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Regular and Discontinuous Solutions in a Reaction-Diffusion Model for Hair Follicle Spacing

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***Abstract*—Solutions of a model reaction-diffusion system inspired by a model for hair follicle initiation in mice are constructed and analysed for the case of a one-dimensional domain. It is shown that all regular spatially heterogeneous solutions of the problem are unstable. Numerical tests show that the only asymptotically stable weak solutions are those with large jump discontinuities.**

***Keywords*-dynamical systems; reaction-diffusion equation; stationary solutions; weak solutions**

I. Introduction

A parabolic reaction-diffusion system is proposed in [14] to model the WNT signaling pathway in primary hair follicle initiation in mice. The authors in [14] use a modified version of the well-known activator-inhibitor (Gierer-Meinardt) model [3], [4] with saturation and without source terms. An important characteristic of the model is that both species share the same (up to scaling) non-linear production term for both activator and inhibitor.

A modified version of this model was studied in [12] as a proxy to reduce the parameter complexity and to capture the dynamics of the original model. Global existence of solutions of both the original and the modified systems was demonstrated by estimating time-independent upper bounds for the solutions. A parameter space analysis indicated the range of the existence of Turing patterns. It is demonstrated that heterogeneous solutions arise not only because of diffusion-driven instability, but also due to convergence to far-from-equilibrium solution branches.

This short note compares stationary solutions in the singularly perturbed problem (letting the inhibitor's diffusion rate tend to 0) and the reduced problem (setting the inhibitor's diffusion rate equal to 0) based on the modified equations from [12] for the case of a one-dimensional domain.

Stability of the stationary solutions is analysed. We show that all strictly positive, spatially heterogeneous, regular solutions of the reduced problem are unstable. Furthermore, for some parameter values, the spatially homogeneous solution is also unstable. The only asymptotically stable solutions are weak solutions where the activator exhibits jump discontinuities.

This work is organised as follows: first we define the model system and its reduced variant as a coupled ODE-reaction-diffusion system. Then we restrict our attention to a one dimensional domain and convert the problem to an *auxiliary* two-point boundary value problem. Energy methods are employed to construct the regular and weak stationary solutions. Finally we establish the stability properties of the different solutions.

II. The model problem

Let $\Omega \in \mathbb{R}^n$ be a bounded domain with sufficiently regular boundary $\partial\Omega$. Consider the following problem that describes the spatio-temporal dynamics of two interacting species

$$\begin{aligned} u_t &= \epsilon^2 \Delta u + f(u,v), \\ v_t &= d\Delta v + g(u,v), \\ \partial_x u(\cdot,x) &= \partial_x v(\cdot,x) = 0, \quad x \in \partial\Omega, \end{aligned} \tag{1}$$

with nonlinearities f, g given by

$$\begin{aligned} f(u,v) &= \rho_u \frac{u^2}{v(1+\kappa u^2)} - \mu_u u, \\ g(u,v) &= \rho_v \frac{u^2}{v(1+\kappa u^2)} - \mu_v v. \end{aligned} \tag{2}$$

The functions $u = u(t,x), v = v(t,x)$ describe the concentrations of the species at $x \in \Omega$ for time $t > 0$. The initial conditions $u(0,\cdot), v(0,\cdot)$ are sufficiently smooth so that the second derivatives in space are well-defined.

The model parameters $\rho_u, \rho_v, \mu_u, \mu_v, \kappa$ have the following physical interpretation. κ is saturation parameter for the production law for u and v, which is scaled respectively by ρ_u, ρ_v. μ_u, μ_v denote the decay rates of u and v. The diffusion constants ϵ, d describe the diffusion speeds in the domain Ω. The model equations are based on the equations proposed in [14] to model hair follicle spacing in mice.

Of particular interest are the properties of the non-negative *stationary solutions* of (1), i.e. those pairs (u,v) such that $u_t = v_t = 0$. These are those pairs (u,v) solving the problem of two coupled elliptic PDEs

$$\begin{aligned} 0 &= \epsilon^2 \Delta u + f(u,v), \\ 0 &= d\Delta v + g(u,v), \\ \partial_x u(\cdot,x) &= \partial_x v(\cdot,x) = 0, \quad x \in \partial\Omega. \end{aligned} \tag{3}$$

A. *Diffusion-driven instability*

The mechanism of diffusion-driven (or Turing) instability has been used used in mathematical and biological models to motivate the emergence of patterns and forms (spatial heterogeneities) in development processes. The classical form of the mechanism is described by a reaction-diffusion model system with two morphogens that react and diffuse in the domain producing heterogeneous spatial patterns [10].

Let us recall the conditions for diffusion-driven instability of a steady state $(\hat{u}, \hat{v})$ of (3). The Jacobian of the reaction-kinetic system $u_t = f(u,v), v_t = g(u,v)$ evaluated at this steady state is

$$J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}. \tag{4}$$

From the definition of diffusion-driven instability, in the absence of diffusion $d = 0$, the steady state $(\hat{u}, \hat{v})$ must be locally unstable to spatially inhomogeneous perturbations $\tilde{u}(t,x) = u(t,x) - \hat{u}, \tilde{v}(t,x) = v(t,x) - \hat{v}$, but locally stable to spatially homogeneous perturbations $\tilde{u}(t) = u(t) - \hat{u}, \tilde{v}(t) = v(t) - \hat{v}$.

Under the *Ansatz*

$$\begin{aligned} \tilde{u}(t,x) &= \mathbf{u} e^{ikx} e^{\lambda t}, \\ \tilde{v}(t,x) &= \mathbf{v} e^{ikx} e^{\lambda t}, \end{aligned}$$

where $\mathbf{u}, \mathbf{v}$ are scalars, $\tilde{u}(t,x), \tilde{v}(t,x)$ will be growing in time t if the eigenvalue λ associated to the wave number $k > 0$ satisfies $\mathrm{Re}\lambda > 0$. For the spatially homogeneous perturbation ($k = 0$) the eigenvalue λ associated to the wave number $k = 0$ satisfies $\mathrm{Re}\lambda < 0$.

