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Mathematical results of an adaptive transport network with double edges of Plasmodium

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1 Introduction

The plasmodium of true slime mold *Physarum polycephalum* is a large amoeba-like organism. Its body contains a tube network by means of which nutrients and signals circulate through the body in effective manner.

When food sources were presented to a starved plasmodium that was spread over the entire agar surface, it concentrated at every food source, respectively. Almost the entire plasmodium accumulated at the food sources and covered each of them in order to absorb nutrients [3]. Only a few tube remained connecting the quasi-separated components of the plasmodium through the short path. Nakagaki *et al.* showed that this simple organism had the ability to find the minimum-length solution of a maze [4, 5]. The connecting tube traces the shortest path even in a complicated maze. Hydrodynamics theory implies that thick short tubes are in principle the most effective for transportation. And this adaptation process of the tube network is based on an underlying physiological mechanism, that is, a tube becomes thicker as a flux in the tube is larger. This insight might be based on the research on the rhythmic oscillation of *Physarum polycephalum* [6]. Tero *et al.* made a mathematical model in consideration of the qualitative mechanisms clarified by experiments [7]. According to numerical simulation results, the minimum-length solution of a maze can be obtained as an asymptotic steady state of the ODEs model [7, 8].

In 2006, we have proved that the equiribrium point corresponding to the shortest path in the system is globally asymptotically stable in two kind of simpler networks, namely, the ring-shaped network and the Wheatstone bridge-shaped network [1]. Especially in the Wheatstone bridge-shaped case, we have proved it without constructing any Lyapunov function. Therefore this is also a kind of interesting work from a mathematically technical point of view.

In this note, we consider about the problem in which network has double edges. In some cases of nonlinear terms, it is well-known that the shortest path does not survive, if the initial condition is taken adequately. This fact has been proved mathematically rigorously in the ring-shaped network also in [1]. We first prove

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it in triangle shaped network in this note, too. But our real interest of this note is in the case of network with double edges. In some actual chemical experiment, if there are double edges, they often see the transfering point of stability changing, namely, a longer path survives longer time than in single edge case. We would like to investigate such a kind of case mathematically. In this note, we report some mathematically regorous results gotten by the authors. About disscussions from the more applied-mathematical point of view, please see the forthcoming paper [2].

2 Triangle-shaped network without double edge

We consider the triangle-shaped network with three nodes N_1, N_2, N_3 and three edges M_{12}, M_{13}, M_{32}. To simplify the notation, we introduce new variables

$$a = \frac{D_{12}}{L_{12}}, b = \frac{D_{13}}{L_{13}}, c = \frac{D_{32}}{L_{32}}. \tag{2.1}$$

Then, the adaptation equation with adaptation function $f(\xi) = \xi^\mu$ becomes

$$\begin{cases} \dot{a} = \dfrac{1}{L_{12}}\left(I_0 \dfrac{ab+ac}{ab+bc+ca}\right)^\mu - a, \\ \dot{b} = \dfrac{1}{L_{13}}\left(I_0 \dfrac{bc}{ab+bc+ca}\right)^\mu - b, \\ \dot{c} = \dfrac{1}{L_{32}}\left(I_0 \dfrac{bc}{ab+bc+ca}\right)^\mu - c. \end{cases} \tag{2.2}$$

In this section, we treat the case of $\mu > 1$. We prove that there exist two heteroclinic orbits.

Notice that $Q_{13} = Q_{32}$ from the conservation law of flux. So we obtain

$$\dot{D}_{13} - \dot{D}_{32} = -(D_{13} - D_{32}). \tag{2.3}$$

Hence, the set

$$\{(a,b,c) \in \mathbf{R}^3_+ | L_{13} b = L_{32} c\} \tag{2.4}$$

is exponentially attracting and invariant. We restrict the system on this subset. The adaptation equation can be rewritten as

$$\begin{cases} \dot{a} = \dfrac{1}{L_{12}}(1+s^{-1})^\mu \left(\dfrac{I_0 a}{(1+s^{-1})a + s^{-1}b}\right)^\mu - a, \\ \dot{b} = \dfrac{1}{L_{13}} s^{-\mu} \left(\dfrac{I_0 b}{(1+s^{-1})a + s^{-1}b}\right)^\mu - b, \end{cases} \tag{2.5}$$

where $s = L_{13}/L_{32}$.

Notice that the rectangular domain

$$\left\{(a,b) \in \mathbf{R}^2_+ | a \in \left[0, \frac{I_0^\mu}{L_{12}}\right], b \in \left[0, \frac{I_0^\mu}{L_{13}}\right]\right\} \tag{2.6}$$

is attracting and invariant because $-a \le \dot{a} \le I_0^\mu / L_{12} - a$ and $-b \le \dot{b} \le I_0^\mu / L_{13} - b$ hold.

