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Steadily propagating waves of a chemotaxis model

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ABSTRACT

This paper studies the existence, asymptotic decay rates, nonlinear stability, wave speed and chemical diffusion limits of traveling wave solutions to a chemotaxis model describing the initiation of angiogenesis and reinforced random walk. By transforming the chemotaxis system, via a Hopf-Cole transformation, into a system of conservation laws, the authors studied the traveling wave solutions of the transformed system in previous papers. One of the purposes of this paper is to transfer the results of the transformed system to the original Keller–Segel chemotaxis model. It turns out that only partial results of the transformed system have physical meaning when they are passed back to the original system. Thus the transformed system is not entirely equivalent to the original system. Particularly the chemical growth rate parameter appeared in the original system vanishes in the transformed system. Hence to understand the role of this parameter, one has to go back to the original system. Numerical simulations of steadily propagating waves are shown.

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1. Introduction

Chemotaxis describes the oriented movement of cells toward the chemical concentration gradient. The prototype of the population-based chemotaxis model was proposed by Keller–Segel in the 1970s [13,14] to describe the aggregation of cellular slime molds *Dictyostelium discoideum* in response to the chemical cyclic adenosine monophosphate (cAMP). The first mathematical model describing the traveling waves was also proposed by Keller and Segel [15], as follows

$$\begin{cases} u_t = (Du_x - \chi u c^{-1} c_x)_x, \\ c_t = \varepsilon c_{xx} - u c^m, \end{cases}$$
(1.1)

where $(x, t) \in \mathbb{R} \times [0, \infty)$, u(x, t) denotes the cell density and c(x, t) the chemical (or oxygen) concentration. D > 0 and $\varepsilon \ge 0$ are diffusion coefficients of cells and the chemical, respectively. χ is a positive constant often referred to as chemosensitivity. The model (1.1) aimed at describing the propagation of traveling bands of bacteria observed in a pioneering experiment by Adler [1,2], where the bacteria move toward the chemical concentration gradient and consume the chemical along the movement. A vast amount of results on the traveling wave solutions of model (1.1) have been developed subsequently for the case $0 \le m < 1$, cf. [31,32,29,30,28,23,26] and references therein, which led to a traveling pulse in *u* that explains

the traveling band formation of bacterial chemotaxis. In this paper, we consider the traveling wave solutions of the following chemotaxis model

$$\begin{cases} u_t = (Du_x - \chi u c^{-1} c_x)_x, \\ c_t = \varepsilon c_{xx} - u c + \beta c, \end{cases}$$
(1.2)

with initial data

$$(u(x,0), c(x,0)) = (u_0(x), c_0(x)) \to (u_{\pm}, c_{\pm}) \text{ as } x \to \pm \infty.$$
 (1.3)

When $\beta = 0$, the model (1.2) may be used to describe the directed movement of endothelial cells toward the signaling molecule vascular endothelial growth factor (VEGF) during the initiation of angiogenesis [4,5,16,6,34], where *u* denotes the density of endothelial cells and *c* stands for the concentration of VEGF. When $\varepsilon = 0$ and β > 0, then the model (1.2) describes a model of reinforced random walk derived in [17], where *u* is the particle density and *c* accounts for the concentration of a non-diffusive "active agent". Formally the model (1.2) with $\beta = 0$ becomes a special case of model (1.1) when m = 1. We shall show in the paper that the model (1.2) generates a traveling wavefront in u and interprets an "invasive" pattern, which is in contrast to the case $0 \le m < 1$ where the traveling pulse explains traveling band formation of bacterial chemotaxis. Before proceeding, it is helpful to discuss the physical region of (u, c) in (1.2). Since both u and c in denote densities, we assume $u(x,t) \ge 0$, $c(x,t) \ge 0$ for all $(x,t) \in \mathbb{R} \times [0,\infty)$. Hence we suppose that $u_0(x) \ge 0$, $c_0(x) \ge 0$ and consider (1.2) in the region

$$\mathscr{X}_1 = \{(u, v) | u \ge 0, \ c \ge 0, \ u_{\pm} \ge 0, \ c_{\pm} \ge 0\}.$$

$$(1.4)$$

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The traveling wave solution of (1.2) and (1.3) subject to (1.4) is a particular solution in the form

 $(u(x,t),c(x,t))=(U,C)(z), \quad z=x-st,$

which is bounded and satisfies differential equations

$$\begin{cases} -sU_z = (DU_z - \chi UC^{-1}C_z)_z, \\ -sC_z = \varepsilon C_{zz} - UC + \beta C \end{cases}$$
(1.5)

and boundary conditions

$$U(\pm\infty) = u_{\pm}, \quad C(\pm\infty) = c_{\pm}, \quad U_z(\pm\infty) = C_z(\pm\infty) = 0, \quad (1.6)$$

where z is called the traveling wave variable and s is the traveling wave speed.

It is difficult to solve (1.5) directly due to the singularity term and high dimensionality. In a series of studies in [17,18,35,20-22], a Hopf-Cole type transformation (2.1) was skillfully employed to transform the system (1.2) into a system of conservation laws which was then extensively studied, see system (2.2) in Section 2. However the translation of the results from the transformed system to the original Keller–Segel model (1.2) was not examined yet. Moreover the transformed system (2.2) no longer contains the parameter β and thus the role of β to the original chemotaxis model(1.2) is not displayed in (2.2). In the present paper, we show that only partial results of the transformed system (2.2) have physical meaning. Indeed, certain conditions on the end states are needed in order to obtain the physically meaningful results for the original system (1.2). We compare the differences between the original and transformed models. Next, we first state the main results obtained for the system (1.2) and (1.3) based on the results for the transformed system (2.2) and leave the proofs in Section 3.

