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ENERGY CONSIDERATIONS IN A MODEL OF NEMATODE SPERM CRAWLING

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Abstract. In this paper we propose a mathematical model for nematode sperm cell crawling. The model takes into account both force and energy balance in the process of lamellipodium protrusion and cell nucleus drag. It is shown that by specifying the (possibly variable) efficiency of the major sperm protein biomotor one completely determines a self-consistent problem of the lamellipodium-nucleus motion. The model thus obtained properly accounts for the feedback of the load on the lamellipodium protrusion, which in general should not be neglected. We study and analyze the steady crawling state for a particular efficiency function and find that all nonzero modes, up to a large magnitude, are linearly asymptotically stable, thus reproducing the experimental observations of the long periods of steady crawling exhibited by the nematode sperm cells.

1. **Introduction.** In this paper we present a model of cell crawling achieved via the process of polymerization/depolymerization of a lamellipod with the nucleus (or the cell body) carried above it. Our model is specific to the motion of a nematode sperm cell, which crawls in a cycle of protrusion, adhesion and retraction. Although this cycle is similar to that of other eucaryotic cells, such as amoebae, the nematode sperm lacks the machinery of actin cytoskeleton and motor proteins of these eucaryotic cells. Instead, the nematode sperm cell uses major sperm protein (MSP), which can act as a biomotor by itself [B, W]. The ability of MSP to act as a biomotor in the absence of other proteins makes the nematode sperm cell the simplest biological crawling system and an easy object for a quantitative analysis.

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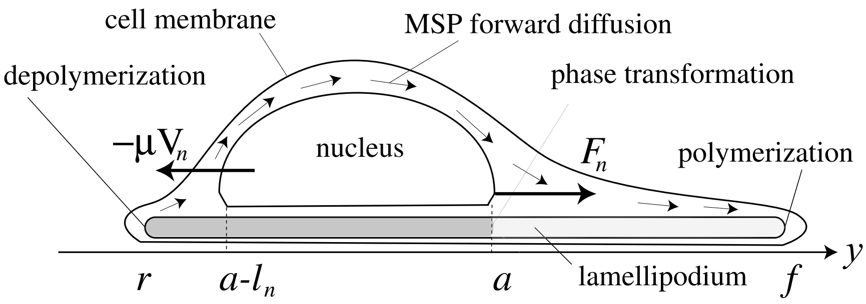

FIGURE 1. Schematic diagram of a crawling nematode sperm cell.

In [B] and [W] the motor action of MSP was related to the process of MSP gel contraction, initiated by the change of pH value near the nucleus. In a broader sense, as the major sperm protein molecules circulate around the cell in the process of crawling, the MSP gel undergoes the same thermodynamic cycle of contraction and expansion, accompanied by an input of external energy (chemical energy in this case) and production of mechanical work, as any medium in a heat engine. From the thermodynamic point of view, the contraction of the gel is a particular case of the phase transitions encountered in the work of other known engines, e.g., the water to vapor transition used the steam engine or the chemical transition associated with the burning of gas in the combustion engine. The main goal of the present paper is to make the MSP biomotor model self-consistent by taking into account not only the difference between the elastic states of the gel before and after the transition [B, W], but also the balance of energy released in the contraction process and in the mechanical work required to drag the nucleus forward.

We consider the one-dimensional model of cell motion. As depicted in Figure 1 the lamellipod extends from the rear end $r = r(t)$ to the front end at $f = f(t)$, while the nucleus lies over the lamellipod with its front end at $a = a(t)$ and its rear end at $a(t) - l_n$; here l_n is a fixed parameter. The nucleus is viewed as a solid-like body, moving with velocity $V_n = V_n(t)$, so that, in particular, $a(t)$ moves with the same velocity V_n. The total resistance of the outside world to this motion acts as a force μV_n, where μ is a fixed parameter. A forward force F_n acting on the nucleus is produced by the biomotor. In the high viscosity (low Reynolds number) regime, the equation of motion of the cell nucleus is $F_n = \mu V_n$. As the nucleus moves forward, the pH gradient moves with it and forces the new portions of the MSP gel to undergo the phase transformation. That releases more chemical energy stored in the gel and allows the biomotor to continue its operation.

The motion of the lamellipod can be described as follows. The main reasons for the leading edge protrusion and rear end retraction are the polymerization and depolymerization of the gel.

The lamellipodium protrudes to the right in the polymerization process and contracts on the left by depolymerization. The forward diffusion of depolymerized proteins completes the cycle of MSP rotation. The MSP gel undergoes a phase transition under the leading edge of the nucleus. The tensile stress produced in the transition is converted into the force F_n, dragging the nucleus to the right. This force is balanced by the total viscous friction μV_n acting on the nucleus. The actual speed of the gel relative to the ground is very small, and its motion is similar to the motion of the lower part of the tractor tracks. To continue the analogy with tractor tracks, one notices that the forward diffusion of depolymerized MSP through the cell volume completes the rotation cycle and plays the role of the upper part of the tracks (Figure 1). The phase transformation of the gel in the middle of the cell is not required for the lamellipodium motion. If there were no phase transformation and no need to carry the nucleus, the motion of the gel would be exactly like the one of the tractor tracks: a piece of the gel would be created when the front of the lamellipodium reaches a certain point. Then it would not move until the rear end of the lamellipodium reached its location and the piece depolymerized. The purpose of the gel phase transformation is to transfer the motion from the lamellipodium to the cell nucleus. When present, the phase transition allows for the work of the biomotor, which produces a force dragging the nucleus. There is of course a feedback effect: the opposite force acts on the gel and modifies it's motion.

In the steady-state motion, the speed of the nucleus V_n is equal to the speed of protrusion and retraction, and thus the nucleus has to slide forward over the lamellipodium. The exact mechanism that couples the nucleus to the zone of phase transformation in the lamellipodium is not yet clear. To highlight the nontriviality of the motor action, we note that it is not enough to couple the nucleus to any fixed piece of the gel, because the nucleus has to move faster than any point of the lamellipodium. This complication was already acknowledged by Bottino et al. [B, Sec. “Contraction” of the Appendix]. In the absence of the explicit model of the biomotor, many different mathematically consistent descriptions of the nematode sperm crawling can be proposed [B, W]. For example, the model of Bottino et al. assumes that the force F_n is generated at the rear end of the lamellipodium, away from the contraction zone, and is independent of V_n. The model of Wolgemuth et al. calculates the motion of the gel with a phase transformation, but ignores the modifications due to the presence of the load.

However, an additional set of constraints on the motor action has yet to be used in the studies of crawling. These are the constraints imposed by energy conservation. In the present paper we show that if an explicit assumption about the efficiency of the biomotor is added to the gel state equations on both sides of the phase transformation, the equations of motion of the lamellipod-nucleus system can be uniquely determined. We then choose a particular form of efficiency and search for the travelling-wave solution of the resulting problem. Such a solution describes the steady crawling of the cell. We finally study the stability of this solution and find that it is stable and thus reproduces the behavior of the actual nematode sperm cells.

New experimental evidence in the literature suggests that the nematode sperm produces force by depolymerization of the gel (cf. [M]), which was modelled by Wolgemuth et al. [WM]. They suggest a slightly different model for the force generation.

2. **The model.**

2.1. **Differential equations of gel motion.**

We denote by $w(y,t)$ the velocity of the gel (i.e., the polymerized MSP) within the lamellipod, by $\varphi(y,t)$ the volume fraction of the gel, and by γ the density of the gel. The gel motion is assumed to happen at constant temperature. Then the stress $\sigma = \sigma(\varphi)$ of the elastic gel is a function of the volume fraction and is related to its free energy $\mathcal{E}(\varphi)$ as (see [O], also [W]):

$$\sigma = \varphi \frac{\partial \mathcal{E}}{\partial \varphi} - \mathcal{E}. \tag{2.1}$$

In the low Reynolds number regime, the motion of the elastic medium is described by two equations:

$$\frac{\partial (\gamma\varphi)}{\partial t} + \frac{\partial j}{\partial y} = 0, \tag{2.2}$$

$$\frac{\partial \sigma}{\partial y} = -\varsigma w. \tag{2.3}$$

Here $j = \gamma\varphi w$ is the flux of mass, and ς is the constant friction coefficient between the lamellipodim and the substrate assumed to be large [B, W]. As was assumed in [B] and justified in [W], the motion of water in the cell crawling process can be ignored.

For the purposes of this paper we will assume the following form of the stress function in the two states of the gel:

$$\sigma(\varphi) = \begin{cases} \sigma_0 - \dfrac{E}{\varphi} & \text{if } y < a(t), \\ \sigma_0 - \dfrac{E}{\varphi} + \tau & \text{if } y > a(t), \end{cases} \tag{2.4}$$

where σ_0, E, τ are positive constants; this form is similar to the one used by [B], and may also be viewed as an approximation to the form used by [W] for small φ. The free energies corresponding to this stress function are given by

$$\mathcal{E}(\varphi) = \begin{cases} -\sigma_0 + \dfrac{E}{2\varphi} & \text{if } y < a(t), \\ -\sigma_0 + \dfrac{E}{2\varphi} - \tau + C\varphi & \text{if } y > a(t), \end{cases} \tag{2.5}$$

where C has a sense of the chemical energy difference between the states of the gel before and after the phase transition.

From (2.2) and (2.3) one can derive the following energy flow equation:

$$\frac{\partial \mathcal{E}}{\partial t} + \frac{\partial Q}{\partial y} = -\varsigma w^2, \tag{2.6}$$

where $Q = (\sigma + \mathcal{E})w$ is the energy flux and the term on the right-hand side represents the energy dissipation due to the friction between the gel and the substrate.

2.2. **Boundary conditions and the motion of the nucleus.** As explained in the introduction, we assume that the phase transformation happens in a very narrow zone and will be approximated by an abrupt phase change at the leading edge point of the nucleus $a(t)$. We also assume that the MSP biomotor acts at the same point and therefore there is a force $F = -F_n = -\mu V_n$ applied to the gel at $a(t)$. When two phases of the material are in contact at the phase transition point $a(t)$, equations (2.3) and (2.6) acquire additional terms proportional to $\delta(y-a)$, where δ is the Dirac function:

$$\frac{\partial \sigma}{\partial y} = -\varsigma w + F\delta(y-a), \tag{2.7}$$

$$\frac{\partial \mathcal{E}}{\partial t} + \frac{\partial Q}{\partial y} = -\varsigma w^2 - P\delta(y-a). \tag{2.8}$$

Here P is the energy dissipation at the contact point. There is no universal expression for P; P depends on actual details of the phase transition and biomotor operation.