Three equilibrium points are written as

$$A_1 = \left(\frac{I_0^\mu}{L_{12}}, 0\right), A_2 = \left(0, \frac{I_0^\mu}{L_{13}}\right),$$
$$C = \left(\frac{T-1}{L_{13}+L_{32}}\left(\frac{I_0}{T}\right)^\mu, \frac{1}{L_{13}}\left(\frac{I_0}{T}\right)^\mu\right),$$

where

$$T = 1 + (L_{13} + L_{32}) \left[\frac{(L_{13} + L_{32})^{\mu}}{L_{12}} \right]^{\frac{1}{1-\mu}}.$$

Under the assumption of $\mu > 1$, the Jacobi matrices for these equilibrium points are calculated as

$$J(A_1) = \begin{pmatrix} -1 & \frac{-\mu}{1+s^{-1}} \\ 0 & -1 \end{pmatrix}, J(A_2) = \begin{pmatrix} -1 & 0 \\ -\mu s & -1 \end{pmatrix},$$

$$J(C) = \begin{pmatrix} \frac{\mu s}{r+s+rs} - 1 & \frac{-\mu r}{r+s+rs} \\ \frac{-\mu s(s+1)}{r+s+rs} & \frac{\mu r(s+1)}{r+s+rs} - 1 \end{pmatrix},$$

where

$$r = L_{32} \left(\frac{(L_{13} + L_{32})^{\mu}}{L_{12}} \right)^{\frac{1}{1-\mu}}.$$

$J(A_1)$ and $J(A_2)$ have an eigenvalue -1 with multiplicity 2. Hence, A_1 and A_2 are asymptotically stable on phase plane. The eigenvectors of $J(A_1), J(A_2)$ associated with -1 are ${}^t(1,0)$ and ${}^t(0,1)$, respectively. On the other, $J(C)$ has two eigenvalues $(\mu - 1)$ and -1. Hence, C_1 is a saddle point if $\mu > 1$. The following equalities hold:

$$J(C)\begin{pmatrix} rs^{-1} \\ 1 \end{pmatrix} = -\begin{pmatrix} rs^{-1} \\ 1 \end{pmatrix}, \quad J(C)\begin{pmatrix} \frac{-1}{s+1} \\ 1 \end{pmatrix} = (\mu - 1)\begin{pmatrix} \frac{-1}{s+1} \\ 1 \end{pmatrix}. \tag{2.7}$$

Notice that the straight line spaned by the eigenvector associated with the stable eigenvalue of C is invariant. This implication is obtaind by solving $\frac{d}{dt}(b/a) = 0$ with respect to (b/a). On the phase plane, a-axis and b-axis are invariant for the system, and A_1, A_2 are located there. Any solution for the system starting from the first quadrant is attracted to a bounded rectangular domain. And the inner equilibrium point C is saddle. Therefore, any limit cycle cannot exist. Because the unstable manifold of C transeversally intersects with the stable manifold of C, there exists two heteroclinic orbit from C to A_1 and to A_2.

3 Triangle-shaped network with double edge

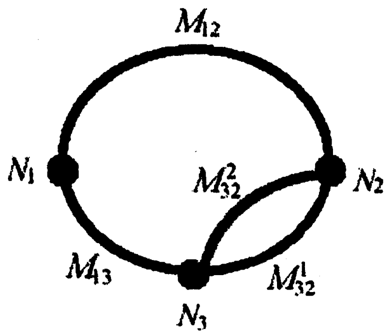

図 3.1: graph

We consider the graph as shown in Figure 3.1. For simplicity, we introduce four variables

$$a = \frac{D_{12}}{L_{12}}, b = \frac{D_{13}}{L_{13}}, c = \frac{D^1_{32}}{L^1_{32}}, d = \frac{D^2_{32}}{L^2_{32}}. \tag{3.1}$$

The network Poisson equation for pressure is

$$\begin{cases} a(p_1 - p_2) + b(p_1 - p_3) = I_0, \\ a(p_1 - p_2) + (c+d)(p_3 - p_2) = I_0, \\ b(p_1 - p_3) = (c+d)(p_3 - p_2). \end{cases} \tag{3.2}$$

By setting $p_2 = 0$, we obtain

$$p_1 = I_0 \frac{b+c+d}{ab+ac+ad+bc+bd}, \quad p_3 = I_0 \frac{b}{ab+ac+ad+bc+bd}. \tag{3.3}$$