The first result concerns the existence of traveling wave solutions.

Theorem 1.1. Let $\beta \ge 0$. Then the model (1.2) and (1.3) has a unique (up to a translation) monotone traveling wave solution (U, C)(x - st) with $U_z < 0$, $C_z > 0$ such that $c_+ > c_- = 0$, $u_- > u_+ = \beta \ge 0$ provided that $\varepsilon \ge 0$ is small, where the wave speed s is given by

$$s = \chi \left[\frac{u_{-}}{\chi + \varepsilon (1 - u_{+}/u_{-})} \right]^{1/2} = \begin{cases} \chi \sqrt{\frac{u_{-}}{\chi + \varepsilon}}, & \beta = 0, \\ \chi \sqrt{\frac{u_{-}}{\chi + \varepsilon (1 - \beta/u_{-})}}, & \beta > 0. \end{cases}$$
(1.7)

Moreover the solution has the following asymptotic behavior

$$U(z) \sim \begin{cases} u_{-} + \alpha e^{\lambda_{+} z}, \text{ as } z \to -\infty, \\ u_{+} + \alpha e^{\lambda_{-} z}, \text{ as } z \to \infty \end{cases}$$

and

$$C(z) \sim \begin{cases} \alpha e^{-\nu_{-Z} - \frac{\alpha}{\lambda_{+}} e^{\lambda_{-} Z}}, \text{ as } z \to -\infty, \\ c_{+} e^{-\frac{\alpha}{\lambda_{-}} e^{\lambda_{+} Z}}, \text{ as } z \to \infty, \end{cases}$$

where α is an arbitrary generic positive constant, $\lambda_{-} < 0$, $\lambda_{+} > 0$ and

$$v_- = \frac{\mathsf{s}(\beta - u_-)}{\chi u_-}$$

Remark 1.1. The explicit formula (1.7) for wave speed implies that: (1) the wave speed *s* does not depend on the asymptotic states of the chemical *c*; (2) the wave speed *s* is enhanced by the chemosensitivity χ and suppressed by the chemical diffusion ε ; (3) the wave speed $s \neq 0$ if $\chi \neq 0$.

Remark 1.2. The smallness assumption on chemical diffusion ε imposed in Theorem 1.1 can be removed by a distinct approach if $u_+ = 0$, see [34]. However the approach in [34] does not apply to the case $u_+ > 0$ even for small ε . Hence the existence of traveling wave solutions for $u_+ > 0$ and for large $\varepsilon > 0$ still remains open.

Next we shall present the asymptotic nonlinear stability results of traveling wave solutions. To state the stability theorem, we introduce some notations. Let ||f|| denote the L^2 norm of any function $f \in L^2(\mathbb{R})$ where $||f|| = (\int_{\mathbb{R}} |f(x)|^2 dx)^{1/2}$. Let $H^p(\mathbb{R})$ denote the usual Sobolev space $W^{p,2}(\mathbb{R})$, and let $||f||_p$ denote the H^p norm for any $f \in H^p(\mathbb{R})$ where $||f||_p = (\int_{\mathbb{R}} \sum_{i=0}^p |\frac{d^i}{dx^i} f(x)|^2 dx)^{1/2}$, $p \ge 1$.

The stability theorem is as follows:

Theorem 1.2. Let (U, C)(x - st) be a traveling wave profile of (1.2) and (1.3) obtained in Theorem 1.1. If $\varepsilon \ge 0$ is small $u_+ > 0$, then there exists a constant $\varepsilon_0 > 0$ such that if $||u_0 - U||_1 + ||(\ln c_0)_x - (\ln C)_x||_1 + ||(\phi_0, \psi_0)|| \le \varepsilon_0$, where

$$\phi_0(x) = \int_{-\infty}^x (u_0 - U)(y) dy, \quad \psi_0(x) = -\ln c_0(x) + \ln C(x),$$

then the Cauchy problem (1.2) and (1.3) has a unique global solution (u, c)(x, t) satisfying $u(x, t) > \delta_0$ for all $x \in \mathbb{R}$, $t \ge 0$ for some $\delta_0 > 0$, with

 $(u - U, c_x/c - C_x/C) \in C([0, \infty); H^1) \cap L^2([0, \infty); H^1)$

and the following asymptotic behavior

 $\sup|(u,c)(x,t) - (U,C)(x-st)| \rightarrow 0 \text{ as } t \rightarrow \infty.$

The last theorem addresses the chemical diffusion limits of traveling wave solutions as $\varepsilon \to 0$.

Theorem 1.3. Let $(U^{\varepsilon}, C^{\varepsilon})$ be the traveling wave solution of system (1.2) and (1.3) with $\varepsilon \ge 0$. Then for each $z = x - st \in \mathbb{R}$

$$|(U^{\varepsilon}, C^{\varepsilon})(z) - (U^{0}, C^{0})(z)| \to 0$$
, as $\varepsilon \to 0$,

provided that $C^{\varepsilon}(0) = C^{0}(0)$.