For any function ψ we shall denote by ψ_L the restriction of ψ to the left of $y = a(t)$ and by ψ_R the restriction of ψ to the right of $y = a(t)$.

To obtain transition conditions from (2.7) (the Rankine-Hugoniot conditions associated with this equations), we integrate it along a small interval (y_1, y_2) such that $a(t) \in (y_1, y_2)$:

$$\sigma_R(y_2) - \sigma_L(y_1) = -\int_{y_1}^{y_2} \varsigma w(y)dy + F.$$

When $y_2 - y_1 \to 0$, the integral $\int_{y_1}^{y_2} \varsigma w(y)dy$ converges to zero, and we are left with

$$\sigma_R(a(t)) - \sigma_L(a(t)) = F.$$

If we denote by $[X]$ the jump $X_R - X_L$ of a function X at $a(t)$, then we can express the transition condition for (2.7) in the form

$$[\sigma] = F.$$

The mass is conserved, so from (2.2) we get $[j - \gamma\varphi V_n] = 0$ and similarly from (2.8) we get $[Q - \mathcal{E}V_n] = -P$. For later references we rewrite the three jump relations at $a(t)$:

$$[j - \gamma\varphi V_n] = 0, \quad j = \gamma\varphi w, \tag{2.9}$$

$$[\sigma] = F = -\mu V_n, \tag{2.10}$$

$$[Q - \mathcal{E}V_n] = -P, \ Q = (\sigma + \mathcal{E})\, w. \tag{2.11}$$

Using (2.10), equation (2.11) can be rewritten as

$$[(\sigma + \mathcal{E})(w - V_n)] = -P_0, \tag{2.12}$$

where $P_0 = P + FV_n = P - \mu V_n^2$ has a sense of the energy that could not be used by the biomotor and was dissipated in the form of heat or chemical energy that leaves the gel. The useful work of the biomotor is given by $F_n V_n = -FV_n = \mu V_n^2$.

Next, we need to write the boundary conditions at the rear and front endpoints of the lamellipod. As in [W] we take

$$\sigma\,|_{r(t)} = 0, \quad \sigma\,|_{f(t)} = 0, \tag{2.13}$$

$$\frac{dr}{dt} = V_d + w\,|_{r(t)}, \quad \frac{df}{dt} = V_p(l) + w\,|_{f(t)}, \tag{2.14}$$

where V_d is the speed of depolymerization at the rear, which is assumed to be constant, $l = l(t)$ is the length $f(t) - r(t)$ of the lamellipod, and $V_p(l)$, the speed of polymerization at the front, is a function of l, which is decreasing as l increases; for example [W],

$$V_p(l) = \frac{V_p^0}{l - d} L, \tag{2.15}$$

where V_p^0, d, L are constants.

Finally, we recall that the motion of the nucleus is given by

$$\mu V_n = -F \tag{2.16}$$

and governs the position of the phase transformation point according to

$$\frac{\partial a}{\partial t} = V_n. \tag{2.17}$$

We complete the model by imposing initial conditions

$$r(0) = r_0, \quad f(0) = f_0, \quad a(0) = a_0, \quad \varphi(y,0) = \varphi_0(y). \tag{2.18}$$

The system of equations (2.2), (2.3) with the jump conditions (2.9)–(2.11) at point $a(t)$, boundary conditions (2.13), (2.14) at points $r(t)$ and $f(t)$, respectively, the nucleus motion equations (2.16), (2.17), and initial data (2.18) form the system of equations describing the crawling. The problem is completely determined if the function $P_0(\varphi_L, \varphi_R, w_L, w_R, V_n)$ is known. Alternatively, one can specify the efficiency of the biomotor $\eta = \mu V_n^2/(\mu V_n^2 + P_0)$.

We are now going to specialize to a particular form of P_0. In view of the lack of knowledge about the biomotor operation, our main goal is to choose an expression which would not contradict the laws of physics and would correspond to some model of the energy production at the phase transition point. We represent the energy of the gel in the front part of the lamellipodium (2.5) as

$$\begin{aligned} \mathcal{E} &= \mathcal{E}_1 + \mathcal{E}_2 \\ \mathcal{E}_1 &= -\sigma_0 + \frac{E}{2\varphi} \\ \mathcal{E}_2 &= -\tau + C\varphi. \end{aligned}$$

We then formally assume that the gel in front of the lamellipodium consists of two elastic components with the energies $\mathcal{E}_1$ and $\mathcal{E}_2$, and stresses $\sigma_1 = \sigma_0 - E/\varphi$ and $\sigma_2 = \tau$, respectively. The first component is responsible for the whole density of the gel, while the second component is massless. The state of the gel for $y > a$ is determined by the equilibrium between the two components, which creates strain in both of them. We then assume that at the phase transition component "2" is discarded and component "1" remains in the gel in its strained (expanded) state. Now the stress of this component is no longer balanced by the presence of component "2", and its release can provide the energy for the biomotor operation. It is clear with such assumptions that P_0 equals to the total energy $\mathcal{E}_2$ of the second component discarded per second, namely,

$$P_0 = \mathcal{E}_{2R}(V_n - w_R). \tag{2.19}$$

Using this expression and (2.10), one transforms (2.12) into

$$[(\sigma + \mathcal{E}_1)(w - V_n)] = 0, \tag{2.20}$$

which will now be used as a jump condition.

3. **Characteristic parameter values and the dimensionless form of equations.**

We will use the following values for the gel and nucleus parameters. The elastic modulus of the gel is cited in [B, p. 380] for the stress-strain relation of the form $\sigma = Y\partial u/\partial x$ and equals $Y \sim 10^2 pN/\mu m^2$. We relate it to the elastic modulus E used in our formulae by equating the stress increments corresponding to infinitesimal deformations of the gel. A small deformation with a change of volume fraction $\delta\varphi$ produces the strain $(\partial u/\partial x)\delta x = -\delta\varphi/\varphi$. This gives

$$\frac{E}{\varphi} = Y \sim 10^2 pN/\mu m^2. \tag{3.1}$$

The values of σ_0 and τ are then obtained from the boundary conditions (2.13), and the values of the gel volume fraction at the rear and front of the lamellipodium cited in [W, p. 149, Fig. 3(a)],

$$\varphi(r) \sim 4 \times 10^{-2}, \tag{3.2}$$

$$\varphi(f) \sim 3 \times 10^{-2}. \tag{3.3}$$

For definiteness we assume that (3.1) applies at the rear end of the lamellipodium and get

$$\sigma_0 \sim 10^2 pN/\mu m^2, \tag{3.4}$$

$$\tau = \left(\frac{\varphi(r)}{\varphi(f)} - 1\right)\sigma_0 \sim 0.32 \times 10^2 pN/\mu m^2. \tag{3.5}$$

In our notation the friction coefficient ς is identical to the coefficient ζ_{ex} of Wolgemuth et al. which is estimated as $\zeta_{ex} \sim 6 \times 10^2 pN \cdot sec/\mu m^4$ in [W, p. 157; p. 149, Table 2]. In Bottino *et al.* the same coefficient is denoted by μ and estimated as $\mu \sim 10^2 pN \cdot sec/\mu m^4$ [B, p. 379]. We will use an intermediate value,

$$\varsigma \sim 2 \times 10^2 pN \cdot sec/\mu m^4. \tag{3.6}$$

For the characteristic sizes and velocities we take (cf. [B], [MV])

$$l_n \sim 3\mu m. \tag{3.7}$$

As in [MV, p. 1176] we take

$$V_d \sim 1.25\mu m/\sec, \tag{3.8}$$

and using formula (11) on page 1179 as well as V_0 on page 1176 of [MV] as guides, we take

$$V_p^0 \sim 1.5\mu m/\sec, \quad L \sim 10\mu m; \tag{3.9}$$

we also take $0 < d < l_n$.

Finally we estimate the nucleus friction coefficient μ. As noted in the introduction, this coefficient accounts for all friction processes that impede the motion of the nucleus, and its complete evaluation is difficult. To estimate μ we will use the Stokes formula for the force acting on the spherical body moving in the viscous fluid. Then the total force acting on the nucleus is $f \sim 6\pi\eta R V_n$, where R is the radius of the nucleus. To calculate the characteristic of the drag in the one-dimensional model, we use the formula $\mu = f/(AV_n)$, where A is the area of the gel cross-section that can be estimated as $A \sim Rh$, with h being the thickness of the gel. As a result $\mu \sim 6\pi\eta/h$. The thickness of the lamellipodium is estimated as $h \sim 1\mu m$ [B, p. 380]. The viscosity of the intracellular fluid is given in [W, p. 149, Table 2] as $\eta \sim 10\ pN\ s/\mu m^2$ and is much larger than water viscosity $\eta_{water} \sim 10^{-3}\ pN\ s/\mu m^2$. The effective η has some unknown intermediate value and we conclude that

$$\mu \text{ is between } 2 \times 10^{-2} \text{ and } 2 \times 10^2\ pN\ s/\mu m^3.$$

We can now write the model in the dimensionless form:

$$
\begin{aligned}
&\overline{E} = E/\sigma_0, \quad \overline{\tau} = \tau/\sigma_0, \quad \overline{\sigma} = \sigma/\sigma_0, \quad \overline{F} = F/\sigma_0, \quad \overline{\mathcal{E}}_1 = \mathcal{E}_1/\sigma_0,\\
&\overline{y} = y/l_n, \quad \overline{f}(\overline{t}) = f(t)/l_n, \quad \overline{r}(\overline{t}) = r(t)/l_n, \quad \overline{a}(\overline{t}) = a(t)/l_n,\\
&\overline{t} = tV_d/l_n,\\
&\overline{\varphi}\left(\overline{y},\overline{t}\right) = \varphi\left(y,t\right),\\
&\overline{w}\left(\overline{y},\overline{t}\right) = w\left(y,t\right)/V_d,\\
&\overline{V}_n = V_n/V_d,\\
&\overline{V_p}\left(\overline{l}\right) = V_p\left(l\right)/V_d = \overline{V}_p^0/\left(\overline{l}-\overline{d}\right), \quad \overline{V}_p^0 = LV_p^0/(V_d l_n),\\
&\overline{\varsigma} = \varsigma V_d l_n/\sigma_0,\\
&\overline{\mu} = \mu V_d/\sigma_0,
\end{aligned}
$$

and

$$\overline{\sigma}\left(\overline{\varphi}\right) = 1 - \overline{E}/\overline{\varphi} + \overline{\tau} H\left(\overline{y} - \overline{a}\left(\overline{t}\right)\right), \quad \overline{\mathcal{E}}_1 = -1 + \overline{E}/2\overline{\varphi},$$

where $H(y)$ is the Heaviside function.

