones collected in Section 2 are satisfied when $D(u_{n+1}-2u_n+u_{n-1})$ is replaced by $D_n(u_{n+1}-2u_n+u_{n-1})$ or $D_1(u_n)(u_{n+1}-u_n)+D_2(u_n)(u_{n-1}-u_n)$. This is usually the case.

Corollary 6 should be restated as follows: If for some n, we can find x_1,x_2, y_1,y_2 such that

$$\begin{aligned} & d_1(z_3(F^+(b))-x)+f(x)+F^+(b)<0, && (64)\\ \text{if}\quad & 0=z_1(0)<z_1(F^+(b))<x_2<x<x_1<z_2(F^+(b)), &&\\ & d_2(z_1(F^-(b))-x)+f(x)+F^-(b)>0, && (65)\\ \text{if}\quad & z_2(F^-(b))<y_1<x<y_2<z_3(F^-(b))<z_3(0)=1, && \end{aligned}$$

where $d_1=d_2=D_n$ for (62) and $d_1=D_1(x)$, $d_2=D_2(x)$ for (63), then,

$$u_n(0)\le x_1, \quad u_n(0)\ge y_1,$$

implies

$$u_n(t)\le x_1, \quad u_n(t)\ge y_1,$$

for all $t\ge 0$. In either case initial wave front does not propagate for the dynamics (1)-(2). It becomes pinned at position n.

Corollary 7 holds replacing (33)-(34) and (35)-(36) by

$$\begin{aligned} D_2(A)(z_1(F^-)-A)+f(A)+F^- &\ \ge\ 0, && (66)\\ D_2(A)(z_1(F^-)-v)+D_1(A)(A-v)+f(v)+F^- &\ \ge\ \eta>0, && (67) \end{aligned}$$

where $d_2=D_2(A)$, $d_1=D_1(A)$ for (63) and $d_2=D$, $d_1=d$ for (62), and

$$\begin{aligned} d_1(z_3(F^+)-A)+f(A)+F^+ &\ \le\ 0, && (68)\\ d_1(z_3(F^+)-v)+d_2(A-v)+f(v)+F^+ &\ \le\ -\eta<0. && (69) \end{aligned}$$

where $d_2=D_2(A)$, $d_1=D_1(A)$ for (63) and $d_2=D$, $d_1=d$ for (62), if $0<d<D_n<D$.

Let us turn now to two dimensional models. We consider the two dimensional version of the bistable FitzHugh-Nagumo model:

$$u'_{n,m}=D(u_{n+1,m}+u_{n,m+1}-4u_{n,m}+u_{n-1,m}+u_{n,m-1})+f(u_{n,m})-w_{n,m}, \quad (70)$$

$$w'_{n,m}=\varepsilon(u_{n,m}-bw_{n,m}), \quad (71)$$

for $n, m \in \mathbb{N}$, with $D, b, \varepsilon > 0$.

Theorem 4 still holds keeping the same hypotheses on f. These equations admit constant solutions and satisfy a two dimensional version of the comparison principle stated in Lemma 1. Corollary 5 holds provided pinning and propagation results similar to the ones collected in Section 2 hold for two dimensional diffusion equations. This is likely the case, but a complementary study of propagation failure for two dimensional reaction-diffusion equations should be performed, which is out of the scope of this paper.

Corollary 6 should be restated as follows. If $u_{n,m}(0) \in [z_1, z_3]$ and for some (n, m) we can find x_1,x_2, y_1,y_2 such that

$$\begin{aligned} & 4D(z_3(F^+(b)) - x) + f(x) + F^+(b) < 0, \qquad (72) \\ \text{if} \quad & 0 = z_1(0) < z_1(F^+(b)) < x_2 < x < x_1 < z_2(F^+(b)), \\ & 4D(z_1(F^-(b)) - x) + f(x) + F^-(b) > 0, \qquad (73) \\ \text{if} \quad & z_2(F^-(b)) < y_1 < x < y_2 < z_3(F^-(b)) < z_3(0) = 1, \end{aligned}$$

then,

$$u_{n,m}(0) \leq x_1, \quad u_{n,m}(0) \geq y_1,$$

implies

$$u_{n,m}(t) \leq x_1, \quad u_{n,m}(t) \geq y_1,$$

for all $t \geq 0$. This forbids propagation locally, in regions where the initial data satisfy $y_1 \leq u_{n,m}(0) \leq x_1$.

Travelling wave sub and supersolutions can be constructed in two dimensions by extending one dimensional waves: $l_{n,m}(t) = l(n + ct)$ and $s_{n,m}(t) = s(n - ct)$, with l and s defined in Lemma 3. Any solution of (70)-(71) with initial data $u_{n,m}(0) \geq l_{n,m}(0)$ will propagate to the right if $c < 0$ and l is decreasing or to the left if $c > 0$ and l is increasing. Any solution of (70)-(71) with initial data $u_{n,m}(0) \leq s_{n,m}(0)$ will propagate to the left if $c < 0$ and s is decreasing or to the right if $c > 0$ and s is increasing.

Pinning results extending Theorems 9 and 10 can be proved in a similar way with straightforward modifications.

7 Conclusions

Pinning of the leading fronts of nerve impulses along myelinated axons due to changes in the properties of myelin sheaths is a key mechanism for impulse propagation failure and subsequent illnesses (multiple sclerosis). Standard continuum models fail to reproduce this behavior. Instead, spatially discrete models such as the discrete HH model or the hybrid FHH model describe it. The leading fronts of the nerve impulses are governed by bistable systems with two fast and two slow variables, which can be approximated by bistable systems involving just two components moving in the same time scale. The bistable FitzHugh-Nagumo system has a simpler structure and may be used to understand propagation failure of such wave fronts.

We have derived a comparison principle that relates wave front solutions of the FHN system to wave front solutions of reduced bistable equations, for which propagation failure is better understood. This yields a qualitative understanding of the role of different parameters. Further pinning results are obtained by studying the asymptotic stability of stationary wave front solutions for the full system. Most of these results can be extended to problems with variable coefficients or two dimensions. In more realistic discrete Hodgkin-Huxley models, we have been able to establish existence of stationary wave fronts and a pinning condition derived from the asymptotic stability of such wave fronts. Whether some kind of comparison principle similar to the one established for FHN allowing for more general pinning and propagation predictions can be established for the Hodgkin-Huxley dynamics appears to be open problem.

The discrete Hodgkin-Huxley model is a simplification of the more realistic FitzHugh-Hodgkin-Huxley (FHH) model. However, its predictive value is still limited. The FHH model instead produces predictions of speed values quite similar to the speeds measured experimentally for toads or frogs [11], and includes a variety of parameters such as the resistance and capacitance of the myelin sheath. This model combines a set of discrete equations for the Ranvier nodes with a sequence of parabolic problems for the internodal myelin layers. No rigorous pinning and propagation results for the mixed bistable problems governing the leading fronts of the pulses have been given yet. Only asymptotic predictions are available [11].

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