Before concluding this section, we want to recall some related results on traveling wave solutions of chemotaxis models obtained previously in [27,3,10,8]. First, [27] considered the existence and instability of traveling wave solutions to the same model (1.2) with $\beta > 0$. There are three major differences between [27] and our present studies: (1) the wave profile (U, C) considered in [27] is a (front, pulse), however, a (front, front) is considered in the present paper; (2) [27] proves the instability of traveling wave profile (front, pulse), and the present paper shows the nonlinear stability of traveling wave profile (front, front); (3) In the present paper, the unique wave speed is identified, however in [27] only the minimum wave speed is found. These differences are caused by assuming the integration constant of the first equation of (1.5) to be zero in [27], and nonzero in the present paper. Previously in [10], given that wave profile U is a pulse by assuming a fixed finite cell mass, a class of chemical kinetic function g(u, c) was identified through a constructive approach such that the second equation of (1.2) with $c_t = \varepsilon c_{xx} + g(u, c)$ admits the traveling wave solutions. However the existence result of [10] does not apply to the problem in the present paper whereby the wave profile U is a front. Furthermore without assuming that cell has a fixed finite mass (and hence the integration constant of the first equation of (1.5) can be nonzero), the existence of families of traveling wave solutions was first shown in [3] for a range of g(u, c) for $\varepsilon = 0$. In the present paper, we allow $\varepsilon \ge 0$ and hence the results are not covered by [3]. Finally we mention a work [8] where the transversal stability of traveling wave solutions of a chemotaxis model with a bistable cell growth term and a linear chemical kinetics (i.e. g(u, v) = u - v) was studied, which is different from what we study here. It is worth stressing that the method of Hopf-Cole transformation employed in the paper entirely differs from those developed in afore-mentioned works.

162

The rest of this paper is organized as follows. In Section 2, we transform our problem to a system of conservation laws by a change of variable, and state the main results of the transformed system. In Section 3, we prove the main Theorems 1.1,1.2 and 1.3 using the known results for the transformed system. In Section 4, numerical simulations and biological implications are presented. Several interesting open questions are proposed in Section 5.

2. Preliminary

2.1. Transformation of the problem

The crucial step of establishing our results is to convert the Keller–Segel model (1.2) into a system of conservation law by a Hopf-Cole like transformation

$$\nu = -\frac{c_x}{c} = -(\ln c)_x,\tag{2.1}$$

which was originally introduced in [17] for the model (1.2) with $\varepsilon = 0$ and then in [35] with $\varepsilon > 0$. Indeed with (2.1), we derive a system of viscous conservation laws from (1.2) as follows (see also [22])

$$\begin{cases} u_t - \chi(u\nu)_x = Du_{xx}, \\ \nu_t + (\varepsilon\nu^2 - u)_x = \varepsilon\nu_{xx}. \end{cases}$$
(2.2)

We impose the following initial conditions

$$(u, v)(x, 0) = (u_0, v_0)(x) \to \begin{cases} (u_-, v_-) & \text{as } x \to -\infty, \\ (u_+, v_+) & \text{as } x \to +\infty. \end{cases}$$
(2.3)

Because the chemotaxis model (1.2) describes the directed movement of cells toward the chemical which is consumed by cells when they encounter, the wave is an "invasion" pattern. That is, the wave profile of *u* decreases from its tail to front and that of *c* increases from its tail to the front, which means $c_x > 0$. By transformation (2.1), $v \leq 0$. Hence the physical region of (u, v) is

$$\mathscr{X}_{2} = \{(u, v) | u \ge 0, v \le 0, u_{\pm} \ge 0, v_{\pm} \le 0\}.$$

$$(2.4)$$

In the region \mathscr{X}_2 , we shall prove that the solution of conservation law (2.2) and (2.3) will approach a traveling wave as $t \to \infty$ without the smallness constrains on wave strength. It is worthwhile to remark that the small wave strength is generally an assumption imposed in most of the studies for the conservation laws (e.g. see [19,24]).

The blowup criterion and long-time behavior of classical solutions of (2.2) with $\varepsilon = 0$ in multi-dimensional spaces was recently considered in [18].

2.2. Existence of traveling wave solutions to the transformed problem

In the absence of viscosity terms, the system (2.2) becomes

$$\begin{cases} u_t - \chi(uv)_x = 0, \\ v_t + (\varepsilon v^2 - u)_x = 0, \end{cases}$$
(2.5)

which is hyperbolic and genuinely nonlinear when $0 < \varepsilon < 1$ (see [22]). We now look for traveling waves or viscous shock profiles of (2.2) with the traveling wave ansatz

$$(u, v)(x, t) = (U, V)(z), \quad z = x - st,$$

where *s* denotes the traveling wave speed and *z* the traveling wave variable. Substituting the above ansatz into (2.2), one obtains the wave equations

$$\begin{cases} -sU_z - \chi(UV)_z = DU_{zz}, \\ -sV_z + (\varepsilon V^2 - U)_z = \varepsilon V_{zz}, \end{cases}$$
(2.6)

with boundary conditions

$$(U,V)(z) \to (u_{\pm}, v_{\pm}) \text{ as } z \to \pm \infty,$$
 (2.7)

where $u_{\pm} \ge 0$ and $v_{\pm} \le 0$.

$$\begin{cases} DU_z = -sU - \chi UV + \varrho_1 =: F(U, V), \\ \varepsilon V_z = -sV + \varepsilon V^2 - U + \varrho_2 =: G(U, V), \end{cases}$$
(2.8)

where ϱ_1 and ϱ_2 are constants satisfying

$$\begin{aligned} \varrho_{1} &= su_{-} + \chi u_{-}v_{-} = su_{+} + \chi u_{+}v_{+}, \\ \varrho_{2} &= sv_{-} - \varepsilon(v_{-})^{2} + u_{-} = sv_{+} - \varepsilon(v_{+})^{2} + u_{+}, \end{aligned}$$
which gives
$$(2.9)$$

$$s(u_{+} - u_{-}) = \chi(u_{-}v_{-} - u_{+}v_{+}),$$

$$s(v_{+} - v_{-}) = \varepsilon(v_{+})^{2} - \varepsilon(v_{-})^{2} + u_{-} - u_{+}.$$
(2.10)

Eliminating s from (2.10) yields

$$\frac{u_{+}-u_{-}}{v_{+}-v_{-}} = \frac{\chi(u_{-}v_{-}-u_{+}v_{+})}{\varepsilon(v_{+})^{2}-\varepsilon(v_{-})^{2}+u_{-}-u_{+}}.$$
(2.11)

When u_{\pm} and v_{\pm} fulfill the condition (2.11), we can solve wave speed *s* from (2.10) and obtain two wave speeds with opposite signs, where the negative *s* corresponds to the wave speed of the first characteristic family and the positive one to the second characteristic family of shock waves of (2.5) [22]. We consider only the case s > 0 and the analysis applies to the case s < 0.

