A The Perturbative Approach on Continuous Attractor Neural Networks

A.1 Lowest Order Perturbative Analysis on Static Bump Solutions

Without loss of generality, we let $z = 0$. Substituting Eqs. (5) and (6) into Eq. (1), we get

$$\tau_s e^{-\frac{x^2}{4a^2}} \frac{du_0}{dt} = \frac{\rho J_0 u_0^2}{\sqrt{2}\left(1+\sqrt{2\pi}ak\rho u_0^2\right)} \left[e^{-\frac{x^2}{4a^2}} - p_0\sqrt{\frac{2}{3}}e^{-\frac{x^2}{3a^2}}\right] - u_0 e^{-\frac{x^2}{4a^2}}. \tag{A.1}$$

Using the projection in Eq. (7), we can approximate $\exp\left(-x^2/3a^2\right) \approx \sqrt{6/7}\exp\left(-x^2/4a^2\right)$. This reduces the equation to

$$\tau_s \frac{du_0}{dt} = \frac{\rho J_0 u_0^2}{\sqrt{2}\left(1+\sqrt{2\pi}ak\rho u_0^2\right)} \left[1 - \sqrt{\frac{4}{7}}p_0\right]. \tag{A.2}$$

Introducing the rescaled variables $\overline{u}$ and $\overline{k}$, we arrive at Eq. (8).

Similarly, substituting Eqs. (5) and (6) into Eq. (2), we get

$$\tau_d e^{-\frac{x^2}{2a^2}} \frac{dp_0}{dt} = -p_0 e^{-\frac{x^2}{2a^2}} + \frac{\tau_d \beta u_0^2}{1+\sqrt{2\pi}ak\rho u_0^2}\left(e^{-\frac{x^2}{2a^2}} - p_0 e^{-\frac{x^2}{a^2}}\right). \tag{A.3}$$

Making use of the projection $\exp\left(-x^2/a^2\right) \approx \sqrt{2/3}\exp\left(-x^2/2a^2\right)$, the equation simplifies to

$$\tau_d \frac{dp_0}{dt} = -p_0 + \frac{\tau_d \beta u_0^2}{1+\sqrt{2\pi}ak\rho u_0^2}\left(1 - \sqrt{\frac{2}{3}}p_0\right). \tag{A.4}$$

Introducing the rescaled variables $\overline{u}$, $\overline{k}$, and β, we arrive at Eq. (9).

The steady state solution is obtained by setting the time derivatives in Eqs. (8) and (9) to zero, yielding

$$\overline{u} = \frac{1}{\sqrt{2}}\frac{\overline{u}^2}{B}\left(1 - \sqrt{\frac{4}{7}}p_0\right), \tag{A.5}$$

$$p_0 = \frac{\overline{\beta}\overline{u}^2}{B}\left(1 - \sqrt{\frac{2}{3}}p_0\right), \tag{A.6}$$

where $B \equiv 1 + \overline{k}\overline{u}^2/8$ is the divisive inhibition.

Dividing Eq. (A.5) by (A.6), we eliminate B,

$$\overline{u} = \frac{1}{\sqrt{2}\,\overline{\beta}}\left(\frac{1-\sqrt{4/7}p_0}{1-\sqrt{2/3}p_0}\right)p_0. \tag{A.7}$$

We can eliminate $\overline{u}$ from Eq. (A.6). This gives rise to an equation for p_0

$$\frac{1}{2\overline{\beta}}\left(1-\sqrt{\frac{4}{7}}p_0\right)^2\left[1-\left(\sqrt{\frac{2}{3}}+\frac{\overline{k}}{8\overline{\beta}}\right)p_0\right]p_0 - \left(1-\sqrt{\frac{2}{3}}p_0\right)^2 = 0. \tag{A.8}$$

Rearranging the terms, we have

$$\overline{k} = \frac{8}{p_0}\left(1-\sqrt{\frac{2}{3}}p_0\right)\overline{\beta} - \frac{16}{p_0^2}\left(\frac{1-\sqrt{2/3}p_0}{1-\sqrt{4/7}p_0}\right)^2\overline{\beta}^2. \tag{A.9}$$

Therefore, for each fixed p_0, we can plot a parabolic curve in the phase diagram $\overline{\beta}$ versus $\overline{k}$. As shown in figure A.1, the dashed lines are parabolas for different values of p_0. The family of all parabolas map out the region of existence of the steady state solutions.