Both conditions can be written in terms of the dispersion relation $M(\lambda, k)$ relating the eigenvalue λ to the wavenumber k. The conditions for diffusion-driven instability can be formulated as follows. First, we require the equation $M(\lambda, 0) = 0$ to have solutions with $\mathrm{Re}\lambda < 0$. Second, there must exist at least one $k_0 > 0$ such that the equation $M(\lambda, k_0) = 0$ has a solution with $\mathrm{Re}\lambda > 0$. In particular, this implies that the diffusion constants must be different $d \neq \epsilon^2$.

In particular biological applications the diffusion constant ϵ^2 may be so small to be negligible or u may not diffuse at all. The reduced problem with $\epsilon = 0$ may also exhibit diffusion-driven instability, but the above conditions may have different significance. In particular, the properties of the stationary solutions cannot be derived from a linear stability analysis of the spatially homogeneous steady state because these solutions are *far-from-equilibrium* solutions.

We remark that spatial heterogeneities arise also in reaction-diffusion systems where the nonlinearities *do not* even allow the existence of a spatially homogeneous steady state $(\hat{u}, \hat{v})$ [12].

In this note, our attention is restricted to the one-dimensional case $\Omega = [0, 1]$. For simplicity we set $\rho_u = \rho_v = 1$ in (2).

We begin by providing some *a priori* estimates for the solutions $u, v > 0$ of the stationary problem (3).

B. A priori estimates

Throughout the rest of the discussion we let $\Omega = [0, 1]$.

Lemma 1. *Let f, g be given by* (2)*. Assume that the pair (u, v) with positive $u, v \in C^2(\Omega)$ solves* (3)*. Then*

$$\begin{aligned} \max_\Omega u &\leq e^{\sqrt{\mu_u}/\epsilon} \min_\Omega u, \\ \max_\Omega v &\leq e^{\sqrt{\mu_v/d}} \min_\Omega v. \end{aligned}$$

Proof: For shortness we shall prove this for v. The computations for $u > 0$ are analogous. Since we are looking for a solution $(u, v) > 0$, we can divide both sides of the equation for v in (3) by v and integrate over Ω,

$$\mu_v = d \int_0^1 \frac{\Delta v}{v}\, dx + \int_0^1 \frac{u^2}{v^2(1 + \kappa u^2)}\, dx.$$

Integration by parts using the boundary condition $\partial_x v(0) = \partial_x v(1) = 0$ gives

$$\mu_v = d \int_0^1 \left(\frac{\partial_x v}{v}\right)^2 dx + \int_0^1 \frac{u^2}{v^2(1 + \kappa u^2)}\, dx,$$

whence

$$\int_0^1 \left(\frac{\partial_x v}{v}\right)^2 dx \leq \frac{\mu_v}{d}.$$

Choose $x_{\min}, x_{\max} \in \Omega$ such that

$$v(x_{\min}) = \min_\Omega v, \quad v(x_{\max}) = \max_\Omega v.$$

Then

$$\begin{aligned} &\log \max v - \log \min v = \int_{x_{\min}}^{x_{\max}} \frac{\partial_x v}{v}\, dx \\ &\leq |x_{\min} - x_{\max}|^{1/2} \cdot \left| \int_{x_{\min}}^{x_{\max}} \left(\frac{\partial_x v}{v}\right)^2 dx \right|^{1/2} \\ &\leq \sqrt{\frac{\mu_v}{d}}, \end{aligned}$$

implying $\max v \leq e^{\sqrt{\mu_v/d}} \min v$. ∎

Theorem 1. *Let $(u, v) \in C^2(\Omega)$ solve* (3)*. Then there exist monotone functions $\psi_\uparrow, \psi_\downarrow, \alpha$ such that $\alpha, \psi_\uparrow$ are monotone increasing, $\psi_\downarrow$ is monotone decreasing, and*

$$\psi_\uparrow(\epsilon) < \quad u(x) \quad < \psi_\downarrow(\epsilon), \tag{5}$$

$$\alpha(\min_\Omega u) \leq \quad v(x) \quad \leq \alpha(\max_\Omega u). \tag{6}$$

The functions $\psi_\uparrow, \psi_\downarrow, \alpha$ are independent of d.

Proof: Solving the equation $g(u, v) = 0$ (2), v can be expressed in terms of u as

$$v = \alpha(u) :\equiv \left(\frac{u^2}{\mu_v(1 + \kappa u^2)}\right)^{1/2}.$$

$\alpha(u)$ is a monotone increasing function of u. Observe that for a fixed u $g(u, v) < 0$ iff $v > \alpha(u)$ and $g(u, v) > 0$ iff $v < \alpha(u)$.

Choose $x_{\min}, x_{\max} \in \Omega$ such that

$$v(x_{\min}) = \min_\Omega v,$$
$$v(x_{\max}) = \max_\Omega v.$$

Because $\Delta v(x_{\min}) \geq 0, \Delta v(x_{\max}) \leq 0$ the equality $d\Delta v + g(u,v) = 0$ implies

$$g(u(x_{\min}), v(x_{\min})) \leq 0,$$
$$g(u(x_{\max}), v(x_{\max})) \geq 0.$$

Therefore,

$$\min v = v(x_{\min}) \geq \alpha(u(x_{\min})),$$
$$\min v = v(x_{\max}) \leq \alpha(u(x_{\max})),$$

and due to monotonicity of α we obtain

$$\min_{\Omega} v \geq \alpha(\min_{\Omega} u),$$
$$\max_{\Omega} v \leq \alpha(\max_{\Omega} u),$$

whence

$$\alpha(\min_{\Omega} u) \leq v(x) \leq \alpha(\max_{\Omega} u), \quad x \in \Omega. \quad (7)$$

From the equation $f(u,v) = 0$ we express

$$v = \beta(u) :\equiv \frac{u}{(1+\kappa u^2)\mu_u},$$

for $u > 0$. Observe that for a fixed $u > 0$ $f(u,v) < 0$ iff $v > \beta(u)$ and $f(u,v) > 0$ iff $v < \beta(u)$.