To simplify notations we shall henceforth drop all the bars in the above notations. Then our model problem consists of the differential equations

$$\frac{\partial\varphi}{\partial t} + \frac{\partial}{\partial y}\left(\varphi w\right) = 0, \quad \varsigma w = -\frac{\partial\sigma}{\partial y}, \tag{3.10}$$

the jump conditions at $a\left(t\right)$ (using (2.20))

$$
\begin{aligned}
&\left[\left(w - V_n\right)\varphi\right] = 0, \quad [\sigma] = F, \quad F = -\mu V_n,\\
&\left[\left(\sigma + \mathcal{E}_1\right)\left(w - V_n\right)\right] = 0, \quad V_n = \frac{da}{dt},
\end{aligned} \tag{3.11}
$$

boundary conditions

$$
\begin{aligned}
&\sigma\mid_{r(t)} = 0, \quad \sigma\mid_{f(t)} = 0,\\
&\frac{dr}{dt} = V_d + w\mid_{r(t)}, \quad \frac{df}{dt} = V_p\left(l\right) + w\mid_{f(t)},
\end{aligned} \tag{3.12}
$$

and initial conditions

$$r = r_0, \quad f = f_0, \quad a = a_0, \quad \varphi = \varphi_0(y) \quad \text{at } t = 0, \tag{3.13}$$

where

$$\sigma\left(\varphi\right) = 1 - E/\varphi + \tau H\left(y - a\left(t\right)\right), \quad \mathcal{E}_1 = -1 + E/\left(2\varphi\right), \tag{3.14}$$

and

$$V_d = 1, \quad V_p(l) = \frac{V_p^0}{l - d_0}, \quad 0 < d_0 < 1. \tag{3.15}$$

The dimensionless constants in the new notations are:

$$\varsigma \sim 7.5, \quad E \sim 0.04, \quad \tau \sim 0.32, \quad V_p^0 \sim 4.0, \tag{3.16}$$

$$\mu \text{ is between } 2\times 10^{-4} \text{ and } 2.0. \tag{3.17}$$

4. **Travelling wave solutions.** In this section we consider solutions of (3.10)–(3.12) that travel with uniform velocity V. We introduce the new spatial variable $z = y - Vt$ and set $r(t) = Vt$, $a(t) = a_0 + Vt$, $f(t) = l_0 + Vt$, $\varphi(y,t) = u(z)$, $w(y,t) = \widetilde{w}(z)$. Since now $\varphi_t = -u_z V$, we get the equations

$$\frac{\partial}{\partial z}\left(\left(\widetilde{w} - V\right) u\right) = 0, \tag{4.1}$$

$$\varsigma \widetilde{w} = -\frac{\partial \sigma}{\partial z}, \tag{4.2}$$

the jump relations at $z = a_0$

$$\left[u\left(\widetilde{w} - V\right)\right] = 0, \quad [\sigma] = -\mu V, \quad \left[\left(\sigma + \mathcal{E}_1\right)\left(\widetilde{w} - V\right)\right] = 0, \tag{4.3}$$

and the boundary conditions

$$u(0) = E, \quad u(l_0) = \frac{E}{1+\tau}, \quad V = 1 + \widetilde{w}(0), \quad V = V_p(l_0) + \widetilde{w}(l_0) \tag{4.4}$$

where

$$\sigma(u) = 1 - E/u + \tau H(z - a_0), \quad \mathcal{E}_1 = -1 + E/2u.$$

From (4.1) and the first jump relation in (4.3), we obtain $u\left(\widetilde{w} - V\right) = const. = c_1$, and from the boundary conditions it follows $c_1 = -E$, so that $u(V - \widetilde{w}) = E$, and $V_p(l_0) = E/u(l_0) = 1 + \tau$. Then, by (3.15), l_0 is uniquely determined:

$$l_0 = d_0 + \frac{V_p^0}{1+\tau} \sim d_0 + 3. \tag{4.5}$$

It will be convenient to work with the function $\psi(z) = 1/u(z)$. Clearly

$$\psi(0) = \frac{1}{E}, \quad \psi(l_0) = \frac{1+\tau}{E}, \tag{4.6}$$

$$\widetilde{w} = V - E\psi, \tag{4.7}$$

and from the second equation in (4.2)

$$\frac{d\psi}{dz} + \varsigma\psi = \frac{\varsigma V}{E} \quad on \quad 0 < z < a_0,\, a_0 < z < l_0. \tag{4.8}$$

Solving for ψ we get

$$\psi(z) = \frac{1}{E}\Big(V + (1 - V)\, e^{-\varsigma z}\Big), \quad 0 < z < a_0, \tag{4.9}$$

$$\psi(z) = \frac{1}{E}\Big(V + (1 + \tau - V)\, e^{-\varsigma z + \varsigma l_0}\Big), \quad a_0 < z < l_0. \tag{4.10}$$

To write the jump relations, we introduce the notations $f_L(a_0) = f(a_0 - 0)$, $f_R(a_0) = f(a_0 + 0)$ for any function f. By (4.6),

$$\psi_L(a_0) = \frac{1}{E}\Big(V + (1 - V)\, e^{-\varsigma a_0}\Big), \tag{4.11}$$

$$\psi_R(a_0) = \frac{1}{E}\Big(V + (1 + \tau - V)\, e^{\varsigma(l_0 - a_0)}\Big). \tag{4.12}$$

The last two jump conditions in (4.3) can be written in the form

$$-E\psi_R(a_0) + \tau + E\psi_L(a_0) = -\mu V, \tag{4.13}$$

$$\left(\tau - \frac{E}{2}\psi_R(a_0)\right)\left(\widetilde{w}_R(a_0) - V\right) + \frac{E}{2}\psi_L(a_0)\left(\widetilde{w}_L(a_0) - V\right) = 0. \tag{4.14}$$

Using (4.7) we can reduce (4.14) to

$$\tau\psi_R(a_0) - \frac{E}{2}\left(\psi_R^2(a_0) - \psi_L^2(a_0)\right) = 0. \tag{4.15}$$

Solving $\psi_R(a_0)$ and $\psi_L(a_0)$ from (4.15), (4.13), we get

$$\psi_L(a_0) = \left(\frac{\tau}{2\mu V} - \frac{1}{2}\right)\frac{\tau + \mu V}{E}, \tag{4.16}$$

$$\psi_R(a_0) = \left(\frac{\tau}{2\mu V} + \frac{1}{2}\right)\frac{\tau + \mu V}{E}. \tag{4.17}$$

Comparing (4.11) with (4.16), we get

$$\frac{1}{2\mu V}\left(\tau^2 - (\mu V)^2\right) - V = (1 - V)\, e^{-\varsigma a_0}. \tag{4.18}$$

Similarly, comparing (4.13) with (4.17), we find that

$$\frac{1}{2\mu V}(\tau + \mu V)^2 - V = (1 + \tau - V)\, e^{\varsigma(l_0 - a_0)}. \tag{4.19}$$

Physically the value of V should be larger than the velocity of depolymerization; i.e., $V > 1$. Dividing (4.19) by (4.18) we obtain the equation

$$\frac{1 + \tau - V}{1 - V} e^{\varsigma l_0} = \frac{(\tau + \mu V)^2 - 2\mu V^2}{\tau^2 - \mu^2 V^2 - 2\mu V^2}. \tag{4.20}$$

Suppose we can solve V from (4.20). Then we can determine a_0 uniquely from (4.18), and, if a_0 lies in the interval $1 < a_0 < l_0$, then we obtain a travelling wave

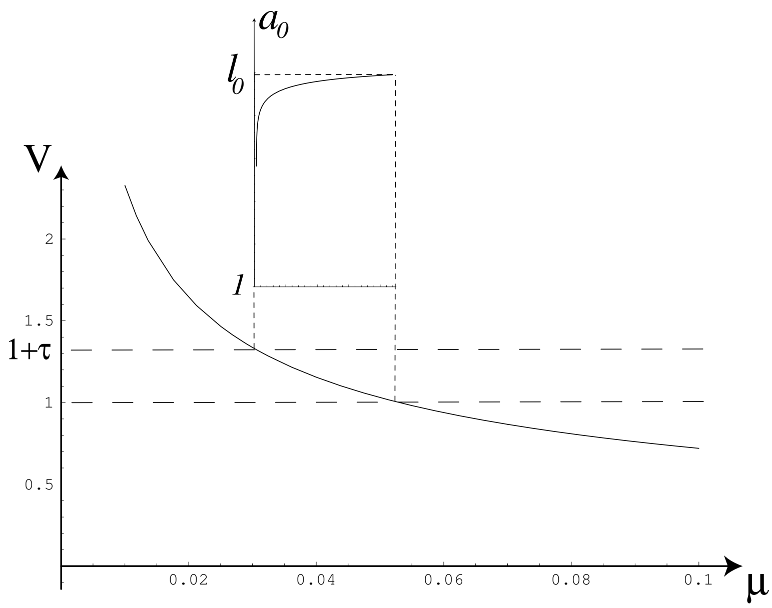

FIGURE 2. Velocity of the travelling wave solution as a function of nucleus friction coefficient μ. The inset shows the behavior of $a_0(\mu)$ in the interval where the solution exists and satisfies $1 < a_0 < l_0$.

solution. The solution (V, a_0) will depend on the parameter μ, which is a friction coefficient that depends on the environment where the cell is moving.

Using the value $d_0 = 0.5$ we solve l_0 from (4.5): $l_0 = 3.5303$, so that the length of the lamellipod is $3.5303 \cdot l_n = 10.59 \mu m$. The solution for the travelling wave velocity is shown in Figure 2. We see that for $1 < V < 1 + \tau$, parameter a_0 indeed resides within the limits $1 < a_0 < l_0$. Thus there is an interval of friction coefficients supporting the travelling wave solution. Numerically we find this interval to be $\mu \in (0.03, 0.05)$. A travelling wave solution was also found in the model [B]. We note that the model of [MV] (which is based on entirely different assumptions) also has travelling wave solutions, and it was shown numerically to be stable.

We also study the linear stability of this travelling wave solution. Our computations (Appendices I–III) show that, for a certain range of parameters, all nonzero modes are linearly asymptotically stable, and thus our model can describe the continuous stable crawling of the nematode sperm.