We have the following existence of traveling wave results for the transformed system (2.2).

Proposition 2.1. Let $\varepsilon > 0$ be small. Assume that u_{\pm} and v_{\pm} satisfy (2.11). Then there exists a monotone shock profile (U, V)(x - st) to system (2.6) and (2.7), which is unique up to a translation and satisfies $U_z < 0$, $V_z > 0$, where the wave speed s is given by

$$s = -\frac{\chi v_{-}}{2} + \frac{1}{2} \sqrt{\chi^2 v_{-}^2 + 4u_{+} \chi \left[1 - \varepsilon \frac{v_{+}^2 - v_{-}^2}{u_{+} - u_{-}}\right]}.$$
 (2.12)

Moreover the solution profile (U,V) decays exponentially at $\pm\infty$ with rates

$$\begin{pmatrix} U\\V \end{pmatrix} \sim \begin{pmatrix} u_{\pm}\\v_{\pm} \end{pmatrix} + \begin{pmatrix} C_{1\pm}\\C_{2\pm} \end{pmatrix} e^{\sigma_{\pm}z}, \text{ as } z \to \pm \infty,$$

where $C_{1\pm}$ and $C_{2\pm}$ are constants and

$$\sigma_{\pm} = -\left(\frac{s + \chi v_{\pm}}{2D} + \frac{s - 2\varepsilon v_{\pm}}{2\varepsilon}\right) + \sqrt{\left(\frac{s + \chi v_{\pm}}{2D} - \frac{s - 2\varepsilon v_{\pm}}{2\varepsilon}\right)^2 + \frac{\chi u_{\pm}}{\varepsilon D}}$$

Proof. The existence of traveling wave solutions as well as the wave speed have been given in [22, Theorem 2.1]. It only remains to derive the asymptotic decay rates. This can be done by linearizing the system (2.8) around the equilibrium (u_{\pm}, v_{\pm}) , which leads to a Jacobian matrix

$$J(u_{\pm}, v_{\pm}) = \begin{bmatrix} \frac{-s - \chi v_{\pm}}{D} & -\frac{\chi u_{\pm}}{D} \\ -\frac{1}{\varepsilon} & \frac{-s + 2\varepsilon v_{\pm}}{\varepsilon} \end{bmatrix},$$

whose eigenvalue σ satisfies

$$\sigma^{2} + \left(\frac{s + \chi v_{\pm}}{D} + \frac{s - 2\varepsilon v_{\pm}}{\varepsilon}\right)\sigma + \frac{1}{\varepsilon D}((s + \chi v_{\pm})(s - 2\varepsilon v_{\pm}) - \chi u_{\pm}) = 0.$$
(2.13)

Denote the two roots of (2.13) by σ_1 and σ_2 . Since $0 \le u_+ < u_-, v_- < v_+ \le 0$, $s + \chi v_{\pm} > 0$ (see [22]), then

$$\sigma_1 + \sigma_2 = -\left(\frac{s + \chi v_{\pm}}{D} + \frac{s - 2\varepsilon v_{\pm}}{\varepsilon}\right) < 0.$$

Furthermore it was shown in [22] that

 $\sigma_1 \sigma_2|_{(u_-,v_-)} < 0, \quad \sigma_1 \sigma_2|_{(u_+,v_+)} > 0.$

Therefore the equilibrium (u_-, v_-) is a saddle and (u_+, v_+) is a stable node. Computing the eigenvalues of (2.13), we obtain the results directly by the standard argument of phase plane analysis. \Box

2.3. Stability of traveling wave solutions to the transformed problem

Now we study the asymptotic stability of traveling wave solutions obtained in Proposition 2.1 under the small initial perturbations of the form

$$\int_{-\infty}^{+\infty} \begin{bmatrix} u_0(x) - U(x) \\ v_0(x) - V(x) \end{bmatrix} dx = x_0 \begin{bmatrix} u_+ - u_- \\ v_+ - v_- \end{bmatrix} + \eta \mathbf{r}_1(u_-, v_-),$$
(2.14)

where $\mathbf{r_1}(u_-, v_-)$ denotes the first eigenvector evaluated at (u_-, v_-) of the Jacobian matrix of the system (2.5) corresponding to the first characteristic field of shock waves. The coefficients x_0 and η are uniquely determined by the initial data $(u_0(x), v_0(x))$. For the stability of small-amplitude waves of conservation laws corresponding to the case $\eta \neq 0$, the reader is referred to [25,33] and references therein. In this paper, we assume that $\eta = 0$ as in [9,12] but consider the large-amplitude waves in contrast to the small-amplitude waves in [9,12]. Now by the systems (2.2) and (2.6), we derive that

$$\int_{-\infty}^{+\infty} \begin{bmatrix} u(x,t) - U(x+x_0 - st) \\ v(x,t) - V(x+x_0 - st) \end{bmatrix} dx = \int_{-\infty}^{+\infty} \begin{bmatrix} u_0(x) - U(x+x_0) \\ v_0(x) - V(x+x_0) \end{bmatrix} dx = \int_{-\infty}^{+\infty} \begin{bmatrix} u_0(x) - U(x) \\ v_0(x) - V(x) \end{bmatrix} dx + \int_{-\infty}^{+\infty} \begin{bmatrix} U(x) - U(x+x_0) \\ V(x) - V(x+x_0) \end{bmatrix} dx = \int_{-\infty}^{+\infty} \begin{bmatrix} u_0(x) - U(x) \\ v_0(x) - V(x) \end{bmatrix} dx - x_0 \begin{bmatrix} u_+ - u_- \\ v_+ - v_- \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$