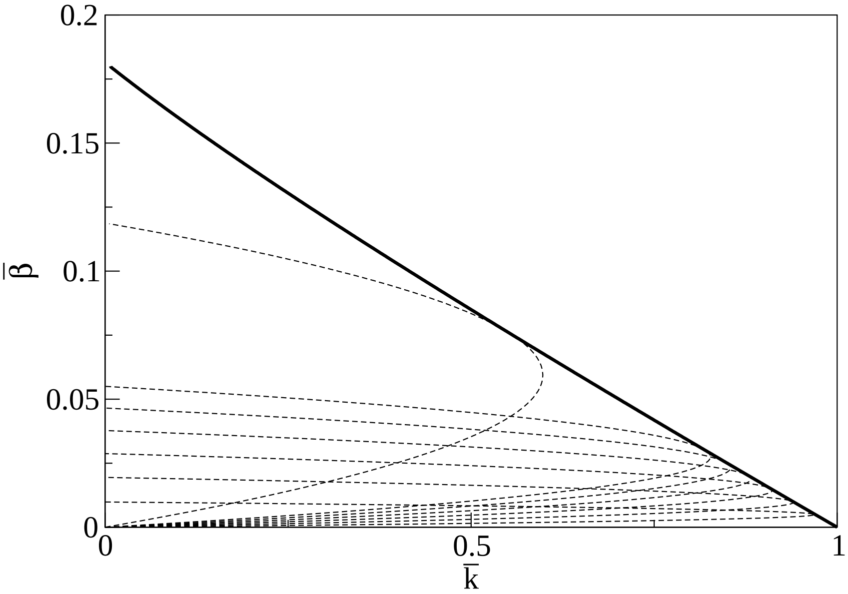

Figure A.1: The region of existence of static bump solutions. Solid line: the boundary of existence of static bump solutions. Dashed lines: the parabolic curves for different constant values of p_0.

A.2 Stability of the Static Bump

To analyze the stability of the static bump, we consider the time evolution of $\epsilon = \overline{u}(t) - \overline{u}^*$ and $\delta = p_0(t) - p_0^*$, where $(\overline{u}^*, p_0^*)$ is the fixed point solution of Eqs. (A.5) and (A.6). Then, we have

$$\frac{d}{dt}\begin{pmatrix} \epsilon \\ \delta \end{pmatrix} = \begin{pmatrix} -\frac{1}{\tau_s}\left[1 - \frac{\sqrt{2}\overline{u}}{B^2}\left(1 - \sqrt{\frac{4}{7}}p_0\right)\right] & -\frac{\overline{u}^2}{\tau_s B}\sqrt{\frac{2}{3}} \\ \frac{2\overline{\beta}\overline{u}}{\tau_d B^2}\left(1 - \sqrt{\frac{2}{3}}p_0\right) & -\frac{1}{\tau_d}\left(1 + \frac{\overline{\beta}\overline{u}^2}{B}\sqrt{\frac{2}{3}}\right) \end{pmatrix}\begin{pmatrix} \epsilon \\ \delta \end{pmatrix}. \tag{A.10}$$

The stability condition is determined by the eigenvalues of the stability matrix, $\left(T \pm \sqrt{T^2 - 4D}\right)/2$, where D and T are the determinant and the trace of the matrix respectively. The determinant is given by

$$\begin{aligned} D &= \frac{1}{\tau_s \tau_d}\left\{\left[1 - \frac{\sqrt{2}\overline{u}}{B^2}\left(1 - \sqrt{\frac{4}{7}}p_0\right)\right]\left(1 + \frac{\overline{\beta}\overline{u}^2}{B}\sqrt{\frac{2}{3}}\right)\right. \\ &\quad \left. + \sqrt{\frac{2}{7}}\frac{2\overline{\beta}\overline{u}^3}{B^3}\left(1 - \sqrt{\frac{2}{3}}p_0\right)\right\}. \end{aligned} \tag{A.11}$$

Using Eqs. (A.5) and (A.6), the determinant can be simplified to

$$D = \frac{1}{\tau_s \tau_d B}\left(\frac{2\sqrt{4/7}p_0}{1 - \sqrt{4/7}p_0} - \frac{2 - B}{1 - \sqrt{2/3}p_0}\right). \tag{A.12}$$

The trace is given by

$$T = \frac{1}{\tau_s}\left[\frac{2}{B} - \frac{\tau_s}{\tau_d\left(1 - \sqrt{2/3}p_0\right)} - 1\right]. \tag{A.13}$$