For simplicity, let $S = ab+ac+ad+bc+bd$. Then the fluxes along each edge are calculated as

$$\begin{cases} Q_{12} = \frac{I_0}{S}(ab+ac+ad) \\ Q_{13} = \frac{I_0}{S}(bc+bd) \\ Q^1_{32} = \frac{I_0}{S}bc \\ Q^2_{32} = \frac{I_0}{S}bd \end{cases} \tag{3.4}$$

Remark 1. *If $b = c = d = 0$, the numerator and denominator of Q_{ij}'s become zero. But Q_{ij}'s have finite limit value when $b, c, d \to 0$. First, we can calculate Q_{12} as*

$$Q_{12} = \frac{I_0(ab+ac+ad)}{ab+ac+ad+bc+bd} = \frac{I_0 a}{a + (bc+bd)/(b+c+d)}.$$

Notice that

$$0 \le \frac{bc+bd}{b+c+d} \le \frac{b(c+d)}{c+d} = b \to 0 \quad (b, c, d \to 0).$$

Hence we obtain $Q_{12} \to I_0$ as $b, c, d \to 0$. Similarly, we obtain

$$Q_{13} = \frac{I_0}{a(b+c+d)/(bc+bd)+1} \to 0 \quad (b, c, d \to 0).$$

Since $0 \le Q^i_{32} \le Q_{13} (i = 1, 2)$, we also have $Q^i_{32} \to 0$ as $b, c, d \to 0$.

Remark 2. *In a similar way, we obtain $p_1 \to I_0/a$ as $b, c, d \to 0$. However, the limit of p_3 is not always same value. This is caused by the fact that the limit of $(c+d)/b$ changes by how to approach. But it becomes finite when $a > 0$, in fact, $0 \le p_3 \le p_1 \le I_0/a$ holds.*

3.1 $\mu = 1$(*Physarum* solver)

First, we use *Physarum* solver. So we study the adaptation equation

$$\begin{cases} \dot{a} = \frac{I_0}{L_{12}S}(ab+ac+ad) - a \\ \dot{b} = \frac{I_0}{L_{13}S}(bc+bd) - b \\ \dot{c} = \frac{I_0}{L^1_{32}S}bc - c \\ \dot{d} = \frac{I_0}{L^2_{32}S}bd - d \end{cases} \tag{3.5}$$

There are three equilibrium points corresponding to three paths connecting N_1 and N_2. They are

$$A_1 = \left(\frac{I_0}{L_{12}}, 0, 0, 0\right), A_2 = \left(0, \frac{I_0}{L_{13}}, \frac{I_0}{L_{32}^1}\right), A_3 = \left(0, \frac{I_0}{L_{13}}, 0, \frac{I_0}{L_{32}^2}\right). \tag{3.6}$$

In this case, we can restrict the system on two-dimensional rectangle.

Lemma 1. *Let*

$$W = \left\{(a, b, c, d) \in \mathbf{R}_+^4; L_{12}a + L_{13}b = I_0, L_{13}b = L_{32}^1 c + L_{32}^2 d\right\}. \tag{3.7}$$

Then W is an attracting invariant subset of (3.19).

Proof. Let $P_1 = L_{12}a + L_{13}b$ and $P_2 = L_{13}b - L_{32}^1 c - L_{32}^2 d$. From the network Poisson equation, we obtain $\dot{P}_1 = I_0 - P_1$ and $\dot{P}_2 = -P_2$. This implies that W is exponentially attracting and invariant for the flow of (3.19). □

Therefore, we only have to consider the behavior of two variables (c, d). Then we can determine a and b by $L_{13}b = L_{32}^1 c + L_{32}^2 d$ and $L_{12}a + L_{13}b = I_0$. Three equilibrium points are represented by

$$A_1 = (0, 0), A_2 = \left(\frac{I_0}{L_{32}^1}, 0\right), A_3 = \left(0, \frac{I_0}{L_{32}^2}\right) \tag{3.8}$$

Lemma 2. *Let*

$$R = \left\{(c, d) \in \mathbf{R}_+^2; 0 \le c \le \frac{I_0}{L_{32}^1}, 0 \le d \le \frac{I_0}{L_{32}^2}\right\} \tag{3.9}$$

Then R is an attracting invariant subset of (3.19) *restricted on W.*

Proof. Obviously, $-D_{32}^i \le \dot{D}_{32}^i \le I_0 - D_{32}^i (i = 1, 2)$ holds. Therefore, c and d are attracted to R and this rectangle is invariant. □