Since (2.2) is a system of conservation laws, we make use of the technique of taking anti-derivatives of the perturbations. We decompose the solution (u, v) as

$$(u, v)(x, t) = (U, V)(x - st + x_0) + (\phi_x, \psi_x)(x, t),$$
(2.15)

where

$$(\phi(x,t),\psi(x,t)) = \int_{-\infty}^{x} (u(y,t) - U(y + x_0 - st), v(y,t) - V(y + x_0 - st))dy$$
(2.16)

for all $x \in \mathbb{R}$ and $t \ge 0$. It then holds that

 $\phi(\pm\infty,t) = 0$, $\psi(\pm\infty,t) = 0$ for all t > 0.

We further assume, without loss of generality, that the translation constant $x_0 = 0$. Then (2.14) becomes

$$\int_{-\infty}^{+\infty} \begin{bmatrix} u_0(x) - U(x) \\ v_0(x) - V(x) \end{bmatrix} dx = \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$
(2.17)

The initial conditions of the perturbation (ϕ, ψ) are thus given by

$$\phi_0(x) = \int_{-\infty}^x (u_0 - U)(y) dy$$
 (2.18)

and by the Hopf-Cole transformation (2.1)

$$\begin{split} \psi_0(x) &= \int_{-\infty}^x (\nu_0 - V)(y) dy = -\int_{-\infty}^x ((\ln c_0)_y - (\ln C)_y)(y) dy \\ &= -\ln c_0(x) + \ln C(x). \end{split}$$
(2.19)

The asymptotic stability of traveling wave solutions of (2.2) means that $(u - U, v - V)(x, t) = (\phi_x, \psi_x)(x, t) \rightarrow 0$ as $t \rightarrow \infty$.

The theorem of the asymptotic stability for the transformed system (2.2) is as follows, see [22, Theorem 2.1].

Proposition 2.2 [22]. Let (U, V)(x - st) be a viscous shock profile of (2.2) obtained in Theorem 2.1. If $\varepsilon > 0$ is small and $u_+ > 0$, then there exists a constant $\varepsilon_0 > 0$ such that if $||u_0 - U||_1 + ||v_0 - V||_1 + ||(\phi_0, \psi_0)|| \le \varepsilon_0$, the Cauchy problem (2.2) and (2.3) has a unique global solution (u, v)(x, t) satisfying $u(x, t) \ge \delta_0 > 0$ for some $\delta_0 > 0$ for all $x \in \mathbb{R}, t \ge 0$, and

$$(u - U, v - V) \in (C([0, \infty); H^1) \cap L^2([0, \infty); H^1))^2$$
.

Furthermore, the solution (u, v) has the following asymptotic nonlinear stability

$$\sup_{x\in\mathbb{R}}|(u,v)(x,t)-(U,V)(x-st)|\to 0 \text{ as } t\to\infty.$$
(2.20)

When $\epsilon = 0$, the existence and stability of traveling wave solutions were proved in [20].

3. Passing the results to the original system

In this section, we prove the main theorems stated in the Introduction by passing the results of the transformed system (2.2) back to the original Keller–Segel model (1.2) and (1.3).

Proof of Theorem 1.1. Noting that u remains the same in systems (1.2) and (2.2), we only need to transform the results from V to C. Recalling the transformation (2.1), we have

$$V(z) = -(\ln C)_z,$$

which yields that

 $C(z)=C(0)e^{-\int_0^z V(y)dy},$

where C(0) is a positive number.

Since $V(z) \leq 0$, then $\int_0^z V(y)dy \to \infty$ as $z \to -\infty$ and hence $C(-\infty) = c_- = 0$. However for the right end state $c_+ = C(\infty)$, there are two cases to consider.

Case 1. If $v_+ < 0$, then $|v^+| \le -V \le |v_-|$ and hence $C(0)e^{|v_+|^2} \le C(z) \le C(0)e^{|v_-|^2}$ which leads to $C(\infty) = c_+ = \infty$. In this case, there is no bounded traveling wave solution *C*.

Case 2. If $v_+ = 0$, then $-\int_0^{\infty} V(y)dy$ is bounded since $V(z) \rightarrow v_+ = 0$ exponentially as $z \rightarrow \infty$. Let $-\int_0^{\infty} V(y)dy = M$, then $C(\infty) = c_+ = C(0)e^M > 0$. In this case, we obtain a uniformly bounded traveling wave solution *C* with

$$C(z) \rightarrow 0$$
, as $z \rightarrow -\infty$,
 $C(z) \rightarrow c_+$, as $z \rightarrow \infty$.