The static bump is stable only if

$$\text{Re}\left[\left(T \pm \sqrt{T^2 - 4D}\right)/2\right] < 0. \tag{A.14}$$

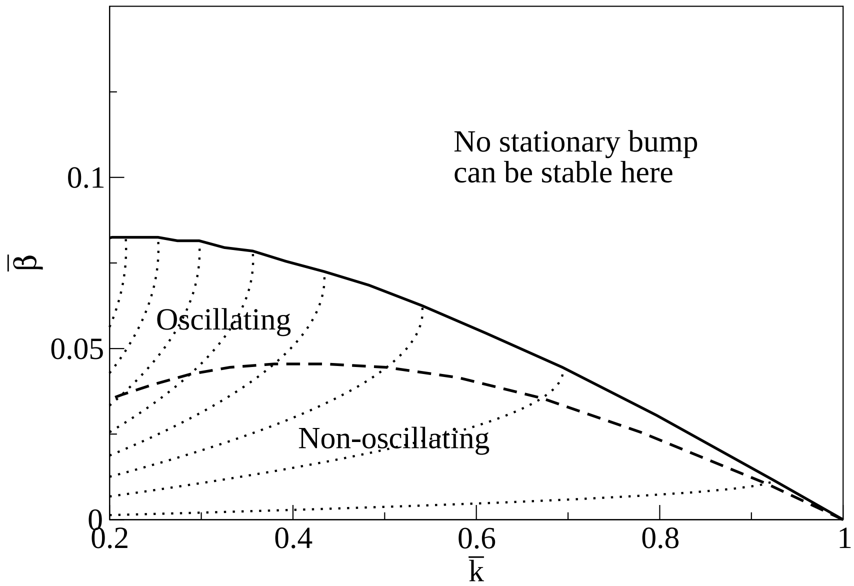

Figure A.2: The region of stable solutions of the static bump for $\tau_d/\tau_s = 50$. Solid line: the boundary of stable static bumps. Dash line: the boundary separating the oscillating and non-oscillating convergence. Dotted lines: the curves for different constant values of p_0.

The eigenvalues are real and negative when $T^2 \geq 4D$. This corresponds to non-oscillating solutions. After some algebra, we obtain the boundary $T^2 = 4D$ given by

$$\left[\overline{\beta} - \frac{p_0\left(1-\sqrt{4/7}p_0\right)^2}{4\left(1-\sqrt{2/3}p_0\right)} + \frac{\tau_s}{\tau_d}\frac{p_0\left(1-\sqrt{4/7}p_0\right)^2}{4\left(1-\sqrt{2/3}p_0\right)^2}\right]^2 = \frac{\tau_s}{\tau_d}\sqrt{\frac{4}{7}}\overline{\beta}\frac{p_0^2\left(1-\sqrt{4/7}p_0\right)}{1-\sqrt{2/3}p_0}. \quad \text{(A.15)}$$

This boundary is shown in figure A.2. Below this boundary, the stability condition can be obtained as

$$\overline{\beta} \leq \frac{p_0\left(1-\sqrt{4/7}p_0\right)^3}{4\left(1-\sqrt{2/3}p_0\right)\left(1-2\sqrt{4/7}p_0+\sqrt{8/21}p_0^2\right)}. \quad \text{(A.16)}$$

This upper bound is identical to the existence condition (A.9), which is above the boundary of non-oscillating solutions. This implies that all non-oscillating solutions are stable.

Above the boundary (A.15), the convergence to the steady state becomes oscillating, and the stability condition reduces to $T \leq 0$, yielding Eq. (10). This condition narrows the region of static bump considerably, as shown in figure A.2.

A.3 Lowest Order Perturbative Analysis of Moving Bump Solution

We substitute Eqs. (11) can (12) into Eqs. (1) and (2). Eq. (1) becomes an equation containing $\exp\left[-(x-vt)^2/4a^2\right]$ and $\exp\left[-(x-vt)^2/4a^2\right](x-vt)/a$ after we have made use of the projections

$$e^{-\frac{(x-vt)^2}{3a^2}} \approx \sqrt{\frac{6}{7}}e^{-\frac{(x-vt)^2}{4a^2}}, \quad \text{(A.17)}$$

$$e^{-\frac{(x-vt)^2}{3a^2}}\left(\frac{x-vt}{a}\right) \approx \left(\sqrt{\frac{6}{7}}\right)^3 e^{-\frac{(x-vt)^2}{4a^2}}\left(\frac{x-vt}{a}\right). \quad \text{(A.18)}$$