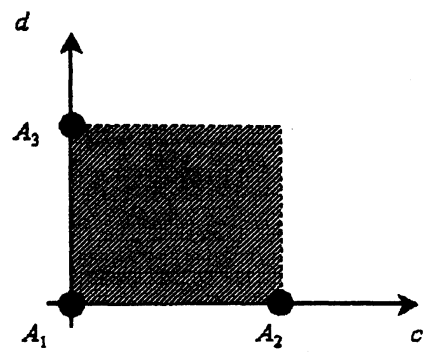

図 3.2: Invariant rectangle

Lemma 3. *1. If the path $M_{13} \to M_{32}^1$ is the shortest, then A_2 is globally asymptotically stable. Othewise, A_2 is unstable.*

2. *If the path $M_{13} \to M_{32}^2$ is the shortest, then A_3 is globally asymptotically stable. Othewise, A_3 is unstable.*

Proof. The path $M_{13} \to M_{32}^1$ is the shortest if

$$L_{13} + L_{32}^1 < L_{12} \quad \text{and} \quad L_{32}^1 < L_{32}^2. \tag{3.10}$$

Eigenvalues of A_2 are calculated as

$$\frac{L_{32}^1 - L_{32}^2}{L_{32}^2}, \quad \frac{L_{32}^1 + L_{13} - L_{12}}{L_{12}}. \tag{3.11}$$

Therefore, if the path $M_{13} \to M_{32}^1$ is the shortest, then A_2 is asymptotically stable. Othewise, A_2 is unstable.

Now we consider the function

$$V = L_{32}^1 \log c - L_{32}^2 \log d. \tag{3.12}$$

The derivative with respect to time is calculated as

$$\dot{V} = L_{32}^2 - L_{32}^1. \tag{3.13}$$

If the path $M_{13} \to M_{32}^1$ is the shortest, we have $\dot{V} > 0$. As the variables are bounded, $d \to 0$ as $t \to \infty$. Then the graph is essentially ring-shaped and we obtain $a \to 0, b \to I_0/L_{13}$ and $c \to I_0/L_{32}^1$. Therefore, the solution converges to A_2 as $t \to \infty$.

On the other, the path $M_{13} \to M_{32}^2$ is the shortest if

$$L_{13} + L_{32}^2 < L_{12} \quad \text{and} \quad L_{32}^2 < L_{32}^1. \tag{3.14}$$

Eigenvalues of A_3 are calculated as

$$\frac{L_{32}^2 - L_{32}^1}{L_{32}^1}, \quad \frac{L_{32}^2 + L_{13} - L_{12}}{L_{12}}. \tag{3.15}$$

Therefore, the stability of A_3 is determined by the length of each path connecting N_1 and N_2.

Similarly, we consider the function V. If the path $M_{13} \to M_{32}^2$ is the shortest, we have $\dot{V} < 0$. As the variables are bounded, $c \to 0$ as $t \to \infty$. Then we obtain $a \to 0, b \to I_0/L_{13}$ and $d \to I_0/L_{32}^2$. Therefore, the solution converges to A_3 as $t \to \infty$. □

We can't determine the linear stability of A_1. However, we can show that A_1 is global asymptotically stable if the path M_{12} is the shortest.

Lemma 4. *If the path M_{12} is the shortest, A_1 is global asymptotically stable.*

Proof. In this case, the length of each edge must satisfy

$$L_{12} < L_{13} + L_{32}^1 \quad \text{and} \quad L_{12} < L_{13} + L_{32}^2. \tag{3.16}$$

Now we consider two functions

$$\begin{cases} V_1 = L_{12} \log a - L_{13} \log b - L_{32}^1 \log c, \\ V_2 = L_{12} \log a - L_{13} \log b - L_{32}^2 \log d. \end{cases} \tag{3.17}$$

The derivatives with respect to time are calculated as

$$\begin{cases} \dot{V}_1 = -L_{12} + L_{13} + L_{32}^1, \\ \dot{V}_2 = -L_{12} + L_{13} + L_{32}^2. \end{cases} \tag{3.18}$$

In this case, we have $\dot{V_1} > 0$ and $\dot{V_2} > 0$. As the variables are bounded and $L_{12} < L_{13} + L_{32}^1$, we obtain $b \to 0$ or $c \to 0$ as $t \to \infty$. As $L_{12} < L_{13} + L_{32}^2$, we obtain $b \to 0$ or $d \to 0$ as $t \to \infty$.