5. **Conclusion.** In this paper we improved the model of nematode sperm crawling based on the MSP gel phase transformation [B, W] by taking into account the conservation of energy which is extracted from the gel in the process of phase transition and partially used by the biomotor to drag the cell body. We showed that the biomotor efficiency function is the last piece of information needed to close the system of equations describing the crawling.

After choosing a consistent expression for the efficiency, we proved the existence of a travelling wave solution in some range of parameters. Our numerical computation suggests that the travelling wave solution we obtained is linearly asymptotically stable in all nonzero modes.

6. **Appendix I. Linearization about the travelling wave solution.** In this section we consider the linearized the system (2.2),(2.3),(2.9)–(2.18) about the travelling wave solution $(u(z), \widetilde{w}(z), a_0, l_0, V)$, and in the next section we shall consider the stability of the linearized system.

For the travelling wave solution, z varies in the interval $0 \le z \le l_0$ and the point of phase transition is $z = a_0$. For the linearized system

$$\begin{aligned} z = 0 \quad & \textit{will change into } z = \varepsilon\rho_1(t), \\ z = l_0 \quad & \textit{will change into } z = l_0 + \varepsilon\rho_2(t), \\ z = a_0 \quad & \textit{will change into } z = a_0 + \varepsilon\rho_3(t). \end{aligned} \tag{6.1}$$

Let $\chi(x)$ be a smooth function such that $\chi(x) = 1$ if $|x| < \delta_0$ and $\chi(x) = 0$ if $|x| > 2\delta_0$ where δ_0 is a small number $(\delta_0 << \min(a_0, l_0 - a_0))$, and set

$$R(x,t) = \rho_1(t)\chi(x) + \rho_3(t)\chi(x - a_0) + \rho_2(t)\chi(x - l_0). \tag{6.2}$$

By the change of variable

$$z = x + \varepsilon R(x,t) \quad (|\varepsilon| \textit{ is small}) \tag{6.3}$$

the three curves in (6.1) become $x = 0$, $x = a_0$ and $x = l_0$, respectively; furthermore, $dz/dx > 0$, and

$$R_x(x,t) = 0 \text{ if } x \text{ lies in the } \delta_0\text{-neighborhood of one of the points } x = 0,\ a_0,\ l_0. \tag{6.4}$$

To derive the linearized system in the fixed interval $0 < x < l_0$ with the phase transition point $x = a_0$, we write the solution $(\varphi(y,t), w(y,t))$ of (2.2),(2.3),(2.9)–(2.18) first in terms of the variable z as in section 4 ($y = z + Vt$), namely,

$$\varphi(y,t) = \varphi(z+Vt,t) \equiv \overline{\varphi}(z,t),$$
$$w(y,t) = w(z+Vt,t) \equiv \overline{w}(z,t),$$

and then rewrite $(\overline{\varphi}, \overline{w})$ as a perturbation of $(u, \widetilde{w})$,

$$\begin{aligned} \overline{\varphi}(z,t) &= u(x) + \varepsilon v(x,t), \\ \overline{w}(z,t) &= \widetilde{w}(x) + \varepsilon \eta(x,t), \end{aligned} \tag{6.5}$$

where x is related to z by (6.3). We have

$$\frac{\partial x}{\partial t} = -\frac{\varepsilon R_t}{1+\varepsilon R_x}, \quad \frac{\partial x}{\partial z} = \frac{1}{1+\varepsilon R_x}.$$

Hence

$$\frac{\partial \overline{\varphi}}{\partial t} = \frac{\partial(u+\varepsilon v)}{\partial x}\frac{\partial x}{\partial t} + \frac{\partial(u+\varepsilon v)}{\partial t} = \varepsilon\left(-\frac{\varepsilon R_t}{1+\varepsilon R_x}\frac{\partial v}{\partial x} + \frac{\partial v}{\partial t}\right) - \frac{\varepsilon R_t}{1+\varepsilon R_x}\frac{\partial u}{\partial x},$$
$$\frac{\partial \overline{\varphi}}{\partial z} = \left(\frac{\partial u}{\partial x} + \varepsilon\frac{\partial v}{\partial x}\right)\frac{1}{1+\varepsilon R_x}.$$

We want to write the linearized system as a parabolic problem for the function v. To do that we shall need to eliminate $\overline{w}$ from the relation

$$\overline{w}(z,t) = -\frac{1}{\varsigma}\frac{E}{\overline{\varphi}^2}\frac{\partial \overline{\varphi}}{\partial z} \tag{6.6}$$

and substitute it into the equation (2.2), written in terms of the (z,t) variables

$$\frac{\partial \overline{\varphi}}{\partial t} - V\frac{\partial \overline{\varphi}}{\partial z} + \frac{\partial}{\partial z}(\overline{\varphi}\,\overline{w}) = 0.$$

We then obtain for $v(x,t)$ the equation

$$\begin{aligned} L(\varepsilon)[v] \equiv \varepsilon\frac{\partial v}{\partial t} - \varepsilon^2\frac{R_t}{1+\varepsilon R_x}\frac{\partial v}{\partial x} - \varepsilon\frac{\partial u}{\partial x}\frac{R_t}{1+\varepsilon R_x} \\ -\frac{1}{1+\varepsilon R_x}\frac{\partial}{\partial x}\left\{(u+\varepsilon v)\left(\frac{E}{\varsigma}\frac{1}{1+\varepsilon R_x}\frac{(u+\varepsilon v)_x}{(u+\varepsilon v)^2} + V\right)\right\} = 0. \end{aligned} \tag{6.7}$$

Recalling (4.8), that

$$\frac{E}{\varsigma}\frac{u_x}{u} + Vu = E \tag{6.8}$$

so that

$$\frac{E}{\varsigma}\frac{u_{xx}}{u} - \frac{E}{\varsigma}\frac{(u_x)^2}{u^2} + Vu_x = 0, \tag{6.9}$$

we find that the zero order terms in ε disappear from (6.7). Dropping also the ε-terms of order ≥ 2, we arrive at the parabolic equation

$$\frac{\partial v}{\partial t} - R_t\frac{\partial u}{\partial x} - \frac{\partial}{\partial x}\left\{\frac{E}{\varsigma}\left(\frac{v_x}{u} - v\frac{u_x}{u^2} - R_x\frac{u_x}{u}\right) + vV\right\} = 0. \tag{6.10}$$

We can simplify this parabolic equation by introducing a dependent variable,

$$\vartheta(x,t) = v(x,t) - \frac{\partial u}{\partial x}R(x,t). \tag{6.11}$$

Then, by (6.9),

$$\frac{\partial\vartheta}{\partial t}=\frac{\partial}{\partial x}\left\{\frac{E}{\varsigma}\left(\frac{1}{u}\frac{\partial\vartheta}{\partial x}-\frac{u_x}{u^2}\vartheta\right)+\vartheta V\right\},$$

or

$$\frac{\partial\vartheta}{\partial t}=\frac{E}{\varsigma}\frac{\partial^2}{\partial x^2}\left(\frac{\vartheta}{u}\right)+V\frac{\partial\vartheta}{\partial x}. \tag{6.12}$$

To express the jump relations at $x=a_0$ we use the notation $[f]=f(a_0+0)-f(a_0-0)$ for any function f. Then the first jump relation in (4.3) is

$$\left[(u+\varepsilon v)\left\{-\frac{E}{\varsigma}\frac{1}{1+\varepsilon R_x}\frac{\partial}{\partial x}\left(\frac{-1}{u+\varepsilon v}\right)-\left(V+\varepsilon\frac{d\rho_3}{dt}\right)\right\}\right]=0.$$

Using (6.8), we obtain (after dropping $\varepsilon-$ terms of order ≥ 2)

$$\left[-\frac{E}{\varsigma}\frac{v_x}{u}+\frac{E}{\varsigma}\frac{u_x}{u}R_x+v\left(\frac{E}{u}-2V\right)-u\frac{d\rho_3}{dt}\right]=0. \tag{6.13}$$

Expressing this condition in terms of ϑ and using (6.8) and (6.9), we reduce this condition to

$$\left[-\frac{E}{\varsigma}\frac{\vartheta_x}{u}+\vartheta\left(\frac{E}{u}-2V\right)-u\frac{d\rho_3}{dt}\right]=0. \tag{6.14}$$

The second jump condition in (4.3) leads to

$$\left[\frac{E}{u^2}\left(\vartheta+\frac{\partial u}{\partial x}\rho_3\right)\right]+\mu\frac{d\rho_3}{dt}=0. \tag{6.15}$$

The third jump condition is $j_3^+(\varepsilon)-j_3^-(\varepsilon)=0$, where

$$j_3^+(\varepsilon)=\left\{\left(\tau-\frac{E}{2(u+\varepsilon v)}\right)\left\{-\frac{E}{\varsigma}\frac{\partial}{\partial x}\left(-\frac{1}{u+\varepsilon v}\right)-\left(V+\varepsilon\frac{d\rho_3}{dt}\right)\right\}\right\}_{x=a_0+0},$$

$$j_3^-(\varepsilon)=\left\{-\frac{E}{2(u+\varepsilon v)}\left\{-\frac{E}{\varsigma}\frac{\partial}{\partial x}\left(-\frac{1}{u+\varepsilon v}\right)-\left(V+\varepsilon\frac{d\rho_3}{dt}\right)\right\}\right\}_{x=a_0-0}.$$

After some calculations, using (6.8), we get

$$\left[v_x\mu_1(x)+v\mu_2(x)-\frac{d\rho_3}{dt}\mu_3(x)\right]=0 \tag{6.16}$$

where

$$\begin{aligned}\mu_1(x)&=\frac{E}{\varsigma u^2}\left(\frac{E}{2u}-\tau(x)\right),\quad \tau(x)=\tau H(x-a_0),\\ \mu_2(x)&=\frac{E}{\varsigma}\frac{2u_x}{u^3}\left(\tau(x)-\frac{E}{2u}\right)-\frac{E^2}{2u^3},\\ \mu_3(x)&=\tau(x)-\frac{E}{2u}.\end{aligned} \tag{6.17}$$

Using (6.8), (6.9) we compute

$$\nu_1(x)\equiv u_{xx}\mu_1(x)+u_x\mu_2(x)=\frac{u_x}{u}\Big(\tau(x)\frac{E}{u}-\frac{E^2}{u^2}\Big). \tag{6.18}$$

Hence, expressed in terms of ϑ, the third jump condition in (4.3) takes the form

$$\left[\vartheta_x\mu_1(x)+\vartheta\mu_2(x)+\rho_3\nu_1(x)-\frac{d\rho_3}{dt}\mu_3(x)\right]=0. \tag{6.19}$$