Choose $x_{\min}, x_{\max} \in \Omega$ such that

$$u(x_{\min}) = \min_{\Omega} u,$$
$$u(x_{\max}) = \max_{\Omega} u.$$

Because $\Delta u(x_{\min}) \geq 0, \Delta u(x_{\max}) \leq 0$ the equality $\epsilon^2 \Delta u + f(u,v) = 0$ implies

$$f(u(x_{\min}), v(x_{\min})) \leq 0,$$
$$f(u(x_{\max}), v(x_{\max})) \geq 0.$$

Therefore,

$$v(x_{\min}) > \beta(u(x_{\min})),$$
$$v(x_{\max}) < \beta(u(x_{\max})).$$

We obtain the following estimates

$$\max_{\Omega} v(x) > \beta(\min_{\Omega} u), \quad \min_{\Omega} v(x) < \beta(\max_{\Omega} u). \quad (8)$$

Combining estimates (7) and (8) we have

$$\beta(\min_{\Omega} u) < \alpha(\max_{\Omega} u),$$
$$\beta(\max_{\Omega} u) > \alpha(\min_{\Omega} u).$$

Note that α is monotone increasing in u, so the estimates in Lemma 1 transforms these inequalities to

$$\beta(\min_{\Omega} u) < \alpha(e^{\sqrt{\mu_u}/\epsilon} \min_{\Omega} u),$$
$$\beta(\max_{\Omega} u) > \alpha(e^{-\sqrt{\mu_u}/\epsilon} \max_{\Omega} u).$$

Therefore, $\min u \geq \zeta_1$, where ζ_1 is the solution of

$$\beta(z) = \alpha(e^{\sqrt{\mu_u}/\epsilon} z), \quad (9)$$

and $\max u \leq \zeta_2$, where ζ_2 is the solution of

$$\beta(z) = \alpha(e^{-\sqrt{\mu_u}/\epsilon} z). \quad (10)$$

Hence we obtain the functions $\psi_{\uparrow}, \psi_{\downarrow}$ by setting

$$\psi_{\uparrow}(\epsilon) = \zeta_1(\epsilon), \quad \psi_{\downarrow}(\epsilon) = \zeta_2(\epsilon),$$

and applying Lemma 2 completes the proof. ■

Remark: The functions $\psi_{\uparrow}, \psi_{\downarrow}$ may have jump discontinuities.

To estimate the behaviour of $\zeta_i, i = 1, 2$, we need

Lemma 2. *The equation* (9) *has as unique solution $\zeta_1 = 0$ if $\mu_v < \mu_u^2$. Otherwise, the equation* (9) *has a unique non-negative solution $\zeta_1(\epsilon)$ which is an increasing function of ϵ. Furthermore, as $\epsilon \to 0$, $\zeta_1(\epsilon) \to 0$, and as $\epsilon \to \infty$, $\zeta_1(\epsilon) \to \frac{1}{\kappa}(\frac{\mu_v}{\mu_u^2} - 1)$.*

The equation (10) *has a unique non-negative solution $\zeta_2(\epsilon)$ which is a decreasing function of ϵ. Furthermore, as $\epsilon \to 0$, $\zeta_2(\epsilon) \to \infty$, and as $\epsilon \to \infty$, $\zeta_2(\epsilon) \to 0$ if $\mu_v < \mu_u^2$ and $\zeta_2(\epsilon) \to \frac{1}{\kappa}(\frac{\mu_v}{\mu_u^2} - 1)$ else.*

Proof: Note that $\alpha(0) = \beta(0) = 0$, and $\alpha' > 0$, while β has a maximum at $z = \frac{1}{\sqrt{k}}$.

Let $s = e^{\pm\sqrt{\mu_u}/\epsilon}, C = \frac{\mu_v}{\mu_u^2}$. The problem reduces to solving the equation $\beta(z) = \alpha(sz)$ or

$$\frac{C}{(1+\kappa z^2)^2} = \frac{s^2}{1+\kappa s^2 z^2}.$$

This is a quadratic in z^2,

$$s^2 - C + (2-C)\kappa s^2 z^2 + \kappa^2 s^2 z^4 = 0. \quad (11)$$

This quadratic has real solutions if its discriminant $D = \kappa^2 s^2 (C^2 s^2 + 4C - 4Cs^2) \geq 0$.

First, note that $s = e^{\sqrt{\mu_u}/\epsilon} \geq 1$, so by Descartes' rule of signs (11) has no positive solutions for $C < 1$. For $1 \leq C < 2$ (11) has a positive solution iff $C > s^2$. The positive solution of (9) is the positive square root $\zeta_1 = \sqrt{Z}$ where

$$Z(s) = \frac{C-2}{2\kappa} + \frac{\sqrt{C^2 s^2 + 4C - 4Cs^2}}{2\kappa s}.$$

For $C \geq 2$ (11) has at least one positive solution iff $D > 0$.

Observe that as $\epsilon \to \infty, s \to 1$ so the positive solution ζ_1 tends to the square root of

$$\lim_{s\to 1} Z(s) = \frac{C-1}{\kappa}.$$

Second, note that $s = e^{-\sqrt{\mu_u}/\epsilon} \leq 1$, so $D > 0$ (solutions are always real). For $C < 1$, Descartes' rule of signs shows (11) has a positive solution iff $s^2 < C$. For $C \geq 1$ Descartes' rule of signs shows that (11) has always one non-negative solution.

Hence we conclude that for $\frac{\mu_v}{\mu_u^2} < 1$, $\zeta_1 = 0$, and for $\frac{\mu_v}{\mu_u^2} \geq 1$, the solution ζ_1 of (9) is an increasing function of ϵ, and

$$\lim_{\epsilon\to 0} \zeta_1(\epsilon) = 0,$$
$$\lim_{\epsilon\to\infty} \zeta_1(\epsilon) = \sqrt{\frac{1}{\kappa}(\frac{\mu_v}{\mu_u^2} - 1)}.$$

Furthermore, $\zeta_2(\epsilon) \to \infty$ as $\epsilon \to 0$, while

$$\lim_{\epsilon\to\infty} \zeta_2(\epsilon) = 0 \quad \text{for } \frac{\mu_v}{\mu_u^2} < 1,$$

but

$$\lim_{\epsilon\to\infty} \zeta_2(\epsilon) = \sqrt{\frac{1}{\kappa}(\frac{\mu_v}{\mu_u^2} - 1)} \quad \text{for } \frac{\mu_v}{\mu_u^2} \geq 1.$$

■

In the *singular-perturbation* limit $\epsilon \to 0$, the problem (3) will exhibit spike solutions with the spikes in u having small support in Ω. We refer to [2], [15] for construction and analytic properties of such solutions. Fig. 1 shows a typical spike solution.