First, we assume $b \to 0$. As we consider the dynamics on W, we have $a \to I_0/L_{12}, c \to 0$ and $d \to 0$. Next, we assume $c \to 0$ and $d \to 0$. For the same reason, we have $a \to I_0/L_{12}$ and $b \to 0$. Therefore, the solution converges to A_1 as $t \to \infty$. □

Theorem 5. *Physarum solver can find the shortest path connecting N_1 and N_2 on the graph as shown in Figure 3.1.*

3.2 $\mu > 1$

Next, we use $f(\xi) = \xi^\mu (\mu > 1)$ as an adaptaion function. In this subsection, we study the adaptation equation

$$\begin{cases} \dot{a} = \dfrac{1}{L_{12}} \left(\dfrac{I_0}{S}(ab + ac + ad) \right)^\mu - a, \\ \dot{b} = \dfrac{1}{L_{13}} \left(\dfrac{I_0}{S}(bc + bd) \right)^\mu - b, \\ \dot{c} = \dfrac{1}{L_{32}^1} \left(\dfrac{I_0}{S} bc \right)^\mu - c, \\ \dot{d} = \dfrac{1}{L_{32}^2} \left(\dfrac{I_0}{S} bd \right)^\mu - d. \end{cases} \tag{3.19}$$

3.2.1 Equilibrium points and their stability

The system (3.19) has seven equilibrium points. The situations in which only one of three paths survives and the others vanish correspond to equilibrium points

$$A_1 = \left(\frac{I_0^\mu}{L_{12}}, 0, 0, 0 \right), A_2 = \left(0, \frac{I_0^\mu}{L_{13}}, \frac{I_0^\mu}{L_{32}^1}, 0 \right), A_3 = \left(0, \frac{I_0^\mu}{L_{13}}, 0, \frac{I_0^\mu}{L_{32}^2} \right).$$

The situation in which only the edge M_{12} vanishes and the other edges survive corresponds to

$$B = \left(0, \frac{I_0^\mu}{L_{13}}, \frac{1}{L_{32}^1} \left[\frac{I_0}{1 + (L_{32}^2/L_{32}^1)^{\frac{1}{\mu-1}}} \right]^\mu, \frac{1}{L_{32}^2} \left[\frac{I_0}{1 + (L_{32}^1/L_{32}^2)^{\frac{1}{\mu-1}}} \right]^\mu \right).$$

The situation in which only the edge M_{32}^1 vanishes and the other edges survive corresponds to

$$C_1 = \left(\frac{T_1 - 1}{L_{13} + L_{32}^1} \left(\frac{I_0}{T_1} \right)^\mu, \frac{1}{L_{13}} \left(\frac{I_0}{T_1} \right)^\mu, \frac{1}{L_{32}^1} \left(\frac{I_0}{T_1} \right)^\mu, 0 \right),$$

where

$$T_1 = 1 + (L_{13} + L_{32}^1) \left[\frac{(L_{13} + L_{32}^1)^\mu}{L_{12}} \right]^{\frac{1}{1-\mu}}.$$

Similarly, the situation in which only the edge M_{32}^2 vanishes and the other edges survive corresponds to

$$C_2 = \left(\frac{T_2 - 1}{L_{13} + L_{32}^2} \left(\frac{I_0}{T_2} \right)^\mu, \frac{1}{L_{13}} \left(\frac{I_0}{T_2} \right)^\mu, 0, \frac{1}{L_{32}^2} \left(\frac{I_0}{T_2} \right)^\mu \right),$$

where

$$T_2 = 1 + (L_{13} + L_{32}^2)\left[\frac{(L_{13} + L_{32}^2)^{\mu}}{L_{12}}\right]^{\frac{1}{1-\mu}}.$$

Finally, the situation in which all edges surveve corresponds to

$$D = (\alpha d_D, \beta d_D, \gamma d_D, d_D),$$

where

$$d_D = \frac{1}{L_{32}^2}\left(\frac{I_0\beta}{\alpha + \beta + \alpha\beta + \beta\gamma + \gamma\alpha}\right)^{\mu},$$

and α, β and γ are given by

$$\alpha = \left[\frac{L_{12}}{L_{32}^2}\left(\frac{\beta}{\beta + \gamma + 1}\right)^{\mu}\right]^{\frac{1}{\mu-1}}, \beta = \frac{L_{32}^2}{L_{13}}(\gamma + 1)^{\mu}, \gamma = \left(\frac{L_{32}^1}{L_{32}^2}\right)^{\frac{1}{\mu-1}}.$$

First, we analyze linear stability of these equilibrium points.

Lemma 6. *If $\mu > 1$, the followings hold:*

1. *A_2 and A_3 are asymptotically stable.*
2. *B is a saddle point.*
3. *C_1 and C_2 are saddle points.*
4. *D is a saddle point.*

Proof. 1. Let $J(A_2)$ be a Jacobi matrix at A_2. $J(A_2)$ is calculate as

$$J(A_2) = \begin{pmatrix} -1 & 0 & 0 & 0 \\ -\mu(L_{13} + L_{32}^1)/L_{13} & -1 & 0 & 0 \\ -\mu(L_{13} + L_{32}^1)/L_{32}^1 & 0 & -1 & -\mu \\ 0 & 0 & 0 & -1 \end{pmatrix}.$$

The characteristic equation of $J(A_2)$ is

$$\det(\lambda I - J(A_2)) = (\lambda + 1)^4 = 0,$$

and we obtain $\lambda = -1$. Therefore, A_2 is linear stable.