We now turn to the boundary conditions. Since $v = 0$ at $x = 0$ and $x = l_0$,

$$\vartheta\,|_{x=0} = -\frac{\partial u}{\partial x}(0)\,\rho_1(t), \tag{6.20}$$

$$\vartheta\,|_{x=l_0} = -\frac{\partial u}{\partial x}(l_0)\,\rho_2(t). \tag{6.21}$$

The free boundary condition at $x = 0$ is

$$\frac{d\rho_1}{dt} + \left\{\frac{E}{\varsigma}\frac{1}{u^2}\left(\frac{\partial\vartheta}{\partial x} + \frac{\partial^2 u}{\partial x^2}\rho_1\right)\right\}_{x=0} = 0. \tag{6.22}$$

Since the velocity of the polymerization $V_p(l)$ depends on the length $l = l_0 + \varepsilon(\rho_2 - \rho_1)$, the second free boundary condition takes the form

$$\frac{d\rho_2}{dt} + \left\{\frac{E}{\varsigma}\frac{1}{u^2}\left(\frac{\partial\vartheta}{\partial x} + \frac{\partial^2 u}{\partial x^2}\rho_2\right)\right\}_{x=l_0} - V_p'(l_0)(\rho_2 - \rho_1) = 0. \tag{6.23}$$

Finally, we complement the system (6.12)–(6.23) with initial conditions

$$\rho_j(0) = \rho_{j0}, \quad (j = 1, 2, 3), \quad \vartheta(x, 0) = \vartheta_0(x). \tag{6.24}$$

We would like to eliminate ρ_3 and $d\rho_3/dt$ from the jump conditions (6.14), (6.15) and (6.19). To do that we write (6.19) and (6.15) in the form

$$\frac{d\rho_3}{dt}[\mu_3] - \rho_3[\nu_1] = [\vartheta_x\mu_1 + \vartheta\mu_2], \tag{6.25}$$

$$\mu\frac{d\rho_3}{dt} + \rho_3\left[E\frac{u_x}{u^2}\right] = -\left[E\frac{\vartheta}{u^2}\right]. \tag{6.26}$$

If

$$D \equiv \begin{vmatrix} [\mu_3] & -[\nu_1] \\ \mu & [E\frac{u_x}{u}] \end{vmatrix} \neq 0, \tag{6.27}$$

then we can solve the two equations for ρ_3 and $d\rho_3/dt$:

$$\frac{d\rho_3}{dt} = \frac{1}{D}\left\{\left[E\frac{u_x}{u}\right][\vartheta_x\mu_1 + \vartheta\mu_2] + \left[E\frac{\vartheta}{u^2}\right][\nu_1]\right\}, \tag{6.28}$$

$$\rho_3 = \frac{1}{D}\left\{-[\mu_3]\left[E\frac{\vartheta}{u^2}\right] - \mu[\vartheta_x\mu_1 + \vartheta\mu_2]\right\}. \tag{6.29}$$

Next we write the jump condition (6.14) in the form

$$\frac{d\rho_3}{dt} = \frac{1}{[u]}[\vartheta_x\nu_2 + \vartheta\nu_3] \qquad (\text{assuming } [u] \neq 0), \tag{6.30}$$

where

$$\nu_2(x) = -\frac{E}{\varsigma u}, \qquad \nu_3 = \frac{E}{u} - 2V, \tag{6.31}$$

and compare it with (6.26). We obtain

$$\rho_3\left[E\frac{u_x}{u}\right] = -\left[E\frac{\vartheta}{u^2}\right] - \frac{\mu}{[u]}[\vartheta_x\nu_2 + \vartheta\nu_3]. \tag{6.32}$$

Finally we compare $d\rho_3/dt$ from (6.30) and (6.28) and ρ_3 from (6.32) and (6.29). This leads to the following jump relations for ϑ at $x = a_0$:

$$[\vartheta_x a_1(x) + \vartheta b_1(x)] = 0, \tag{6.33}$$

$$[\vartheta_x a_2(x) + \vartheta b_2(x)] = 0, \tag{6.34}$$

where

$$a_1(x) = \frac{1}{D}\left[E\frac{u_x}{u}\right]\mu_1(x) - \frac{\nu_2(x)}{[u]},$$
$$a_2(x) = \frac{\mu}{\left[E\frac{u_x}{u}\right]}\left(\frac{1}{D}\left[E\frac{u_x}{u}\right]\mu_1(x) - \frac{\nu_2(x)}{[u]}\right),$$
$$b_1(x) = \frac{1}{D}\left[E\frac{u_x}{u}\right]\mu_2(x) - \frac{\nu_3(x)}{[u]} + \frac{E[\nu_1]}{Du^2}, \tag{6.35}$$
$$b_2(x) = \frac{\mu}{\left[E\frac{u_x}{u}\right]}\left(\frac{1}{D}\left[E\frac{u_x}{u}\right]\mu_2(x) - \frac{\nu_3(x)}{[u]}\right) + \frac{E[\mu_3]}{Du^2} - \frac{1}{\left[\frac{u_x}{u}\right]u^2}.$$

Since $a_2 = \mu\left(E\left[\frac{u_x}{u}\right]\right)^{-1}a_1$, by multiplying the equation (6.33) by $\mu\left(\left[E\frac{u_x}{u}\right]\right)^{-1}$ and subtracting from (6.34), we get

$$[\vartheta c(x)] = 0, \tag{6.36}$$

where

$$u^2(x)c(x) = \frac{1}{\left[\frac{u_x}{u}\right]}\left(\frac{\mu}{D}[\nu_1] + 1\right) - \frac{E[\mu_3]}{D} \equiv c_0, \tag{6.37}$$

where c_0 is a constant. If $c_0 \neq 0$, then (6.36) is equivalent to

$$\left[\frac{\vartheta}{u^2(x)}\right] = 0. \tag{6.38}$$

Substituting ρ_1 and $d\rho_1/dt$ from (6.20) into (6.22), we obtain

$$\left\{-\vartheta_t + \frac{E}{\varsigma u^2}(\vartheta_x u_x - \vartheta u_{xx})\right\}_{x=0} = 0. \tag{6.39}$$

Similarly, substituting ρ_2 and $d\rho_2/dt$ from (6.21)–(6.22) into (6.23), we obtain

$$\left\{-\vartheta_t + \frac{E}{\varsigma u^2}(\vartheta_x u_x - \vartheta u_{xx})\right\}_{x=l_0} + V_p'(l_0)\left\{\vartheta(l_0,t) - \vartheta(0,t)\frac{u_x(l_0)}{u_x(0)}\right\} = 0. \tag{6.40}$$

Summary: The linearized problem consists of the parabolic equation (6.12) for ϑ, the jump conditions (6.38), (6.33), the nonlocal boundary conditions (6.39)–(6.40), and the initial conditions (6.24).

7. **Appendix II. Expressing solutions through the hypergeometric functions.** Using the Pochhammer symbol

$$(x)_n = \frac{\Gamma(x+n)}{\Gamma(x)} = x(x+1)\cdots(x+n-1),$$

the hypergeometric function F, or ${}_2F_1$, is defined by

$$F(a,b,c,z) \equiv {}_2F_1(a,b,c,z) = \sum_{k=0}^{\infty}\frac{(a)_k(b)_k}{(c)_k}\frac{z^k}{k!},$$

where a, b, and c are complex numbers. The function $y = F(a,b,c,z)$ is a solution of the differential equation

$$(z-z^2)y'' + \{c-(a+b+1)z\}y' - aby = 0. \tag{7.1}$$

If $c \neq 1$, a second linearly independent solution of (7.1) is given by

$$z^{1-c}F(a-c+1, b-c+1, 2-c, z). \tag{7.2}$$

For any constant k the functions

$$\widetilde{y} = F(a,b,c,kz), \quad \text{and } \widetilde{y} = z^{1-c}F(1+a-c, 1+b-c, 2-c, kz) \tag{7.3}$$

satisfy the equation

$$\Big(-\frac{1}{k}z+z^2\Big)\widetilde{y}\,''+\Big\{-\frac{c}{k}+(a+b+1)z\Big\}\widetilde{y}\,'+ab\widetilde{y}=0. \tag{7.4}$$

Using Stirling's formula one can readily check (see [G, p. 1066, 9.102]) that

$$\text{if } a,b,c,z\in\mathbb{C} \text{ and } c\neq -n\ (n=0,1,2,3,\cdots), \text{ then the power series for } F(a,b,c,z) \text{ converges in the unit circle } |z|<1. \tag{7.5}$$

We also have (see [WW, p. 281, 14.1]) that

$$\frac{d}{dz}\,F(a,b,c,z)=\frac{ab}{c}\,F(a+1,b+1,c+1,z). \tag{7.6}$$

8. **Appendix III. Stability.** By Section 4,

$$\frac{1}{u(x)}=\psi\,(x)=\frac{V}{E}+\frac{1-V}{E}e^{-\varsigma x}\equiv\frac{V}{E}+d_1e^{-\varsigma x},\quad 0<x<a_0, \tag{8.1}$$

$$\frac{1}{u(x)}=\psi\,(x)=\frac{V}{E}+\frac{1+\tau-V}{E}e^{-\varsigma x+\varsigma l_0}\equiv\frac{V}{E}+d_2e^{-\varsigma x},\quad a_0<x<l_0, \tag{8.2}$$

where

$$d_1=\frac{1-V}{E}<0,\quad d_2=e^{\varsigma l_0}\frac{1+\tau-V}{E}>0. \tag{8.3}$$

A direct computation shows

$$\frac{u_x(0)}{u^2(0)}=\frac{\varsigma(1-V)}{E},\quad \frac{u_{xx}(0)}{u^2(0)}=\frac{\varsigma^2(V-1)}{E}(2V-1), \tag{8.4}$$

$$\frac{u_x(l_0)}{u^2(l_0)}=\frac{\varsigma(1+\tau-V)}{E},\quad \frac{u_{xx}(l_0)}{u^2(l_0)}=\frac{\varsigma^2(1+\tau-V)}{E}\,\frac{1+\tau-2V}{1+\tau}, \tag{8.5}$$

and

$$\frac{u_x(l_0)}{u_x(0)}=\frac{1}{(1+\tau)^2}\,\frac{1+\tau-V}{1-V}. \tag{8.6}$$