Equating the coefficients of $\exp\left[-(x-vt)^2/4a^2\right]$ and $\exp\left[-(x-vt)^2/4a^2\right](x-vt)/a$, and rescaling the variables, we arrive at

$$\begin{aligned} \tau_s \frac{d\overline{u}}{dt} &= \frac{\overline{u}^2}{\sqrt{2}B}\left(1-\sqrt{\frac{4}{7}}p_0\right)-\overline{u}, && \text{(A.19)} \\ \frac{v\tau_0}{2a} &= \frac{\overline{u}}{B}\left(\frac{2}{7}\right)^{\frac{3}{2}} p_1. && \text{(A.20)} \end{aligned}$$

Similarly, making use of the projections

$$\begin{aligned} e^{-\frac{(x-vt)^2}{a^2}} &\approx \sqrt{\frac{2}{3}} e^{-\frac{(x-vt)^2}{2a^2}}, && \text{(A.21)} \\ e^{-\frac{(x-vt)^2}{a^2}}\left(\frac{x-vt}{a}\right) &\approx \left(\sqrt{\frac{2}{3}}\right)^3 e^{-\frac{(x-vt)^2}{2a^2}}\left(\frac{x-vt}{a}\right), && \text{(A.22)} \end{aligned}$$

we find that Eq. (2) gives rise to

$$\begin{aligned} -\tau_d\frac{dp_0}{dt}-\frac{v\tau_d}{2a}p_1 &= p_0-\frac{\overline{\beta}\overline{u}^2}{B}\left(1-\sqrt{\frac{2}{3}}p_0\right), && \text{(A.23)} \\ \tau_d\frac{dp_1}{dt}-\frac{v\tau_d}{a}p_0 &= -\left[1+\frac{\overline{\beta}\overline{u}^2}{B}\left(\frac{2}{3}\right)^{\frac{3}{2}}\right]p_1. && \text{(A.24)} \end{aligned}$$

After some algebra, the solution can be parametrized by $\xi \equiv \overline{\beta}\overline{u}^2/B$,

$$\begin{aligned} p_0 &= \frac{\frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]}{\left(\frac{4}{7}\right)^{\frac{3}{2}}+\sqrt{\frac{4}{7}}\frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]}, && \text{(A.25)} \\ \frac{\overline{u}}{B} &= \sqrt{2}+\frac{7}{\sqrt{8}}\frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right], && \text{(A.26)} \\ \frac{v\tau_s}{a} &= \sqrt{2\frac{\tau_s}{\tau_d}\left\{\left(\frac{4}{7}\right)^{\frac{3}{2}}\xi-\frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]\left[1+\left(\sqrt{\frac{2}{3}}-\sqrt{\frac{4}{7}}\right)\xi\right]\right\}}, && \text{(A.27)} \\ p_1 &= \sqrt{2\frac{\tau_s}{\tau_d}}\frac{\sqrt{\left(\frac{4}{7}\right)^{\frac{3}{2}}\xi-\frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]\left[1+\left(\sqrt{\frac{2}{3}}-\sqrt{\frac{4}{7}}\right)\xi\right]}}{\left(\frac{4}{7}\right)^{\frac{3}{2}}+\sqrt{\frac{4}{7}}\frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]}. && \text{(A.28)} \end{aligned}$$

Real solution exists only if Eq. (13) is satisfied.

The solution enables us to plot the contours of constant ξ in the space of $\overline{k}$ and $\overline{\beta}$. Using the definition of ξ, we can write

$$\overline{k} = \frac{8}{\xi}\overline{\beta}-\frac{8}{\xi^2}\left(\frac{\overline{u}}{B}\right)^2\overline{\beta}^2, \tag{A.29}$$

where the quandratic coefficient can be readily obtained from Eq. (A.26). Figure A.3 shows the family of these cures with constant ξ. The lowest curve saturates the inequality in Eq. (13), and yields the boundary between the static and metastatic or moving regions in Fig. 3.