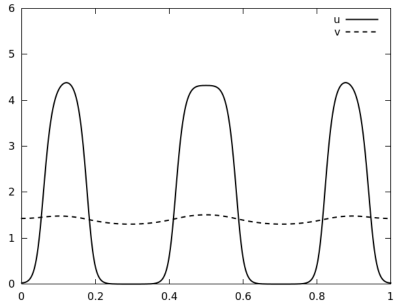

Fig. 1. A pattern with spikes. Parameter values are $\epsilon = 0.01, d = 0.1, \mu_u = 1, \mu_v = 1.2$.

C. Reduced problem

We show that the reduced problem ($\epsilon = 0$) admits another class of solutions. By setting $\epsilon = 0$ in (3) the resulting reduced problem is an algebraic-PDE system

$$\begin{aligned} 0 &= f(U, V), \\ 0 &= d\Delta V + g(U, V), \\ 0 &= \partial_x V, \quad x \in \partial\Omega. \end{aligned} \tag{12}$$

In the following, we shall characterise solutions of (12) and their stability properties.

Let us recall some basic definitions. A solution (U, V) to the problem (12) is called *regular* if there exists a function $h \in C^1(\mathbb{R})$ such that the a solution $U(x)$ of $f(U, V) = 0$ given by $U(x) = h(V(x))$ for all $x \in \Omega$.

If the function h is not unique, there is more than one way to choose the solution for U in the first equation in (12), so the problem may have only piecewise continuous solutions U on Ω. Hence it is convenient to study such solutions in a weak sense. The *weak* solution (U, V) of (12) belongs to the class $L^\infty(\Omega) \times H^1(\Omega)$ and satisfies

$$\begin{gathered} 0 = f(U, V), \text{ a.e. } x \in \Omega, \\ d\langle \nabla V, \nabla \psi \rangle = \langle g(U, V), \psi \rangle, \quad \psi \in H^1(\Omega), \end{gathered} \tag{13}$$

where $\langle \cdot, \cdot \rangle$ denotes the H^1-scalar product.

Proposition 1. *Suppose the problem* (3) *has a spatially homogeneous steady state* $(\hat{u}, \hat{v})$. *Diffusion-*

driven (Turing) instability at $(\hat{u}, \hat{v})$ occurs if u is self-activating there, in other words, $f_u(\hat{u}, \hat{v}) > 0$.

Proof: The dispersion relation is a quadratic in λ. Solving the dispersion relation $M(\lambda, 0) = 0$ for λ we obtain the conditions

$$\mathrm{tr} J = f_u + g_v < 0, \tag{14}$$

$$\det J = f_u g_v - f_v g_u > 0, \tag{15}$$

so that $\mathrm{Re}\lambda_{1,2} < 0$. The derivatives are evaluated at $(\hat{u}, \hat{v})$.

Next we solve the dispersion relation $M(\lambda, k) = 0$ for λ. By Vieta's formulae

$$\lambda_1 + \lambda_2 = -dk^2 + \mathrm{tr} J,$$
$$\lambda_1 \lambda_2 = -f_u dk^2 + \det J,$$

whence $\lambda_1 + \lambda_2 < 0$, for all $k > 0$. If $f_u \leq 0$, $\lambda_1 \lambda_2 > 0$, so $\mathrm{Re}\lambda_{1,2} < 0$ for all $k > 0$, and *no diffusion-driven instability* would be possible. This proves the claim. ∎

III. Auxiliary problem

In this section, we consider an auxiliary elliptic problem when at least one of $U, V > 0$ on some subinterval of Ω. Suppose that the equation $f(U, V) = 0$ can be solved (not necessarily) uniquely on a subset $I \subset \Omega$. Let $U(x) = h(V(x)), x \in I$, with $h \in C^1(\mathbb{R})$.

Then every regular solution of (12) on I satisfies the elliptic problem

$$0 = d\Delta V + \phi(V), \quad x \in I, \tag{16}$$

with $\phi(V) = g(h(V), V)$.

The solutions of (16) can be constructed using an energy method for two-point boundary value problems. There are two cases for the function ϕ, depending on whether $U = 0$ on I or $U > 0$ on I. Let us consider each case separately.

If $U(x) = 0, x \in I$, we have $h \equiv 0$, so $\phi = -\mu_v V$ almost everywhere on I. The problem (16) is reduced to the elliptic problem (17),

$$0 = d\Delta V - \mu_v V, \quad x \in I, \tag{17}$$

which has a non-trivial solution only under Dirichlet or Robin boundary conditions.

Next we classify the solutions when $h \not\equiv 0$ on I.

We solve formally for U in (12),

$$U = h_i(V) = \frac{1 \pm \sqrt{1 - 4\kappa\mu_u^2 V^2}}{2\kappa\mu_u V}, \quad i = 1, 2. \tag{18}$$

and use

$$\frac{U^2}{V(1 + \kappa U^2)} = \mu_u U, \quad x \in I.$$

When $U > 0$, the equation $f(U, V) = 0$ may have locally at most two solutions. Then (16) becomes

$$0 = d\Delta V + \mu_u h_i(V) - \mu_v V, \tag{19}$$

so we must solve a two-point boundary-value problem in two cases $i = 1, 2$ (for each solution branch for U),

$$0 = \Delta V + \frac{1}{d}(\mu_u h_i(V) - \mu_v V), \quad x \in I. \tag{20}$$

We set

$$\begin{aligned} \phi_i(y) &= \frac{1}{d}(\mu_u h_i(y) - \mu_v y) \\ &= \frac{1}{d}\left(\frac{1 \pm \sqrt{1 - 4\kappa\mu_u^2 y^2}}{2\kappa y} - \mu_v y\right) \end{aligned} \tag{21}$$

with ϕ_1 denoting the choice of positive square root and ϕ_2 denoting the choice of negative square root in (21).

The auxiliary elliptic problem is thus formulated: Solve for $V = y(x)$ such that

$$0 = y'' + \phi_i(y), \quad x \in I, \quad i = 1, 2. \tag{22}$$

Recall that only solutions $y \in (0, \frac{1}{2\mu_u\sqrt{k}})$ are considered in order for the square root in (21) to be real-valued.