2. Let $J(B)$ be a Jacobi matrix at B. Since $a = 0$ and $Q_{12} = 0$, the shape of $J(B)$ is as follows:

$$J(B) = \begin{pmatrix} -1 & 0 & 0 & 0 \\ \frac{\partial \dot{b}}{\partial a} & -1 & 0 & 0 \\ \frac{\partial \dot{c}}{\partial a} & 0 & \frac{\partial \dot{c}}{\partial c} & \frac{\partial \dot{c}}{\partial d} \\ \frac{\partial \dot{d}}{\partial a} & 0 & \frac{\partial \dot{d}}{\partial c} & \frac{\partial \dot{d}}{\partial d} \end{pmatrix}.$$

The characteristic polynomial becomes

$$\det(J(B) - \lambda I) = (\lambda + 1)^2 \det\begin{pmatrix} \frac{\partial \dot{c}}{\partial d} - \lambda & \frac{\partial \dot{c}}{\partial d} \\ \frac{\partial \dot{d}}{\partial c} & \frac{\partial \dot{d}}{\partial d} - \lambda \end{pmatrix}.$$

Hence, B has eigenvalue -1. To determine the stability of B, we consider the matrix

$$J'(B) = \begin{pmatrix} \frac{\partial \dot{c}}{\partial d} & \frac{\partial \dot{c}}{\partial d} \\ \frac{\partial \dot{d}}{\partial c} & \frac{\partial \dot{d}}{\partial d} \end{pmatrix}.$$

Let $\gamma = (L_{32}^1/L_{32}^2)^{\frac{1}{\mu-1}}$ and $\tilde{\gamma} = 1/\gamma$, then $J'(B)$ is calculated as

$$J'(B) = \begin{pmatrix} \mu\frac{\tilde{\gamma}}{1+\tilde{\gamma}} - 1 & \frac{-\mu}{1+\tilde{\gamma}} \\ \frac{-\mu}{1+\gamma} & \mu\frac{\gamma}{1+\gamma} - 1 \end{pmatrix}.$$

We can easily caluclate eigenvalues of $J'(B)$ as $-1, \mu-1$. Since $\mu > 1$, the equilibrium point B has one positive eigenvalue.

3. Since $d = 0$ and $Q_{32}^2 = 0$, the shape of $J(C_1)$ is as follows:

$$J(C_1) = \begin{pmatrix} * & * & * & * \\ * & * & * & * \\ * & * & * & * \\ 0 & 0 & 0 & -1 \end{pmatrix}.$$

So -1 is one of the eigenvalues of $J(C_1)$ and we only have to consider the matrix

$$J'(C_1) = \begin{pmatrix} \frac{\partial \dot b}{\partial b} & \frac{\partial \dot b}{\partial c} & \frac{\partial \dot b}{\partial a} \\ \frac{\partial \dot c}{\partial b} & \frac{\partial \dot c}{\partial c} & \frac{\partial \dot c}{\partial a} \\ \frac{\partial \dot a}{\partial b} & \frac{\partial \dot a}{\partial c} & \frac{\partial \dot a}{\partial a} \end{pmatrix}.$$

Now we set

$$r = L_{32}^1 \left(\frac{L_{12}}{(L_{13} + L_{32}^1)^\mu} \right)^{\frac{1}{\mu - 1}}, \quad s = \frac{L_{32}^1}{L_{13}}.$$

$J'(C_1)$ is calculated as

$$J'(C_1) = \begin{pmatrix} \frac{\mu r}{r+s+rs} - 1 & \frac{\mu r s^2}{r+s+rs} & \frac{-\mu s(s+1)}{r+s+rs} \\ \frac{\mu r}{s(r+s+rs)} & \frac{\mu r s}{r+s+rs} - 1 & \frac{-\mu(s+1)}{r+s+rs} \\ \frac{-\mu r}{(s+1)(r+s+rs)} & \frac{-\mu r s^2}{(s+1)(r+s+rs)} & \frac{\mu s}{r+s+rs} - 1 \end{pmatrix}.$$

The characteristic equation becomes

$$\det(\lambda I - J'(C_1)) = (\lambda+1)^2(\lambda - \mu + 1) = 0.$$

Hence, eigenvalues of $J(C_1)$ are -1(multiplicity is 3) and $\mu - 1$. Therefore, C_1 is a saddle point.