From above analysis, we see that only the case $v_+ = 0$ leads to physical traveling wave solutions for *C*. Therefore we assume $v_+ = 0$ which results in $c_+ > 0$. Furthermore by the transformation (2.1), one has

$$V=-\frac{C_z}{C},$$

which yields $C_z = -VC > 0$ due to V < 0 and C > 0 for any $z \in \mathbb{R}$. The fact $U_z < 0$ is inherited from Proposition 2.1 directly. To find the role of the parameter β , we evaluate the second equation of (1.5) at $z = \infty$ and obtain that

$$c_+(eta-u_+)=0,$$

which gives $u_+=eta$ since $c_+>0.$

164

Next we derive the wave speed *s* given in Theorem 1.1. Indeed, the first equation of (2.9) gives

$$v_- = \frac{s(u_+ - u_-)}{\chi u_-}$$

where the fact $v_{+} = 0$ has been used. Substituting the above identity into the second equation of (2.9), we obtain

$$s^{2}[\chi u_{-}(u_{+}-u_{-})-\varepsilon(u_{+}-u_{-})^{2}]=\chi^{2}u_{-}^{2}(u_{+}-u_{-}).$$

Noticing that $\beta = u_+ < u_-$, we get (1.7) immediately. To finish the proof, it remains to derive the asymptotic behavior announced in the theorem, which can be obtained directly from the asymptotic decay rates given in Proposition 2.1. Then the proof of Theorem 1.1 is complete. \Box

Proof of Theorem 1.2. The results for u has been given in Proposition 2.2. It remains to pass the results from v to c.

By the transformation (2.1) and (2.16), one deduces that

$$\frac{c(x,t)}{C(x-st)}=e^{\int_{-\infty}^{x}(V(\xi-st)-\nu(\xi,t))d\xi}=e^{\psi(x,t)}.$$

Next we show that $\psi(x,t) \to 0$ as $t \to \infty$. Indeed it has been shown in [22], see the Proposition 4.3 and the Proof of Theorem 4.1 in [22], that $\|\psi(\cdot,t)\| < \infty$ and $\|\psi_x(\cdot,t)\|_1 \to 0$ as $t \to \infty$. Then

$$\begin{split} \psi^2(x,t) &= 2 \int_{-\infty}^x \psi \psi_y(y,t) dy \\ &\leqslant 2 \Big(\int_{\mathbb{R}} \psi^2 dy \Big)^{1/2} \Big(\int_{\mathbb{R}} \psi_y^2 dy \Big)^{1/2} \to 0 \text{ as } t \to \infty \end{split}$$

which implies $\psi(x, t) \to 0$ as $t \to \infty$ for all $x \in \mathbb{R}$. Note that C(x - st) is a traveling wave solution which is bounded, say, by $M_1 > 0$. Then

$$\begin{aligned} |c(x,t) - C(x - st)| &= |C(x - st)e^{\psi(x,t)} - C(x - st)| \\ &= C(x - st)|1 - e^{\psi(x,t)}| \leqslant M_1 |1 - e^{\psi(x,t)}| \to 0 \\ &\text{ as } t \to \infty \end{aligned}$$

for all $x \in \mathbb{R}$.

The proof is complete. \Box

Proof of Theorem 1.3. We shall employ the geometric singular perturbation theory [7,11] to prove Theorem 1.3. To this end, we rewrite (2.8) as

$$\begin{cases} U' = -\frac{s}{D}U - \frac{\chi}{D}UV + \frac{\varrho_1}{D} =: F(U, V), \\ \varepsilon V' = -sV + \varepsilon V^2 - U + \varrho_2 =: G(U, V, \varepsilon), \end{cases}$$
(3.1)

where $' = \frac{d}{dz}$. System (3.1) is referred to as the slow system [11]. Clearly the solution of (2.6) and (2.7) is the solution of (3.1) connecting (u_-, v_-) and (u_+, v_+) .

Now we define the rescaling $\tau = \frac{z}{\varepsilon^{*}}$ and convert the system (3.1) into a so-called fast system

$$\begin{cases} \dot{U} = \varepsilon F(U, V), \\ \dot{V} = G(U, V, \varepsilon) \end{cases}$$
(3.2)

where $\dot{f} = \frac{df}{d\tau}$.

. .

Setting $\hat{c} = 0$ in (3.1), we obtain an invariant manifold M_0 define by

$$M_0 = \left\{ (U, V) | V = h^0(U) = \frac{\varrho_2 - U}{s} \right\},$$

where $U(z)$ satisfies

$$U' = \frac{\chi}{D}U(U - \varrho_2) - \frac{s}{D}U + \frac{\varrho_1}{D}.$$
(3.3)

It has been shown in [20] that (3.3) has a unique solution U^0 satisfying $U^0(z) \rightarrow u_{\pm}$ as $z \rightarrow \pm \infty$. Therefore (3.1) with $\varepsilon = 0$ has a unique traveling wave solution (U^0, V^0) .

Note that at any point of M_0 , $\frac{\partial G}{\partial V} = -s \neq 0$, see (1.7) and (2.12). Hence M_0 is normally hyperbolic for fast system (3.2) with $\varepsilon = 0$. By Fenichel's invariant manifold theorem [11], for $\varepsilon > 0$ sufficiently small, there is a slow manifold M_{ε} that lies within $O(\varepsilon)$ neighborhood of M_0 and is diffeomorphic to M_0 . Moreover it is locally invariant under the flow of (3.2) and can be written as

$$M_{\varepsilon} = \{ (U, V) | V = h^{\varepsilon}(U) = h^{0}(U) + O(\varepsilon) \}.$$

$$(3.4)$$

Then the slow system (3.1) on M_{ε} can be written as

$$U' = F(U, h^{\varepsilon}(U)) = \frac{\chi}{sD}U(U - \varrho_2) - \frac{s}{D}U + \frac{\varrho_1}{D} + O(\varepsilon),$$
(3.5)

which is a regular perturbation of (3.3).