Problem (22) can be rewritten as the equivalent system (23) of first-order equations

$$y' = z, \quad z' = -\phi_i(y). \tag{23}$$

Note that $y < \frac{1}{2\mu_u\sqrt{\kappa}}$ in order for the square root in (21) to be well-defined in $\mathbb{R}$. Hence, without loss of generality we may assume that $V < \frac{1}{2\mu_u\sqrt{\kappa}}$ on I. Else, we restrict the domain to a subset $\{x : V(x) < \frac{1}{2\mu_u\sqrt{\kappa}}\} \subset I$.

We employ an energy formulation to describe the solutions y, z of (23). We set $\mathcal{E}$ as the total energy, $\mathcal{U}$ as the potential energy. The first integral of (23) is

$$\frac{z^2}{2} + \mathcal{U}(y) = \mathcal{E}, \quad \mathcal{U}' = \phi_i. \tag{24}$$

To see this, differentiate the left-hand side of (24) and apply (22) and (23),

$$\left(\frac{z^2}{2} + \mathcal{U}(y)\right)' = zz' + \mathcal{U}'y' = zz' + \phi_i z = 0.$$

Let $\mathcal{U}$ have a local minimum at y_0. Choose total energy $\mathcal{E}$ such that $\mathcal{U}(0) > \mathcal{E} > \mathcal{U}(y_0)$. According to [1, Satz, p.92], for $\mathcal{E} > \mathcal{U}(y_0)$, the equation (24) defines a closed smooth curve in the (y, z)-plane, which is symmetric with respect to the y-axis. Then there exists some $t > 0$ such that $z(0) = z(t)$, corresponding to a solution of problem (22) under homogeneous Neumann boundary conditions on $(0, t)$.

As in [1] we express the solution y of the ODE using (24) as

$$y' = \pm\sqrt{2(\mathcal{E} - \mathcal{U}(y))}.$$

Choosing the positive value of y' (corresponding to a monotone increasing y), rearranging the above as

$$1 = \frac{y'}{\sqrt{2(\mathcal{E} - \mathcal{U}(y))}} \tag{25}$$

and integrating both sides of (25) over x, we obtain for every $L > 0$,

$$\begin{aligned} L &= \int_0^L \frac{y'(x)}{\sqrt{2(\mathcal{E} - \mathcal{U}(y(x))}} dx \\ &= \int_{y(0)}^{y(L)} \frac{dy}{\sqrt{2(\mathcal{E} - \mathcal{U}(y))}}. \end{aligned} \tag{26}$$

Let $0 < y_1 < y_0 < y_2 < \frac{1}{2\mu_u\sqrt{\kappa}}$ be such that $\mathcal{U}(y_1) = \mathcal{U}(y_2) = \mathcal{E}$, but $\mathcal{U}'(y_i) \neq 0, i = 1, 2$. Then the integral

$$\mathcal{I}(\mathcal{E}) = \int_{y_1}^{y_2} \frac{dy}{\sqrt{2(\mathcal{E} - \mathcal{U}(y))}} := \frac{L}{2}. \tag{27}$$

is convergent [1, p.93]. Then (26) defines implicitly a continuous solution y of (22) such that $y(0) = y_1, y(\frac{L}{2}) = y_2$. This solution can be continued periodically on $\mathbb{R}$ and the periodic function has a period $\frac{L}{2}$.

Therefore, every such closed curve for suitable L will correspond to a solution of the system (23) under homogeneous Neumann boundary conditions on $(0, \frac{L}{2})$. The properties of the solutions of (23) will depend, therefore, on the properties of the integral (27), $\mathcal{I}(\mathcal{E})$. The following lemma is a modification of a well-known result. For the idea of proof we refer to [11, Lemma 3.1] or [5, Lemma 5.3-5.5].

Lemma 3. *Let $\mathcal{U}$ have a local minimum at x_0 and a local maximum at 0. Suppose $0 < x_1 < x_0 < x_2$ are such that $\mathcal{U}(x_1) = \mathcal{U}(x_2) = E, \mathcal{U}'(x_1), \mathcal{U}'(x_2) \neq 0$. Then $\mathcal{I}(E)$ is a continuous function in E, and*

$$\lim_{E \to \mathcal{U}(x_0)} \mathcal{I}(E) = \frac{\pi}{\mathcal{U}''(x_0)}, \quad \lim_{E \to \mathcal{U}(0)} \mathcal{I}(E) = \infty.$$

The extrema of the potential energy $\mathcal{U}_i$ depend on the zeros of the functions ϕ_i. Let us examine ϕ_i's zeros for $i = 1, 2$. Note that in order for the square root in (21) to be real-valued, $y > 0$ is such that $1 - 4\kappa\mu_u^2 y^2 \geq 0$, so we search for zeros in the interval $(0, \frac{1}{2\mu_u\sqrt{k}})$.

Lemma 4. *The equation $\phi_1(y) = 0$ has no solutions in $(0, \frac{1}{2\mu_u\sqrt{k}})$. For $\mu_v < \mu_u^2$ or $\mu_v > 2\mu_u^2$, $\phi_2(y) = 0$ has no solution in $(0, \frac{1}{2\mu_u\sqrt{k}})$. For $\mu_u^2 < \mu_v < 2\mu_u^2$, the solution of $\phi_2(y) = 0$ is $y_0 = \sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_v^2}}$.*

Proof: After rearrangement of the terms and squaring both sides, we obtain

$$1 - 4\kappa\mu_u^2 y^2 = (1 - 2\kappa\mu_v y^2)^2,$$

and after cancellation of y^2 from both sides, $\kappa\mu_v^2 y^2 + \mu_u^2 - \mu_v = 0$. For $\mu_v < \mu_u^2$, the left-hand side is strictly positive, hence neither ϕ_i has a positive root.

If $\mu_v > \mu_u^2$, a direct computation shows that the solution of the above quadratic is $y_0 = \sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_v^2}}$. Yet, y_0 is a root of ϕ_2 only.

When $\mu_v < 2\mu_u^2$,

$$1 - 2\kappa\mu_v y^2 > 1 - 4\kappa\mu_u^2 y^2 \geq 0,$$

so

$$\phi_1(y) = \frac{1}{d}\left(\frac{1 - 2\kappa\mu_v y^2 + \sqrt{1 - 4\kappa\mu_u^2 y^2}}{2\kappa y}\right) > 0.$$

Therefore, for $\mu_u^2 < \mu_v < 2\mu_u^2$, $\phi_1(y) = 0$ has no solution $y \in \mathbb{R}^+$.