4. For simplicity, we denote $P = \alpha + \beta + \alpha\beta + \beta\gamma + \gamma\alpha$. Jacobi matrix $J(D)$ is calculated as

$$\begin{pmatrix} \frac{\mu\beta(\gamma+1)}{P} - 1 & \frac{-\mu\alpha(\gamma+1)^2}{P(\beta+\gamma+1)} & \frac{-\mu\alpha\beta^2}{P(\beta+\gamma+1)} & \frac{-\mu\alpha\beta^2}{P(\beta+\gamma+1)} \\ \frac{-\mu\beta(\beta+\gamma+1)}{P} & \frac{\mu\alpha(\gamma+1)}{P} - 1 & \frac{\mu\alpha\beta^2}{P(\gamma+1)} & \frac{\mu\alpha\beta^2}{P(\gamma+1)} \\ \frac{-\mu\gamma(\beta+\gamma+1)}{P} & \frac{\mu\alpha\gamma(\gamma+1)}{P\beta} & \frac{\mu(\alpha+\beta+\alpha\beta)}{P} - 1 & \frac{-\mu\gamma(\alpha+\beta)}{P} \\ \frac{-\mu(\beta+\gamma+1)}{P} & \frac{\mu\alpha(\gamma+1)}{P\beta} & \frac{-\mu(\alpha+\beta)}{P} & \frac{\mu(\alpha\beta+\beta\gamma+\gamma\alpha)}{P} - 1 \end{pmatrix}.$$

The characteristic equation of $J(D)$ becomes

$$\det(\lambda I - J(D)) = (\lambda+1)^2(-\lambda + \mu - 1)^2 = 0.$$

Hence, eigenvalues of $J(D)$ are -1 and $\mu - 1$ (multiplicity is 2). Therefore, D is a saddle point. $\square$

Remark 3. *Jacobi matrices shown in this section are obtained under the assumption of $\mu > 1$. They do not hold for $\mu < 1$.*

Next, we consider the stability of A_1.

Lemma 7. *A_1 is locally asymptotically stable.*

equilibria	type	n_+	n_-
A_2	stable node	0	4
A_3	stable node	0	4
B	saddle	1	3
C_1	saddle	1	3
C_2	saddle	1	3
D	saddle	2	2

表 1: (Linear) stability types of equilibria. n_+ is a number of unstable eigenvalues and n_- is a number of stable eigenvalues.

Proof. Let $\mathbf{x} = (a, b, c, d)$. We have

$$\begin{aligned}
\frac{(Q_{13})^\mu}{b} &= b^{\mu-1}(p_1 - p_3)^\mu \to 0,\\
\frac{(Q_{32}^1)^\mu}{c} &= c^{\mu-1}p_3^\mu \to 0,\\
\frac{(Q_{32}^2)^\mu}{d} &= d^{\mu-1}p_3^\mu \to 0,
\end{aligned}$$

when $\mathbf{x} \to A_1$. Hence, $\dot{b}, \dot{c}$ and $\dot{d}$ are negative in a sufficiently small neighborhood of A_1 because

$$\dot{b} = -b + o(b), \quad \dot{c} = -c + o(c), \quad \dot{d} = -d + o(d) \tag{3.20}$$

when $\mathbf{x} \to A_1$. Now $\ddot{a}$ is calculated as

$$\begin{aligned}
\ddot{a} &= \frac{\mu}{L_{12}} Q_{12}^{\mu-1}\dot{Q}_{12} - \dot{a}\\
&= \frac{\mu}{L_{12}} Q_{12}^{\mu-1}\left(\frac{\partial Q_{12}}{\partial a}\dot{a} + \frac{\partial Q_{12}}{\partial b}\dot{b} + \frac{\partial Q_{12}}{\partial c}\dot{c} + \frac{\partial Q_{12}}{\partial d}\dot{d}\right) - \dot{a}.
\end{aligned}$$

Note that

$$\begin{aligned}
\frac{\partial Q_{12}}{\partial a} &= \frac{I_0(b+c+d)(bc+bd)}{S} = \frac{Q_{12}Q_{13}}{aI_0}\\
\frac{\partial Q_{12}}{\partial b} &= -\frac{\mu I_0}{L_{12}}\frac{a(c+d)^2}{S^2} \le 0,\\
\frac{\partial Q_{12}}{\partial c} &= \frac{\partial Q_{12}}{\partial d} = -\frac{\mu I_0}{L_{12}}\frac{ab^2}{S^2} \le 0.
\end{aligned}$$