Thus we can rewrite (6.39), (6.40) as

$$\Big\{-\vartheta_t-(V-1)\vartheta_x-\varsigma(V-1)(2V-1)\vartheta\Big\}_{x=0}=0, \tag{8.7}$$

$$\begin{aligned}&\Big\{-\vartheta_t+(1+\tau-V)\vartheta_x-\varsigma(1+\tau-V)\,\frac{1+\tau-2V}{1+\tau}\vartheta\Big\}_{x=l_0}\\&\qquad+V_p'(l_0)\Big\{\vartheta(l_0,t)+\frac{1}{(1+\tau)^2}\,\frac{1+\tau-V}{V-1}\vartheta(0,t)\Big\}=0.\end{aligned} \tag{8.8}$$

We next compute the jump conditions. From (8.1), (8.2) we get

$$\Big(\frac{u(a_0+)}{u(a_0-)}\Big)^2=\Big(\frac{V+(1-V)e^{-\varsigma a_0}}{V+(1+\tau-V)e^{\varsigma(l_0-a_0)}}\Big)^2,$$

and by (4.18)–(4.19), the right-hand side is equal to

$$\Big(\frac{\tau^2-(\mu V)^2}{(\tau+\mu V)^2}\Big)^2.$$

Hence we can rewrite the jump relation (6.38) in the form

$$\vartheta\Big|_{x=a_0+}=\vartheta\Big|_{x=a_0-}\Big(\frac{\tau^2-(\mu V)^2}{(\tau+\mu V)^2}\Big)^2. \tag{8.9}$$

We next express the jump condition (6.33) in a more computable form. We begin by computing

$$\begin{aligned}
u(a_0+) &= \frac{E}{V+(1+\tau-V)e^{\varsigma(l_0-a_0)}},\\
u_x(a_0+) &= \frac{E\varsigma(1+\tau-V)e^{\varsigma(l_0-a_0)}}{(V+(1+\tau-V)e^{\varsigma(l_0-a_0)})^2},\\
u(a_0-) &= \frac{E}{V+(1-V)e^{-\varsigma a_0}},\\
u_x(a_0-) &= \frac{E\varsigma(1-V)e^{-\varsigma a_0}}{(V+(1-V)e^{-\varsigma a_0})^2},
\end{aligned}$$

and

$$\begin{aligned}
\Big[E\frac{u_x}{u}\Big] &= E\Big(\frac{u_x(a_0+)}{u(a_0+)}-\frac{u_x(a_0-)}{u(a_0-)}\Big),\\
[\mu_3] &= \tau-\frac{E}{2u(a_0+)}+\frac{E}{2u(a_0-)},\\
[\nu_1] &= \frac{u_x(a_0+)}{u(a_0+)}\Big(\tau\frac{E}{u(a_0^+)}-\frac{E^2}{u^2(a_0+)}\Big)+\frac{u_x(a_0-)}{u(a_0-)}\frac{E^2}{u^2(a_0-)},\\
D &= \mu[\nu_1]+[\mu_3]\Big[E\frac{u_x}{u}\Big],\\
[u] &= u(a_0+)-u(a_0-).
\end{aligned}$$

We write (6.33) as

$$\begin{aligned}
&\vartheta_x(a_0+,t)a_1(a_0+)+\vartheta(a_0+,t)b_1(a_0+)\\
&\quad-\vartheta_x(a_0-,t)a_1(a_0-)-\vartheta(a_0-,t)b_1(a_0-)=0.
\end{aligned}\tag{8.10}$$

We now proceed to compute the four constants $a_1(a_0+), b_1(a_0+), a_1(a_0-)$, and $b_1(a_0-)$. By (6.17), (6.31),

$$\begin{aligned}
a_1(a_0+) &= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\mu_1(a_0+)-\frac{\nu_2(a_0+)}{[u]}\\
&= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\frac{E}{\varsigma u^2(a_0+)}\Big(\frac{E}{2u(a_0+)}-\tau\Big)+\frac{1}{[u]}\,\frac{E}{\varsigma u(a_0+)},
\end{aligned}$$

$$\begin{aligned}
a_1(a_0-) &= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\mu_1(a_0-)-\frac{\nu_2(a_0-)}{[u]}\\
&= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\frac{E}{\varsigma u^2(a_0-)}\Big(\frac{E}{2u(a_0-)}\Big)+\frac{1}{[u]}\,\frac{E}{\varsigma u(a_0-)},
\end{aligned}$$

$$\begin{aligned}
b_1(a_0+) &= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\mu_2(a_0+)-\frac{\nu_3(a+)}{[u]}+\frac{E[\nu_1]}{Du^2(a_0+)}\\
&= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\left\{\frac{2Eu_x(a_0+)}{\varsigma u^3(a_0+)}\Big(\tau-\frac{E}{2u(a_0+)}\Big)-\frac{E^2}{2u^3(a_0+)}\right\}\\
&\qquad -\frac{1}{[u]}\Big(\frac{E}{u(a_0+)}-2V\Big)+\frac{E[\nu_1]}{Du^2(a_0+)},
\end{aligned}$$

$$\begin{aligned} b_1(a_0-) &= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\mu_2(a_0-) - \frac{\nu_3(a-)}{[u]} + \frac{E[\nu_1]}{Du^2(a_0-)} \\ &= \frac{1}{D}\Big[E\frac{u_x}{u}\Big]\Big\{\frac{2Eu_x(a_0-)}{\varsigma u^3(a_0-)}\Big(-\frac{E}{2u(a_0-)}\Big) - \frac{E^2}{2u^3(a_0-)}\Big\} \\ &\qquad -\frac{1}{[u]}\Big(\frac{E}{u(a_0-)} - 2V\Big) + \frac{E[\nu_1]}{Du^2(a_0-)}. \end{aligned}$$

Introduce a change of variables

$$y = e^{-\varsigma x}.$$

Then

$$\frac{\partial}{\partial x} = -\varsigma y\frac{\partial}{\partial y}, \quad \frac{\partial^2}{\partial x^2} = \varsigma^2 y^2\frac{\partial^2}{\partial y^2} + \varsigma^2 y\frac{\partial}{\partial y},$$

and

$$\frac{1}{u} = \frac{V}{E} + d_j y, \quad \frac{\partial}{\partial x}\Big(\frac{1}{u}\Big) = -d_j\varsigma y, \quad \frac{\partial^2}{\partial x^2}\Big(\frac{1}{u}\Big) = d_j\varsigma^2 y, \tag{8.11}$$

where $j = 1$ for $0 < x < a_0$ and $j = 2$ for $a_0 < x < l_0$. In the new variables the equation (6.12) reduces to

$$\frac{1}{E\varsigma}\vartheta_t = (\frac{V}{E}y^2 + d_j y^3)\vartheta_{yy} + 3d_j y^2\vartheta_y + d_j y\vartheta. \tag{8.12}$$

The boundary conditions (8.7), (8.8) in the new coordinate system take the form

$$\Big\{-\vartheta_t + \varsigma(V-1)\vartheta_y - \varsigma(V-1)(2V-1)\vartheta\Big\}_{y=1} = 0, \tag{8.13}$$

$$\begin{aligned} &\Big\{-\vartheta_t - \varsigma y(1+\tau-V)\vartheta_y - \varsigma(1+\tau-V)\,\frac{1+\tau-2V}{1+\tau}\vartheta\Big\}_{y=e^{-\varsigma l_0}} \\ &\quad -\frac{V_p^0}{(l_0-d_0)^2}\Big\{\vartheta\Big|_{y=1} + \frac{1}{(1+\tau)^2}\,\frac{1+\tau-V}{V-1}\vartheta\Big|_{y=e^{-\varsigma l_0}}\Big\} = 0. \end{aligned} \tag{8.14}$$

We look for (nontrivial) solutions of the form

$$\vartheta(t,y) = e^{st}\xi(y,s).$$

Then

$$\frac{1}{E\varsigma}s\xi = (\frac{V}{E}y^2 + d_j y^3)\xi_{yy} + 3d_j y^2\xi_y + d_j y\xi, \tag{8.15}$$

and

$$\Big\{-\frac{s}{V-1}\xi + \varsigma\xi_y - \varsigma(2V-1)\xi\Big\}_{y=1} = 0, \tag{8.16}$$

$$\begin{aligned} &\Big\{-\frac{s}{1+\tau-V}\xi + \varsigma y\xi_y - \varsigma\,\frac{1+\tau-2V}{1+\tau}\xi\Big\}_{y=e^{-\varsigma l_0}} \\ &\quad -\frac{V_p^0}{(l_0-d_0)^2}\Big\{\frac{1}{1+\tau-V}\xi\Big|_{y=1} + \frac{1}{(1+\tau)^2}\,\frac{1}{V-1}\xi\Big|_{y=e^{-\varsigma l_0}}\Big\} = 0, \end{aligned} \tag{8.17}$$

with (noting that if $y_0 = e^{-\varsigma a_0}$, then $y = y_0+$ corresponds to $x = a_0-$, $y = y_0-$ corresponds to $x = a_0+$, and thus $e^{st}\xi_R(e^{-\varsigma a_0}, s) = \vartheta(a_0-, t)$, $e^{st}\xi_L(e^{-\varsigma a_0}, s) = \vartheta(a_0+, t)$):

$$\xi_L(e^{-\varsigma a_0}, s) = \xi_R(e^{-\varsigma a_0}, s)\Big(\frac{\tau^2 - (\mu V)^2}{(\tau+\mu V)^2}\Big)^2, \tag{8.18}$$

and

$$\beta_1\xi_L(e^{-\varsigma a_0}, s) + \beta_2\frac{\partial\xi_L}{\partial y}(e^{-\varsigma a_0}, s) + \beta_3\xi_R(e^{-\varsigma a_0}, s) + \beta_4\frac{\partial\xi_R}{\partial y}(e^{-\varsigma a_0}, s) = 0, \tag{8.19}$$

where

$$\begin{aligned}\beta_1 &= b_1(a_0+),\\ \beta_2 &= -\varsigma e^{-\varsigma a_0}a_1(a_0+),\\ \beta_3 &= -b_1(a_0-),\\ \beta_4 &= \varsigma e^{-\varsigma a_0}a_1(a_0-).\end{aligned}$$

We make a change of variable $y^\lambda\widetilde{\xi} = \xi$, where $\lambda = \lambda(s)$ is to be determined. Then $\widetilde{\xi}$ satisfies

$$\begin{aligned}(\frac{V}{E}y^2 + d_jy^3)\widetilde{\xi}_{yy} + \Big\{2\lambda(\frac{V}{E}y + d_jy^2) + 3d_jy^2\Big\}\widetilde{\xi}_y\\ +\Big\{\lambda(\lambda-1)(\frac{V}{E} + d_jy) + 3\lambda d_jy + d_jy - \frac{1}{E\varsigma}s\Big\}\widetilde{\xi} = 0.\end{aligned} \tag{8.20}$$