For $\mu_v > 2\mu_u^2$, the number y_0 lies outside the domain of definition of the square root, $(0, \frac{1}{2\mu_u\sqrt{k}})$. Hence none of $\phi_i, i = 1, 2$ has a zero in $(0, \frac{1}{2\mu_u\sqrt{k}})$. ■

Now we are able to characterise the extrema of the potential energies $\mathcal{U}_1, \mathcal{U}_2$ on $(0, \frac{1}{2\mu_u\sqrt{k}})$.

Lemma 5. *Let $\mu_u, \mu_v > 0$. The potential energy $\mathcal{U}_1$ has a maximum at $\frac{1}{2\mu_u\sqrt{k}}$ and no local minima.*

- *for $\mu_v < \mu_u^2$, $\mathcal{U}_2$ has a minimum at 0;*
- *for $\mu_v \in (\mu_u^2, 2\mu_u^2)$, $\mathcal{U}_2$ has a local maximum at 0 and a local minimum at $y_0 = \sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_v^2}}$;*
- *for $\mu_v > 2\mu_u^2$, $\mathcal{U}_2$ has a maximum at 0.*

Proof: Lemma 4 implies that ϕ_1 never changes sign on the interval $(0, \frac{1}{2\mu_u\sqrt{k}})$. Thus, it is clear that $\mathcal{U}_1$ has no local extrema in $(0, \frac{1}{2\mu_u\sqrt{k}})$. In fact,

$$\lim_{y\to 0} \mathcal{U}_1(y) = -\infty,$$

and $\mathcal{U}_1$ has a maximum at $\frac{1}{2\mu_u\sqrt{k}}$.

Furthermore, $\mathcal{U}_2$ has an extremum at $y_0 = \sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_v^2}}$, see Lemma 4. Note that for this y_0,

$$\sqrt{1 - 4\kappa\mu_u^2 y_0^2} = \left|1 - \frac{2\mu_u^2}{\mu_v}\right| = \frac{2\mu_u^2}{\mu_v} - 1.$$

Next, we compute $\mathcal{U}_2''(y_0) = \phi_2'(y_0)$. Note that

$$\phi_2'(y) = \frac{1}{d}\left(\frac{1}{2\kappa y^2\sqrt{1 - 4\kappa\mu_u^2 y^2}} - \frac{1}{2\kappa y^2} - \mu_v\right).$$

If $\mu_v \in (\mu_u^2, 2\mu_u^2)$,

$$\mathcal{U}_2''(y_0) = \phi_2'(y_0) = \frac{2\mu_v(\mu_v - \mu_u^2)}{d(2\mu_u^2 - \mu_v)} > 0.$$

Hence, $\mathcal{U}_2$ has a local minimum at y_0.

If $\mu_v = 2\mu_u^2$, the point $y_0 = \frac{1}{2\mu_u\sqrt{\kappa}}$ coincides with the endpoint of the interval, so it is of no interest.

We compute by L'Hôpital's rule

$$\lim_{y\to 0} \phi_2(y) = 0,$$

showing 0 is an extremum for $\mathcal{U}_2$. Next we examine the extremum properties of 0 by applying again L'Hôpital's rule

$$\lim_{y\to 0} \phi_2'(y) = \frac{1}{d}(\mu_u^2 - \mu_v).$$

Therefore, 0 is a maximum for $\mathcal{U}_2$ if $\mu_u^2 < \mu_v$, and a minimum if $\mu_u^2 > \mu_v$. This completes the proof. ■

Lemma 5 and [1, Satz, p.92] allow us to relate the existence of regular solutions of problem (12) on Ω to the extrema of the potential energies associated to the auxiliary problem (22). We conclude that no regular solutions (U, V) can be constructed using the potential energy $\mathcal{U}_1$ because it does not have local minima. The only possibility to construct regular solutions (U, V) is by using the potential energy $\mathcal{U}_2$ when $\mu_u^2 < \mu_v < 2\mu_u^2$.

The following Lemma provides an important property of the integral $\mathcal{I}(E)$ which will be employed in the construction of regular solutions of (12).

Lemma 6. *$\mathcal{I}(E)$ is monotone in E on $(\mathcal{U}_2(y_0), \mathcal{U}_2(0))$.*

Proof: Using reasoning as in [5, Lemma 5.5] it is enough to show that $\mathcal{U}_2''' \leq 0$ on $(0, \frac{1}{2\mu_u\sqrt{\kappa}})$. Then we estimate

$$\mathcal{U}_2'''(y) = \phi_2''(y) = \frac{2}{y^3}(1 - (1 - 4\mu_u^2\kappa y^2)^{-\frac{1}{2}}) - \frac{4\kappa\mu_u^2}{y}(1 - 4\kappa\mu_u^2 y^2)^{-\frac{3}{2}},$$

but $(1 - 4\mu_u^2\kappa y^2)^{-\frac{1}{2}} \geq 1$ so $\mathcal{U}_2'''(y) < 0$. ■

IV. Stationary solutions

Combining the results on the auxiliary problem, we can classify the regular and the weak solutions of the problem (22).

A. Regular stationary solutions

We first remark on the 'trivial', constant solution to (12). If $\mu_u^2 < \mu_v$, there is a constant solution of (12),

$$\begin{aligned} \hat{u} &= \sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_u^2}}, \\ \hat{v} &= \sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_v^2}}. \end{aligned} \tag{28}$$

For $\mu_u^2 < \mu_v < 2\mu_u^2$ we can construct a regular solution using the auxiliary problem and the potential energy $\mathcal{U}_2$ as follows.

Proposition 2. *Let*

$$L_{\min} := \min_{\mathcal{E}} I(\mathcal{E}) = \frac{\pi}{\sqrt{\mathcal{U}_2''\left(\sqrt{\frac{\mu_v - \mu_u^2}{\kappa\mu_v^2}}\right)}}$$

and set $N = \max\{n \in \mathbb{N} : NL_{\min} \leq 1\}$. *The two-point boundary value problem* (20) *with homogeneous Neumann boundary conditions has the following solutions*

- *the spatially homogeneous solution* $V = \hat{v}$ *given in* (28).
- *if* $L_{\min} \leq 1$, *there exists a unique monotone increasing solution* $V_\uparrow(x)$, *and a unique monotone decreasing solution* $V_\downarrow(x) = V_\uparrow(1-x)$
- *for all* $2 \leq n \leq N$ *there exists a unique* n*-periodic solution* $V_{n,\uparrow}$ *which is monotone increasing on* $(0, \frac{1}{n})$, *as well as a unique* n*-periodic solution* $V_{n,\downarrow}$ *which is monotone decreasing on* $(0, \frac{1}{n})$.