A.4 Stability of the Moving Bump

To study the stability of the moving bump, we consider fluctuations arround the moving bump solution. Suppose

$$\begin{aligned} u(x,t) &= (u_0^*+u_1)\, e^{-\frac{(x-vt-s_1)^2}{4a^2}}, && \text{(A.30)} \\ p(x,t) &= 1-(p_0^*+\epsilon_0)\, e^{-\frac{(x-vt-s_1)^2}{2a^2}}+(p_1^*+\epsilon_1)\left(\frac{x-vt-s_1}{a}\right)e^{-\frac{(x-vt-s_1)^2}{2a^2}}. && \text{(A.31)} \end{aligned}$$

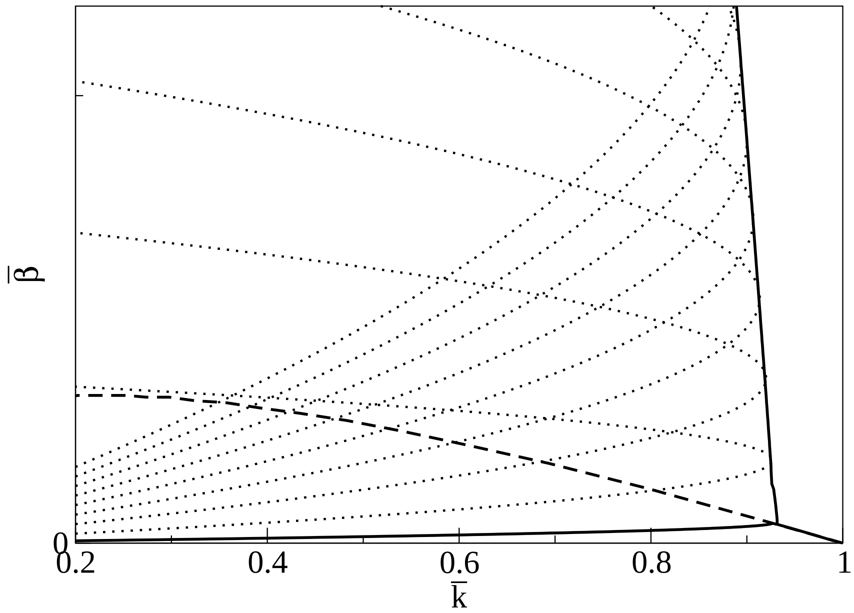

Figure A.3: The family of curves with constant values of ξ at $\tau_d/\tau_s = 50$. Dashed line: phase boundary of the static bump.

These expressions are substituted into the dynamical equations. The result is

$$\tau_s \frac{d\overline{u}_1}{dt} = \frac{\sqrt{2}\overline{u}}{B^2}\left(1-\sqrt{\frac{4}{7}}p_0\right)\overline{u}_1 - \frac{\overline{u}^2}{B}\sqrt{\frac{2}{7}}\epsilon_0 - \overline{u}_1, \tag{A.32}$$

$$\frac{\tau_s}{a}\frac{ds_1}{dt} = -\frac{v\tau_s}{a\overline{u}}\overline{u}_1 + \frac{4p_1}{B^2}\left(\frac{2}{7}\right)^{\frac{3}{2}}\overline{u}_1 + \frac{2\overline{u}}{B}\left(\frac{2}{7}\right)^{\frac{3}{2}}\epsilon_1, \tag{A.33}$$

$$\tau_d \frac{d\epsilon_0}{dt} = \frac{2\overline{\beta}\overline{u}}{B^2}\left(1-\sqrt{\frac{2}{3}}p_0\right)\overline{u}_1 - \left(1+\sqrt{\frac{2}{3}}\xi\right)\epsilon_0 - \frac{v\tau_d}{2a}\epsilon_1 - \frac{\tau_d p_1}{2a}\frac{ds_1}{dt}, \tag{A.34}$$

$$\tau_d \frac{d\epsilon_1}{dt} = -\frac{2\overline{\beta}\overline{u}p_1}{B^2}\left(\frac{2}{3}\right)^{\frac{3}{2}}\overline{u}_1 + \frac{v\tau_d}{a}\epsilon_0 - \left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]\epsilon_1 + \frac{\tau_d p_0}{a}\frac{ds_1}{dt}. \tag{A.35}$$

We first revisit the stability of the static bump. By setting v and p_1 to 0, and considering the asymmetric fluctuations s_1 and ϵ_1 in Eqs. (A.33) and (A.35), we have

$$\frac{\tau_s}{a}\frac{ds_1}{dt} = \frac{2\overline{u}}{B}\left(\frac{2}{7}\right)^{\frac{3}{2}}\epsilon_1, \tag{A.36}$$

$$\tau_d \frac{ds_1}{dt} = -\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]\epsilon_1 + \frac{\tau_d p_0}{a}\frac{d\epsilon_1}{dt}. \tag{A.37}$$