If we choose λ such that

$$\lambda(\lambda-1)\frac{V}{E} - \frac{1}{E\varsigma}s = 0, \tag{8.21}$$

then (8.20) is reduced to

$$\Big(\frac{V}{Ed_j}y + y^2\Big)\widetilde{\xi}_{yy} + \Big\{2\lambda\frac{V}{Ed_j} + (2\lambda+3)y\Big\}\widetilde{\xi}_y + (\lambda^2 + 2\lambda + 1)\widetilde{\xi} = 0, \tag{8.22}$$

so that there are explicit solutions given in terms of the hypergeometric functions

$$\widetilde{\xi}_j(y,s) = F(a_j, b_j, c_j, k_jy), \tag{8.23}$$

or

$$\widetilde{\xi}_j(y,s) = y^{1-c_j}F(a_j - c_j + 1, b_j - c_j + 1, 2 - c_j, k_jy), \tag{8.24}$$

where

$$\frac{1}{k_j} = -\frac{V}{Ed_j}, \quad c_j \equiv c_j(\lambda) = 2\lambda, \tag{8.25}$$

$$a_j + b_j + 1 = 2\lambda + 3, \quad a_jb_j = \lambda^2 + 2\lambda + 1. \tag{8.26}$$

From (8.25), c_j is actually independent of j. It is important to note that, from (8.3),

$$k_1 = \frac{V-1}{V} \in (0,1), \qquad -k_2e^{-\varsigma a_0} = \frac{1+\tau-V}{V}e^{\varsigma(l_0-a_0)} \in (0,1). \tag{8.27}$$

This guarantees the convergence of the series given in (8.23) and (8.24), by (7.5). Actually, for our data $0 < k_1 < 1/4$, and $0 < -k_2e^{-\varsigma a_0} < 2/3$, so the convergence is very fast for numerical computations.

From (8.26)

$$a_j = a_j(\lambda) = \lambda + 1, \quad b_j = b_j(\lambda) = \lambda + 1.$$

We can solve (8.21)

$$\lambda^\pm = \lambda^\pm(s) = \frac{1}{2} \pm \frac{1}{2}\sqrt{1 + \frac{4s}{\varsigma V}}. \tag{8.28}$$

The function $F(a,b,c,y)$ has poles at $c = 0, -1, -2, -3, \cdots$. We take in (8.23) and (8.24) for $\lambda = \lambda^+(s)$. Then, both the functions $F(a_j(\lambda^+), b_j(\lambda^+), c_j(\lambda^+), k_jy)$ and $F(a_j(\lambda^+) - c_j(\lambda^+) + 1, b_j(\lambda^+) - c_j(\lambda^+) + 1, 2 - c_j(\lambda^+), k_jy)$ are smooth functions when

$$\frac{4s}{\zeta V} \neq (n+1)^2 - 1, \quad n = 0, 1, 2, 3, \cdots;$$

i.e.,

$$0 < s < \frac{3}{4}\zeta V, \quad \frac{3}{4}\zeta V < s < 2\zeta V, \cdots, \frac{(n+1)^2-1}{4}\zeta V < s < \frac{(n+2)^2-1}{4}\zeta V, \cdots.$$

Then the general solution of (8.15) is given by:

$$\xi(y,s) = m_{j1} y^{\lambda^+(s)} F(a_j(\lambda^+), b_j(\lambda^+), c_j(\lambda^+), k_j y) + m_{j2} y^{\lambda^+(s)+1-c_j(\lambda^+)} \times F(a_j(\lambda^+) - c_j(\lambda^+) + 1, b_j(\lambda^+) - c_j(\lambda^+) + 1, 2 - c_j(\lambda^+), k_j y), \tag{8.29}$$

where $j = 1$ for $1 > y > e^{-\varsigma a_0}$, $j = 2$ for $e^{-\varsigma a_0} > y > e^{-\varsigma l_0}$. We now want to determine the four coefficients $m_{11} = m_{11}(s)$, $m_{12} = m_{12}(s)$, $m_{21} = m_{21}(s)$, and $m_{22} = m_{22}(s)$ using two boundary conditions and two jump conditions.

In the formula (7.29) we could also use $\lambda = \lambda^-(s)$. Actually, the solution $y^{\lambda^+(s)} F(a_j(\lambda^+), b_j(\lambda^+), c_j(\lambda^+), k_j y)$ is a scalar multiple of $F(a_j(\lambda^-) - c_j(\lambda^-) + 1, b_j(\lambda^-) - c_j(\lambda^-) + 1, 2 - c_j(\lambda^-), k_j y)$.

This is a homogeneous linear system of four equations with four unknowns m_{11}, m_{12}, m_{21}, and m_{22}, of the form

$$q_{p1} m_{11} + q_{p2} m_{12} + q_{p3} m_{21} + q_{p4} m_{22} = 0, \quad p = 1,2,3,4. \tag{8.30}$$

Since we look for nontrivial solutions, the determinant $\det(q_{ij})_{i,j=1}^4$ must be 0, and this is the transcendental equation for s.

We now proceed to compute the 16 coefficients in the matrix (q_{ij}).

From (8.16) and (7.6),

$$\varsigma\Big\{ m_{11}\Big\{\lambda^+ G_{11}(s) + G_{d11}(s)\Big\} + m_{12}\Big\{(\lambda^+ - c_1(\lambda^+) + 1) G_{12}(s) + G_{d12}(s)\Big\}\Big\} = \Big\{\frac{s}{V-1} + \varsigma(2V-1)\Big\}\Big\{m_{11} G_{11}(s) + m_{12} G_{12}(s)\Big\}, \tag{8.31}$$

where

$$\begin{aligned} G_{11}(s) &= F(a_1(\lambda^+), b_1(\lambda^+), c_1(\lambda^+), k_1), \\ G_{d11}(s) &= k_1 \frac{a_1(\lambda^+) b_1(\lambda^+)}{c_1(\lambda^+)} F(a_1(\lambda^+) + 1, b_1(\lambda^+) + 1, 1 + c_1(\lambda^+), k_1), \\ G_{12}(s) &= F(a_1(\lambda^+) - c_1(\lambda^+) + 1, b_1(\lambda^+) - c_1(\lambda^+) + 1, 2 - c_1(\lambda^+), k_1), \\ G_{d12}(s) &= k_1 \frac{(a_1(\lambda^+) - c_1(\lambda^+) + 1)(b_1(\lambda^+) - c_1(\lambda^+) + 1)}{2 - c_1(\lambda^+)} \\ &\quad \times F(a_1(\lambda^+) - c_1(\lambda^+) + 2, b_1(\lambda^+) - c_1(\lambda^+) + 2, 3 - c_1(\lambda^+), k_1); \end{aligned}$$

from this we obtain the equation for $p = 1$:

$$\left\{ \begin{aligned} q_{11} &= \Big\{\varsigma\lambda^+ - \frac{s}{V-1} - \varsigma(2V-1)\Big\} G_{11}(s) + \varsigma G_{d11}(s), \\ q_{12} &= \Big\{\varsigma(\lambda^+ - c_1(\lambda^+) + 1) - \frac{s}{V-1} - \varsigma(2V-1)\Big\} G_{12}(s) + \varsigma G_{d12}(s), \\ q_{13} &= 0, \\ q_{14} &= 0. \end{aligned} \right. \tag{8.32}$$

Similarly, we define

$$
\begin{aligned}
G_{21}(s) &= F(a_2(\lambda^+), b_2(\lambda^+), c_2(\lambda^+), k_2 e^{-\varsigma l_0}), \\
G_{d21}(s) &= k_2 \frac{a_2(\lambda^+) b_2(\lambda^+)}{c_2(\lambda^+)} F(a_2(\lambda^+)+1, b_2(\lambda^+)+1, 1+c_2(\lambda^+), k_2 e^{-\varsigma l_0}), \\
G_{22}(s) &= F(a_2(\lambda^+) - c_2(\lambda^+)+1, b_2(\lambda^+) - c_2(\lambda^+)+1, 2 - c_2(\lambda^+), k_2 e^{-\varsigma l_0}), \\
G_{d22}(s) &= k_2 \frac{(a_2(\lambda^+) - c_2(\lambda^+)+1)(b_2(\lambda^+) - c_2(\lambda^+)+1)}{2 - c_2(\lambda^+)} \\
&\quad \times F(a_2(\lambda^+) - c_2(\lambda^+)+2, b_2(\lambda^+) - c_2(\lambda^+)+2, 3 - c_2(\lambda^+), k_2 e^{-\varsigma l_0});
\end{aligned}
$$

then from (8.17)

$$
\begin{aligned}
&\Big\{ \frac{-s}{1+\tau-V} - \varsigma \frac{1+\tau-2V}{1+\tau} + \frac{V_p^0}{(l_0-d_0)^2(1+\tau)^2(V-1)} \Big\} \\
&\quad \times \Big\{ m_{21} e^{-\varsigma l_0 \lambda^+} G_{21}(s) + m_{22} e^{-\varsigma l_0 \{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{22}(s) \Big\} \\
&+ \varsigma \Bigg\{ m_{21} \Big\{ \lambda^+ e^{-\varsigma l_0 (\lambda^+ - 1)} G_{21}(s) + e^{-\varsigma l_0 \lambda^+} G_{d21}(s) \Big\} \\
&\quad + m_{22} \Big\{ (\lambda^+ - c_2(\lambda^+)+1) e^{-\varsigma l_0 \{\lambda^+ - c_2(\lambda^+)\}} G_{22}(s) \\
&\quad\quad + e^{-\varsigma l_0 \{\lambda^+ - c_2(\lambda^+)+1\}} G_{d22}(s) \Big\} \Bigg\} \\
&= \frac{V_p^0}{(l_0-d_0)^2(1+\tau-V)} \Big\{ m_{11} G_{11}(s) + m_{12} G_{12}(s) \Big\}. \qquad (8.33)
\end{aligned}
$$