Proof: The validity of the first claim is obvious. The remaining claims use the properties of the integral $\mathcal{I}$ in Lemma 3 and 6. These imply that for all $n \leq N$, there exists a unique energy level $\mathcal{E}_n : \mathcal{I}(\mathcal{E}_n) = \frac{1}{n}$, corresponding to a unique monotone increasing solution $V_{n,\uparrow}(x)$ on $(0, \frac{1}{n})$, and a monotone decreasing solution $V_{n,\downarrow} = V_{n,\uparrow}(\frac{1}{n} - x)$ on $(0, \frac{1}{n})$. If $n \geq 2$, either solution can be extended to the entire domain Ω by the folding principle [1], [11]. ■

B. Weak stationary solutions

The previous section showed that for values of μ_u, μ_v such that $\mu_v < \mu_u^2$ (12) has only weak solutions.

These solutions are constructed piecewise using the auxiliary problem for each branch of $U = h_i(V)$. Then $U \in L^\infty(\Omega)$ and V is continuous on Ω.

Start on the y-axis at $x = 0$ and begin tracing along any admissible trajectories defined by

- $(y, z) : z = \pm\sqrt{2\mathcal{E} - \mathcal{U}_0(y)}$,
- $(y, z) : z = \pm\sqrt{2\mathcal{E} - \mathcal{U}_1(y)}$, or
- $(y, z) : z = \pm\sqrt{2\mathcal{E} - \mathcal{U}_2(y)}$.

Here $\mathcal{U}_0(y) = -\frac{\mu_v}{d}y^2$ is the potential energy associated with the problem (17). The potential energies $\mathcal{U}_{1,2}$ are represented in closed form (up to a constant) by

$$\begin{aligned} \mathcal{U}_1(y) &= \frac{1}{d\kappa}\log y + \frac{1}{2d\kappa}\sqrt{1 - 4\kappa\mu_u^2 y^2} - \frac{\mu_v}{2d}y^2 \\ &\quad - \frac{1}{2\kappa}\log\left(\frac{1}{2\mu_u\sqrt{k}} + \sqrt{\frac{1}{4\mu_u^2\kappa} - y^2}\right), \\ \mathcal{U}_2(y) &= -\frac{1}{2d\kappa}\sqrt{1 - 4\kappa\mu_u^2 y^2} - \frac{\mu_v}{2d}y^2 \\ &\quad + \frac{1}{2d\kappa}\log\left(\frac{1}{2\mu_u\sqrt{k}} + \sqrt{\frac{1}{4\mu_u^2\kappa} - y^2}\right). \end{aligned}$$

Continue tracing until returning to the y-axis at $x = 1$ (Fig. 4). In this way we obtain a partitioning of the domain Ω into subintervals I_i. On each I_i the solution V is given by the y-coordinate of the admissible solution trajectories in the (y, z)-space.

Of course, under this construction U may be discontinuous in Ω as on each subinterval I_i U is given by a different branch h_i. However, note that $V := y$ belongs to $C^1(\Omega)$ because by construction $z = y'$ is continuous at the intersection of such trajectories.

On Fig. 2 and Fig. 3 are plotted several solution curves corresponding to an energy level $\mathcal{E}$ for the different cases of potential energies $\mathcal{U}_i$. Note, for example, that a weak solution can be traced by following a trajectory given by $\mathcal{U}_0$,$\mathcal{U}_2$ (in that order) when $\mu_v < \mu_u^2$ or $\mathcal{U}_2$,$\mathcal{U}_1$ (in that order) when $\mu_v > 2\mu_u^2$.

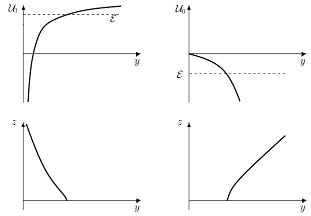

Fig. 2. Solution curves in (y, z)-space associated to potential energies $\mathcal{U}_1$ and $\mathcal{U}_0$.

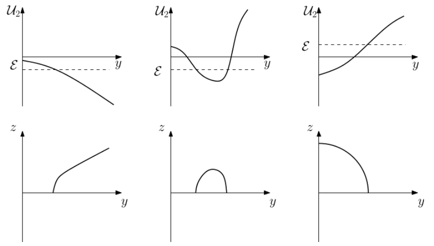

Fig. 3. Solution curves in (y, z)-space associated to potential energies $\mathcal{U}_2$ for the different cases (*from left to right*) $\mu_v > 2\mu_u^2, \mu_u^2 < \mu_v < 2\mu_u^2, \mu_v < \mu_u^2$.

V. Stability of stationary solutions

For a stationary solution (U, V) we can establish linear stability in the classical sense: for small perturbations $\tilde{u}(t, x) = u(t, x) - U(x), \tilde{v}(t, x) = v(t, x) - V(x)$, the behaviour of the solutions u, v of (3) is governed locally by the linear approximation. By setting an *Ansatz*

$$\tilde{u}(t, x) = \mathbf{u}(x)e^{\lambda t},$$
$$\tilde{v}(t, x) = \mathbf{v}(x)e^{\lambda t},$$

for local stability we have to consider the sign of $\mathrm{Re}\lambda$. λ is an eigenvalue of the linearised differential operator $\mathcal{L} = \mathrm{diag}(0, d\Delta) + J$, where

$$J = \begin{pmatrix} \frac{2U}{V(1+\kappa U^2)^2} - \mu_u & -\frac{U^2}{V^2(1+\kappa U^2)} \\ \frac{2U}{V(1+\kappa U^2)^2} & -\frac{U^2}{V^2(1+\kappa U^2)} - \mu_v \end{pmatrix}.$$

If every eigenvalue λ of $\mathcal{L}$ has negative real part, the stationary solution (U, V) is locally stable. Note that the spectrum of $\mathcal{L}$ need not be discrete.