It has been shown in [20] that Eq. (3.3) has a one-dimensional unstable manifold near u_- , denoted by \mathscr{U}^- , and a one-dimensional stable manifold near u_+ , denoted by \mathscr{U}^+ . The transversal intersection $\mathscr{U}^- \cap \mathscr{S}^+$ gives the heteroclinic orbit $U^0(z)$. Then by the geometric singular perturbation theory (see [7] or [11]), for sufficiently small $\varepsilon > 0$, there is a heteroclinic orbit $U^{\varepsilon}(z)$ of (3.1) on M_{ε} , which is a small perturbation of $U^0(z)$ with

$$\|U^{\varepsilon}(z) - U^{0}(z)\|_{L^{\infty}(\mathbb{R})} = O(\varepsilon) \to 0 \text{ as } \varepsilon \to 0.$$
(3.6)

Note that on M_{ε} , $V^{\varepsilon}(z) = \frac{\varrho_2 - U^{\varepsilon}(z)}{s} + O(\varepsilon)$. Moreover $V^0(z) = \frac{\varrho_2 - U^0(z)}{s}$. Then it is evident that

$$\|V^{\varepsilon}(z) - V^{0}(z)\|_{L^{\infty}(\mathbb{R})} = O(\varepsilon) \to 0 \text{ as } \varepsilon \to 0.$$
(3.7)

Now we are only left to prove the convergence of C^{e} . Indeed it follows from (2.1) that

$$\frac{C^{\varepsilon}}{C^0}(Z) = e^{-\int_0^z (V^{\varepsilon} - V^0)(y) dy}$$

provided that $C^{\varepsilon}(0) = C^{0}(0)$. Then (3.7) and the boundedness of $C^{0}(z)$ immediately yield that for each $z \in \mathbb{R}$

$$|C^{\varepsilon}(z) - C^{0}(z)| \to 0$$
, as $\varepsilon \to 0$.

This completes the proof of Theorem 1.3. \Box

4. Simulations and biological implications

Due to the singularity term c^{-1} in model (1.2), it is impossible to obtain the numerical solutions without using the approximation technique. The Hopf-Cole transformation (2.1) enable us not only to analytically study the traveling wave solutions as exposed here, but also to explore numerical solutions using standard numerical schemes without approximation. In this section, we shall illustrate the numerical simulations of propagating traveling waves, and discuss the biological implications.

As the most interesting solution component, the cell density u remains the same in the original model (1.2) and the transformed system (2.2). Hence we find the numerical solution u via the transformed model (2.2) which can be numerically solved based on the finite-difference method. The process of traveling wave propagation will be simulated in a finite spatial domain with Dirichlet conditions to be compatible with the initial data. The parameter values will be chosen to satisfy the Rankine–Hugoniot condition (2.11). In our simulation, the initial data are set as

$$u_0(x) = \tilde{u}(x) = \bar{u} + 1/(1 + \exp(2(x - 20))),$$

$$v_0(x) = \tilde{v}(x) = \bar{v} + 1/(1 + \exp(-2(x - 20))),$$
(4.1)

which is also a wavefront profile with end states $\tilde{u}_{-} = \bar{u} + 1$, $\tilde{u}_{+} = \bar{u}$, $\tilde{v}_{-} = \bar{v}$, $\tilde{v}_{+} = \bar{v} + 1$. In relation to the applications, we hereby

consider two sets of parameter values: (1) $\varepsilon = 0$ and $\beta > 0$; (2) $\varepsilon > 0$ and $\beta = 0$. The former may describe the reinforced random walk and the latter may account for the directed movement of endothelial cells toward the signalling molecules during the initiation of angiogenesis, see Section 1 for details.

In Fig. 1, we simulate the wave propagation of model (2.2) with $\varepsilon = 0$ and $\beta > 0$, where the domain $\Omega = (0, 300)$ with mesh size 0.5. We choose D = 2, $\bar{u} = 1$, $\bar{v} = -1$ and $\chi = 0.5$, hence $\tilde{u}_{-} = 2$, $\tilde{u}_{+} = 1$, $\tilde{v}_{-} = -1$, $\tilde{v}_{+} = 0$. Fig. 1(a) is a three dimensional visualization of traveling waves propagating in the spatial field, and Fig. 1(b) plots the temporal-spatial wave pattern formation. From Fig. 1(a), we see that the solution oscillates for a short time and then quickly evolves to a stable propagating wave with the same end states as those of the initial data. In relation to the biological motivation of model (2.2) with $\varepsilon = 0$, $\beta > 0$, Fig. 1 illustrates a spatial movement pattern of random walkers in response to the chemical signal. Here $\beta > 0$ is reflected by the fact $\beta = u_{+} = 1$.

Fig. 2 plots the propagating waves generated by the model (2.1) with $\varepsilon = 0.1 > 0$, $\chi = 0.9$ and $\beta = 0$, where $\bar{u} = 0$ and other parameters are the same as those in Fig. 1. Here Fig. 2(a) plots the temporal-spatial pattern of traveling waves propagating in the field, and Fig. 2(b) plots the process of the solution *u* evolving from the initial profile to a monotone wavefront, which fits our theoretical

results. In this case the model (1.2) describes the directed migration of endothelial cells toward the signalling molecule VEGF. Such process is exactly shown by our simulations where $\beta = u_+ = 0$. An observable variation between Figs. 1 and 2 is that the transient time taken from initial data to a steady wave in Fig. 1 is longer than that in Fig. 2. This implies that the chemical diffusion ε may enhance the process of wave formation, which is an interesting numerical discovery not proved by our theoretical results.