From this equation we obtain the equation for $p = 2$:

$$
\begin{cases}
q_{21} = \dfrac{-V_p^0}{(l_0-d_0)^2(1+\tau-V)} G_{11}(s), \\
q_{22} = \dfrac{-V_p^0}{(l_0-d_0)^2(1+\tau-V)} G_{12}(s), \\
q_{23} = \Big\{ \dfrac{-s}{1+\tau-V} - \varsigma \dfrac{1+\tau-2V}{1+\tau} + \dfrac{V_p^0}{(l_0-d_0)^2(1+\tau)^2(V-1)} \Big\} e^{-\varsigma l_0 \lambda^+} G_{21}(s) \\
\quad + \varsigma \Big\{ \lambda^+ e^{-\varsigma l_0 (\lambda^+ - 1)} G_{21}(s) + e^{-\varsigma l_0 \lambda^+} G_{d21}(s) \Big\} \\
q_{24} = \Big\{ \dfrac{-s}{1+\tau-V} - \varsigma \dfrac{1+\tau-2V}{1+\tau} + \dfrac{V_p^0}{(l_0-d_0)^2(1+\tau)^2(V-1)} \Big\} \\
\quad \times e^{-\varsigma l_0 \{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{22}(s) \\
\quad + \varsigma \Big\{ (\lambda^+ - c_2(\lambda^+)+1) e^{-\varsigma l_0 \{\lambda^+ - c_2(\lambda^+)\}} G_{22}(s) + e^{-\varsigma l_0 \{\lambda^+ - c_2(\lambda^+)+1\}} G_{d22}(s) \Big\}.
\end{cases}
\qquad (8.34)
$$

We next define

$$
\begin{aligned}
G_{31}(s) &= F(a_1(\lambda^+), b_1(\lambda^+), c_1(\lambda^+), k_1 e^{-\varsigma a_0}),\\
G_{d31}(s) &= k_1 \frac{a_1(\lambda^+) b_1(\lambda^+)}{c_1(\lambda^+)} F(a_1(\lambda^+)+1, b_1(\lambda^+)+1, 1+c_1(\lambda^+), k_1 e^{-\varsigma a_0}),\\
G_{32}(s) &= F(a_1(\lambda^+)-c_1(\lambda^+)+1, b_1(\lambda^+)-c_1(\lambda^+)+1, 2-c_1(\lambda^+), k_1 e^{-\varsigma a_0}),\\
G_{d32}(s) &= k_1 \frac{(a_1(\lambda^+)-c_1(\lambda^+)+1)(b_1(\lambda^+)-c_1(\lambda^+)+1)}{2-c_1(\lambda^+)}\\
&\quad \times F(a_1(\lambda^+)-c_1(\lambda^+)+2, b_1(\lambda^+)-c_1(\lambda^+)+2, 3-c_1(\lambda^+), k_1 e^{-\varsigma a_0});\\
G_{41}(s) &= F(a_2(\lambda^+), b_2(\lambda^+), c_2(\lambda^+), k_2 e^{-\varsigma a_0}),\\
G_{d41}(s) &= k_2 \frac{a_2(\lambda^+) b_2(\lambda^+)}{c_2(\lambda^+)} F(a_2(\lambda^+)+1, b_2(\lambda^+)+1, 1+c_2(\lambda^+), k_2 e^{-\varsigma a_0}),\\
G_{42}(s) &= F(a_2(\lambda^+)-c_2(\lambda^+)+1, b_2(\lambda^+)-c_2(\lambda^+)+1, 2-c_2(\lambda^+), k_2 e^{-\varsigma a_0}),\\
G_{d42}(s) &= k_2 \frac{(a_2(\lambda^+)-c_2(\lambda^+)+1)(b_2(\lambda^+)-c_2(\lambda^+)+1)}{2-c_2(\lambda^+)}\\
&\quad \times F(a_2(\lambda^+)-c_2(\lambda^+)+2, b_2(\lambda^+)-c_2(\lambda^+)+2, 3-c_2(\lambda^+), k_2 e^{-\varsigma a_0}).
\end{aligned}
$$

From (8.18),

$$
\begin{aligned}
&m_{21} e^{-\varsigma a_0 \lambda^+} G_{41}(s) + m_{22} e^{-\varsigma a_0 \{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{42}(s)\\
&= \Big(\frac{\tau^2 - (\mu V)^2}{(\tau + \mu V)^2} \Big)^2 \Big\{ m_{11} e^{-\varsigma a_0 \lambda^+} G_{31}(s) + m_{12} e^{-\varsigma a_0 \{\lambda^+ + 1 - c_1(\lambda^+)\}} G_{32}(s) \Big\}. \qquad (8.35)
\end{aligned}
$$

From this we obtain the equation for $p = 3$:

$$
\left\{
\begin{aligned}
q_{31} &= \Big(\frac{\tau^2 - (\mu V)^2}{(\tau + \mu V)^2} \Big)^2 e^{-\varsigma a_0 \lambda^+} G_{31}(s),\\
q_{32} &= \Big(\frac{\tau^2 - (\mu V)^2}{(\tau + \mu V)^2} \Big)^2 e^{-\varsigma a_0 \{\lambda^+ + 1 - c_1(\lambda^+)\}} G_{32}(s),\\
q_{33} &= -e^{-\varsigma a_0 \lambda^+} G_{41}(s),\\
q_{34} &= -e^{-\varsigma a_0 \{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{42}(s).
\end{aligned}
\right. \qquad (8.36)
$$

Finally, from (8.19),

$$
\begin{aligned}
&m_{21}\beta_1 e^{-\varsigma a_0 \lambda^+} G_{41}(s) + m_{22}\beta_1 e^{-\varsigma a_0 \{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{42}(s)\\
&+ m_{21}\lambda^+ \beta_2 e^{-\varsigma a_0 (\lambda^+ - 1)} G_{41}(s) + m_{22}(\lambda^+ + 1 - c_1(\lambda^+))\beta_2 e^{-\varsigma a_0 \{\lambda^+ - c_2(\lambda^+)\}} G_{42}(s)\\
&+ m_{21}\beta_2 e^{-\varsigma a_0 \lambda^+} G_{d41}(s) + m_{22}\beta_2 e^{-\varsigma a_0 \{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{d42}(s)\\
&+ m_{11}\beta_3 e^{-\varsigma a_0 \lambda^+} G_{31}(s) + m_{12}\beta_3 e^{-\varsigma a_0 \{\lambda^+ + 1 - c_1(\lambda^+)\}} G_{32}(s)\\
&+ m_{11}\lambda^+ \beta_4 e^{-\varsigma a_0 (\lambda^+ - 1)} G_{31}(s) + m_{12}(\lambda^+ + 1 - c_1(\lambda^+))\beta_4 e^{-\varsigma a_0 \{\lambda^+ - c_1(\lambda^+)\}} G_{32}(s)\\
&+ m_{11}\beta_4 e^{-\varsigma a_0 \lambda^+} G_{d31}(s) + m_{12}\beta_4 e^{-\varsigma a_0 \{\lambda^+ + 1 - c_1(\lambda^+)\}} G_{d32}(s) = 0. \qquad (8.37)
\end{aligned}
$$

From this we obtain the equation for $p = 4$:

$$\begin{cases} q_{41} = \beta_3 e^{-\varsigma a_0 \lambda^+} G_{31}(s) + \lambda^+ \beta_4 e^{-\varsigma a_0(\lambda^+ - 1)} G_{31}(s) + \beta_4 e^{-\varsigma a_0 \lambda^+} G_{d31}(s), \\ q_{42} = \beta_3 e^{-\varsigma a_0\{\lambda^+ + 1 - c_1(\lambda^+)\}} G_{32}(s) \\ \qquad +(\lambda^+ + 1 - c_1(\lambda^+))\beta_4 e^{-\varsigma a_0\{\lambda^+ - c_1(\lambda^+)\}} G_{32}(s) \\ \qquad +\beta_4 e^{-\varsigma a_0\{\lambda^+ + 1 - c_1(\lambda^+)\}} G_{d32}(s), \\ q_{43} = \beta_1 e^{-\varsigma a_0 \lambda^+} G_{41}(s) + \lambda^+ \beta_2 e^{-\varsigma a_0(\lambda^+ - 1)} G_{41}(s) + \beta_2 e^{-\varsigma a_0 \lambda^+} G_{d41}(s), \\ q_{44} = \beta_1 e^{-\varsigma a_0\{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{42}(s) \\ \qquad +(\lambda^+ + 1 - c_2(\lambda^+))\beta_2 e^{-\varsigma a_0\{\lambda^+ - c_2(\lambda^+)\}} G_{42}(s) \\ \qquad +\beta_2 e^{-\varsigma a_0\{\lambda^+ + 1 - c_2(\lambda^+)\}} G_{d42}(s). \end{cases} \tag{8.38}$$

Let $Q(s) = \det(q_{ij})$. Then the equation for s is

$$Q(s) = 0. \tag{8.39}$$

First of all, one can show that $Q(0) = 0$ and thus $s = 0$ is an eigenvalue. The presence of a zero eigenvalue is a direct consequence of the invariance symmetry of the travelling wave solution. From (4.8) the travelling wave solution satisfies an equation,

$$\frac{E}{\varsigma}\frac{u_x}{u} + Vu = E\ ,$$

so that

$$\frac{E}{\varsigma}\frac{d^2}{dx^2}\left(\frac{u_x}{u}\right) + V\frac{d^2u}{dx^2} = 0\ . \tag{8.40}$$

This shows that the function $\vartheta = u_x(x)$ is the solution of (6.12). One can check, that $\vartheta = u_x$ and $\rho_k = -1$, $k = 1, 2, 3$, satisfy the boundary conditions (6.22), (6.23) and the jump conditions (6.14), (6.15), and (6.19). (To see that (6.14) and (6.19) are satisfied for $\vartheta = u_x$, note that if $\vartheta = u_x$, (6.14) is equivalent to (6.13) with $v = 0$, and (6.19) is equivalent to (6.16) with $v = 0$.) In other words, $s = 0$ is the eigenvalue of the linearized homogeneous problem with the corresponding eigenvector $(u_x, -1, -1, -1)$. The $\vartheta = u_x$ perturbation corresponds to an infinitesimal shift of the travelling wave solution and thus simply reveals the presence of an infinite number of travelling wave solutions related to each other by a shift along x. Such ambiguity in the choice of the particular travelling wave solution is eliminated by the initial conditions, and therefore the presence of the $s = 0$ eigenvalue represents not a real loss of stability, but an artifact of the linear stability analysis in the translationally invariant systems.

Next, numerical computations show that for $\mu = 0.04$, which is the middle range of our parameter, $d_0 = 0.5$ and the other parameters given by (3.16), with a mesh size of 0.1, $Q(s)$ does not vanish on the node of 100×200 in the range

$$\{s \in \mathbb{C};\quad 0 < \text{Re } s < 10, \quad |\text{Im } s| < 10\}.$$

Thus there are no unstable modes in this range. The same result is also valid for μ near 0.04. Such behavior suggests that there should be no unstable modes in $\{s \in \mathbb{C};\quad \text{Re s} > 0\}$ as well.

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