In the one-dimensional case we formulate results on the stability of spatially nonuniform stationary solutions of the system. Easy linear stability analysis leads to

Proposition 3. *Let $\mu_u^2 < \mu_v < 2\mu_u^2$, the constant solution $(\hat{u}, \hat{v})$ is locally asymptotically unstable. When $\mu_v > 2\mu_u^2$, the constant solution $(\hat{u}, \hat{v})$ is locally asymptotically stable.*

Proof: A linearisation of the right-hand side of (12) at $(\hat{u}, \hat{v})$ gives the following:

$$\mathcal{L} = \mathrm{diag}(0, d\Delta) + \begin{pmatrix} \frac{2\mu_u^3}{\mu_v} - \mu_u & -\mu_v \\ \frac{2\mu_u^3}{\mu_v} & -2\mu_v \end{pmatrix}.$$

Note that the saturation parameter κ does not influence the stability of the constant solution. $\mathcal{L}$ has constant coefficients and its spectrum can be computed by matrix eigenvalue analysis. For values $\mu_v > 2\mu_u^2$, the spectrum of $\mathcal{L}$ lies entirely in the left half-plane. Hence, the constant solution $(\hat{u}, \hat{v})$ is locally asymptotically stable.

For values $\mu_v < 2\mu_u^2$, $\mathcal{L}$ has positive eigenvalues. This proves the claim. ■

The following result establishes the local instability of spatially heterogeneous regular solutions.

Theorem 2. *Let $\mu_u^2 < \mu_v < 2\mu_u^2$. Any spatially heterogeneous regular solution (U, V) of* (12) *on the interval Ω is unstable.*

Proof: For the proof we use a result on the spectrum of $\mathcal{L}$ established in [6, Corollary 2.7],

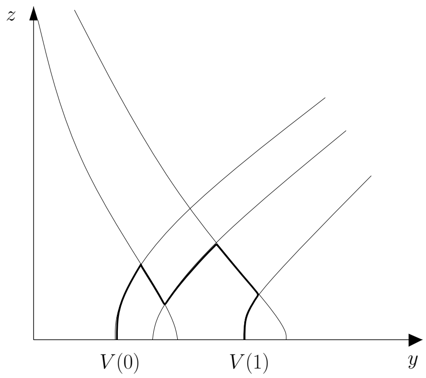

Fig. 4. A weak solution on Ω following different energy trajectories.

namely the effect of autocatalysis in the nonlinearity f which implies that the spectrum of $\mathcal{L}$ comprises eigenvalues with positive real part. This fact implies linear instability of the stationary solution (U, V). Note that $f(0, V) = 0$ for all $V \in \mathbb{R}$. Let (U, V) be a regular solution of (12). Then due to the energy method construction, $U = h_2(V) > 0$ is continuous on I, and so is

$$f_u(U, V) = \frac{2U}{V(1 + \kappa U^2)^2} - \mu_u.$$

Furthermore, using the formula (18) we see that

$$U = h_2(V) < \kappa^{-1/2}.$$

We estimate, first, using the relation $f(U, V) = 0$ on I,

$$f_u(U, V) = \frac{2\mu_u}{1 + \kappa U^2} - \mu_u < \mu_u$$

Second,

$$\begin{aligned} f_u(U, V) &= \frac{2\mu_u}{1 + \kappa U^2} - \mu_u \\ &> \frac{2\mu_u}{1 + 1} - \mu_u = 0. \end{aligned}$$

The result of [6, Corollary 2.7] implies that the linearised differential operator $\mathcal{L}$ has eigenvalues with positive real part. Hence, (U, V) is an unstable solution. ■

The result of Theorem 2 is also a consequence of the results in [7] that establish instability of heterogeneous solutions for semilinear diffusion equations. However, in this particular case instability of the regular solution can be established by direct computation.

Theorem 3. *Let $\mu_v < 2\mu_u^2$. Any weak solution (U, V) of* (12) *such that $U < \kappa^{-1/2}$ on Ω is unstable.*

The proof is identical to that of Theorem 2.

Theorem 4. *Let $n \in \mathbb{N}, 0 \leq x_1 < x_2 < \ldots < x_n \leq 1$. The pair (U, V) defined by $U(x) > 0, x = x_j, U(x) = 0, x \neq x_j$, and V a solution to* (17) *with Robin boundary conditions, is a solution to* (13)*. Moreover, any such (U, V) is locally asymptotically stable.*

Proof: For any (U, V) of the given type, the linearised operator $\mathcal{L}$ looks almost everywhere like

$$\mathcal{L} = \operatorname{diag}(0, d\Delta) + \begin{pmatrix} -\mu_u & 0 \\ 0 & -\mu_v \end{pmatrix}.$$

Therefore, the spectrum of $\mathcal{L}$ is bounded away from 0 in the left halfplane almost everywhere. Hence, any stationary solution (U, V) is locally asymptotically stable. ■

VI. Discussion

Theorem 3 and Theorem 4 imply that the locally stable weak solutions must necessarily exhibit large jump discontinuities of amplitude at least $\kappa^{-1/2}$. In the literature such solutions are said to exhibit *striking patchiness* [8], [9] or *transition layers* [13].

The results show that all spatially heterogeneous, strictly positive, regular solutions of (12) over a one-dimensional domain Ω are unstable. This is in contrast to the singularly perturbed system (3) where stable spike solutions exist [15]. The asymptotically stable solutions, which are different from the homogeneous steady state $(\hat{u}, \hat{v})$ (28) are discontinuous solutions that exhibit large transition layers. Fig. 5 shows such a pattern.

In contrast to the results in [5], [6], the problem (12) does not fulfil the autocatalysis condition in [6, Corollary 2.7], whose estimates do not hold for all bounded weak solutions of (12). That explains the existence of stable weak solutions with large transition layers.

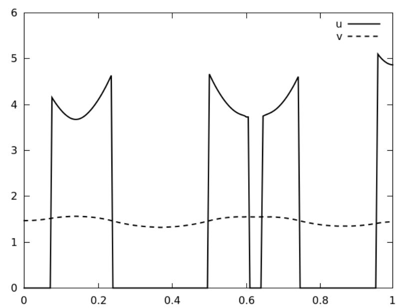

Fig. 5. A discontinuous pattern with large amplitude. Parameter values are $\mu_u = 1, \mu_v = 1.2, \kappa = 0.1, d = 0.1$.

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