We continue to simulate the stability of traveling wave solution. We consider the initial data (u_0, v_0) in the form of

$$u_0(x) = 1 + \frac{1}{1 + \exp(2(x - 100))} + \frac{0.5 \sin x}{((x - 100)/10)^2 + 1},$$

$$v_0(x) = -1 + \frac{1}{1 + \exp(-2(x - 100))} + \frac{0.5 \sin x}{((x - 100)/10)^2 + 1},$$
(4.2)

where the initial perturbation belongs to $H^1(\mathbb{R})$ as required by Proposition 2.2. Then the evolution of the numerical solution u for the case $\varepsilon > 0$ is plotted in Fig. 3. It is clear to visualize that the solution gradually stabilizes to a traveling wavefront, as proved by our theoretical results.

Our numerical simulations indicate that the traveling wavefront, which may interpret the migration of endothelial cells to-



Fig. 1. Numerical simulation of propagation of the traveling wavefronts of cell density u to model (2.2) in the spatial domain as time evolves with a three-dimensional visualization in (a) and two-dimensional visualization in (b), where $\varepsilon = 0$, D = 2, $\chi = 0.5$ and the initial data are $u_0 = 1 + 1/(1 + \exp(2(x - 20)))$, $v_0 = -1 + 1/(1 + \exp(-2(x - 20)))$. The arrow indicates the propagating direction of traveling waves.



Fig. 2. Numerical simulation of propagating traveling wavefront *u* of model (2.2), where $\varepsilon = 0.1$, D = 2, $\chi = 0.9$ and the initial data are $u_0 = 1/(1 + \exp(2(x - 20)))$, $v_0 = -1 + 1/(1 + \exp(-2(x - 20)))$. The arrow indicates the propagating direction of traveling waves.

ward the signalling molecule VEGF during the early stage of angiogenesis, or the propagation of particles toward a non-diffusive chemical field, are stable against perturbations.

5. Open questions

This paper studied various aspects of traveling wave solutions, including the existence, nonlinear stability, asymptotic decay rates and wave speed, to a chemotaxis model describing the initiation of angiogenesis and reinforced random walk. The results are achieved by using a Hopf-Cole transformation of variable which transforms the model into a system of conservation laws. The main results of this paper include: (1) using the backward change of variable to derive the existence and stability of traveling wave solutions to the original Keller–Segel chemotaxis model based on the results for the transformed system, see Theorems 1.1 and 1.2; (2) deriving the explicit wave speed (1.7) in terms of model parameters such as the chemosensitivity χ and chemical diffusion ε , and finding the asymptotic decay rates of traveling wave solutions, see Theorem 1.1; (3) using the geometric singular perturbation method to show the zero chemical diffusion limit of traveling wave solutions, see Theorem 1.3. Our results show that if the right end state of v of the transformed system is non-zero (i.e. $v_+ < 0$), the traveling



Fig. 3. Numerical simulation of the stability of traveling wavefront *u* for $\varepsilon = 0.1 > 0$, where D = 2, $\chi = 0.45$ and the initial data are given by (4.2).



Fig. 4. Numerical simulations of the stability of traveling wavefront *u* to model (2.2) for $u_{+} = 0$ in (a) and for large initial perturbation in (b), where $\varepsilon = 0.1$, D = 2. Other parameter and initial data are: (a) $u_{0} = \frac{1}{1 + \exp(2(x-100))} + \frac{0.5 \sin x}{((x-100)/10)^{2}+1}$, $v_{0} = -1 + \frac{1}{1 + \exp(-2(x-100))} + \frac{0.5 \sin x}{((x-100)/10)^{2}+1}$, $\chi = 0.9$; (b) $u_{0} = 1 + \frac{1}{1 + \exp(2(x-100))} + \frac{\sin x}{((x-100)/10)^{2}+1}$, $v_{0} = -1 + \frac{1}{1 + \exp(-2(x-100))} + \frac{1}{(x-100)/10^{2}+1}$, $\chi = 0.45$. The arrow indicates the propagating direction of traveling waves.

wave solution C(z) corresponding to the original system blows up as $z \to \infty$ and loses physical meaning. The meaningful case is when $v_+ = 0$ which corresponds to $c_+ > 0$. In addition, we show that the parameter β , which represents the growth rate of the chemical but vanishes in the transformed system, is indeed also a parameter equivalent to the right end of cell density (i.e. $\beta = u_+$).

Despite various results obtained in current and previous studies [35,20–22], there are still many interesting open questions. The existence of traveling wave fronts of model (1.2) has been established for both $u_+ > 0$ and $u_+ = 0$. However the nonlinear stability of traveling wave solutions was derived only for the case $u_+ > 0$, where the method of energy estimates was employed (see [20,21]). This method no longer applies for the case $u_+ = 0$. The simulation presented in Fig. 4(a) illustrates that traveling wave solutions are still stable when $u_+ = 0$. Hence novel approach needs to be developed to prove the stability of traveling wave solution for the case $u_+ = 0$.

As commented in Remark 1.2 and results given in Theorem 1.2, the existence and stability of traveling wave solutions with $u_+ > 0$ for large $\varepsilon > 0$ still largely remain unsolved. All approaches appeared in existing literature seem to fail. The numerical simulation (not shown here) illustrates that the solution behavior for $u_+ > 0$ for large $\varepsilon > 0$ is different from the case of small ε . One reason is that system (2.2) changes its type and is no longer hyperbolic for large ε . Hence new method is needed to examine the solution behavior for large ε .

Another interesting question is the stability of traveling wave solutions for large perturbations. The stability Theorem 1.2 requires the initial perturbations to be small and the method of energy estimates in [20–22] made use of this assumption. However the numerical simulation in Fig. 4(b) shows that stability still holds for large perturbations, which raises a challenging question for the future.

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