Eliminating s_1,

$$\tau_s \frac{d\epsilon_1}{dt} = \left\{\frac{2\overline{u}}{B}\left(\frac{2}{7}\right)^{\frac{3}{2}}p_0 - \frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right]\right\}\epsilon_1. \tag{A.38}$$

Hence the static bump remains stable when

$$\frac{2\overline{u}}{B}\left(\frac{2}{7}\right)^{\frac{3}{2}}p_0 - \frac{\tau_s}{\tau_d}\left[1+\left(\frac{2}{3}\right)^{\frac{3}{2}}\xi\right] \le 0. \tag{A.39}$$

Using Eqs. (A.25) and (A.26) to eliminate p_0 and $\overline{u}/B$, we recover the condition in Eq. (13). This shows that the bump becomes a moving one as soon as the static bump becomes unstable against asymmetric fluctuations, as described in the main text.

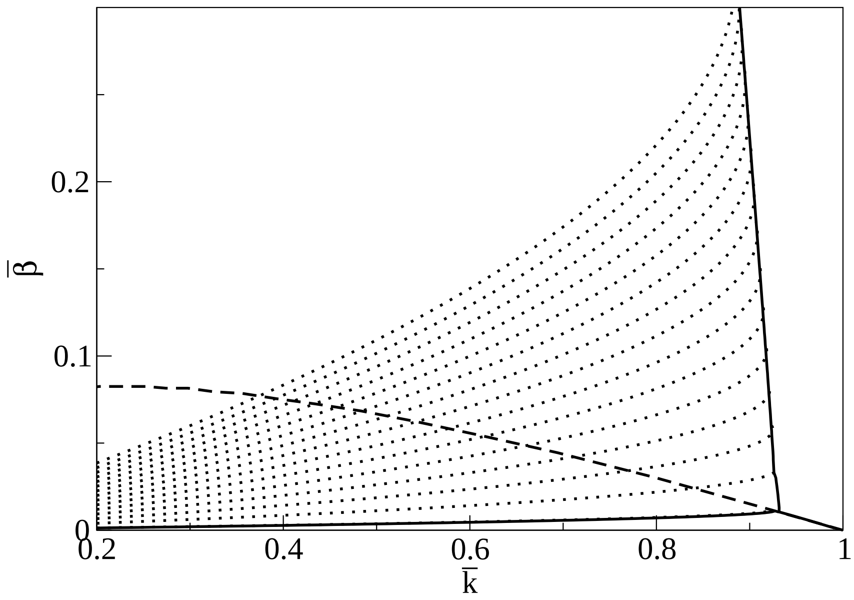

Figure A.4: The stable branches of the family of the curves with contant values of ξ at $\tau_d/\tau_s = 50$. The dashed line is the phase boundary of the static bump.

Now we consider the stability of the moving bump. Eliminating ds_1/dt and summarizing the equations in matrix form,

$$\tau_s \frac{d}{dt} \begin{pmatrix} \overline{u}_1 \\ \epsilon_0 \\ \epsilon_1 \end{pmatrix} = \begin{pmatrix} \frac{2}{B} - 1 & -\frac{\overline{u}^2}{B}\sqrt{\frac{2}{7}} & 0 \\ \frac{2p_0\tau_s}{B\overline{u}\tau_d} + \frac{v\tau_s p_1}{2a\overline{u}} & \frac{v\tau_s p_1}{2ap_0} - \frac{\overline{\beta}\overline{u}^2\tau_s}{Bp_0\tau_d} & -\frac{v\tau_s}{a} \\ \frac{2p_1\tau_s}{B\overline{u}\tau_d} - \frac{v\tau_s p_0}{a\overline{u}} & \frac{v\tau_s}{a} & 0 \end{pmatrix} \begin{pmatrix} \overline{u}_1 \\ \epsilon_0 \\ \epsilon_1 \end{pmatrix}. \tag{A.40}$$

For the moving bump to be stable, the real parts of the eigenvalues of the stability matrix should be non-positive. The stable branches of the family of curves are shown in figure A.4. The results show that the boundary of stability of the moving bumps is almost indistinguishable from te envelope of the family of curves. Higher order perturbations produce phase boundaries that have better agreement with simulation results, as shown in Fig. 3. The derivation will be reported elsewhere.