Hence, we obtain

$$\begin{aligned}
\ddot{a} &\ge \frac{\mu}{L_{12}} Q_{12}^{\mu-1}\frac{\partial Q_{12}}{\partial a}\dot{a} - \dot{a}\\
&= \frac{\mu}{L_{12}}(Q_{12})^\mu Q_{13}\frac{\dot{a}}{aI_0} - \dot{a}\\
&= \mu(\dot{a} + a)Q_{13}\frac{\dot{a}}{aI_0} - \dot{a}\\
&= \mu\frac{Q_{13}}{aI_0}(\dot{a})^2 + \left(\mu\frac{Q_{13}}{I_0} - 1\right)\dot{a}\\
&\ge \left(\mu\frac{Q_{13}}{I_0} - 1\right)\dot{a}.
\end{aligned}$$

Because Q_{13} converges to 0 as $\mathbf{x} \to A_1$, we can choose $\mathbf{x} = (a, b, c, d)$ such that the coefficient of $\dot{a}$ becomes negative. Therefore, $\dot{a} \geq 0$ holds asymptotically, in a sufficiently small neighborhood of A_1. Then, the derivative of square of the distance between $\mathbf{x} = (a, b, c, d)$ and A_1 is calculated as

$$\begin{aligned}\frac{1}{2}\frac{d}{dt}|\mathbf{x} - A_1|^2 &= \frac{1}{2}\frac{d}{dt}\left((\frac{I_0^\mu}{L_{12}} - a)^2 + b^2 + c^2 + d^2\right) \\ &= -\left(\frac{I_0^\mu}{L_{12}} - a\right)\dot{a} + b\dot{b} + c\dot{c} + d\dot{d} \leq 0.\end{aligned}$$

Hence, $|\mathbf{x} - A_1| \to 0$ as $t \to \infty$. Thus, A_1 is locally asymptotically stable. □

3.2.2 Heteroclinic orbits

In this section, we consider about the existence of heteroclinic orbits connecting each equilibrium point. As shown in the previous section, A_2 and A_3 have no unstable manifold, B, C_1 and C_2 have one-dimensional unstable manifold, and that of D is two-dimensional.

First, we study heteroclinic orbits from B.

Lemma 8. *Let $J(B)$ be a Jacobi matrix at B and $\mathbf{v}_B = {}^t(0, 0, -1, 1)$, then*

$$J(B)\mathbf{v}_B = (\mu - 1)\mathbf{v}_B \tag{3.21}$$

holds, that is, $\mathbf{v}_B$ is an eigenvector of $J(B)$ associated with $\mu - 1$.

Proof. This can be obtained by straightforward calculation. □

This implies that the straight line $E^u(B)$ which is sppaned by $\mathbf{v}_B$ tangents to the unstable manifold of B at B. Now we can easily verify that a subset

$$\left\{(a, b, c, d) \in \mathbf{R}_+^4 | a = 0, b = I_0^\mu / L_{13}\right\}$$

is invariant for (3.19). In fact, if $a = 0$ and $b = I_0^\mu / L_{13}$, then $\dot{a} = \dot{b} = 0$. We consider two-dimensional dynamics on this invariant subset. As this case is obviously equivalent to the ring-shaped case, the following is trivial.

Proposition 9. *There are heteroclinic orbits from B to A_2 and from B to A_3.*

Next, we study heteroclinic orbits from C_1. The unstable manifold of C_1 tangents to the straight line $E^u(C_1)$ which is spanned by

$$\mathbf{v}_{C1} = {}^t\left(\frac{-s}{s+1}, s, 1, 0\right)$$

at C_1. It is obvious that a subset

$$\left\{(a, b, c, d) \in \mathbf{R}_+^4 | d = 0\right\}$$

is invariant for (3.19). We consider the dynamics on this invariant subset. This case is equivalent to the triangle-shaped case, the following holds.

Proposition 10. *There are heteroclinic orbits from C_1 to A_1 and to A_2.*

Similarly, a subset

$$\left\{(a, b, c, d) \in \mathbf{R}_+^4 | c = 0\right\}$$

is also invariant, and the system restricted on this subset is equivalent to the triangle-shaped case. So we obtain the following.

Proposition 11. *There are heteroclinic orbits from C_2 to A_1 and to A_3.*

Heteroclinic orbits from B, C_1 and C_2 are completely specified as shown above, because their unstable manifolds are one-dimensional. Next, we consider about heteroclinic orbits from D. Complete detection might be difficult, but some of them can be discovered as follows.

Lemma 12. *The set*

$$\{(a,b,c,d)|c=\gamma d, b=\beta b\} \tag{3.22}$$

is invariant.

Proof. Differentiate c/d with respect to time:

$$\begin{aligned}\frac{d}{dt}\left(\frac{c}{d}\right) &= \frac{1}{d^2}(\dot{c}d - c\dot{d}) \\ &= \frac{c}{d}\left(\frac{I_0 b}{S}\right)^{\mu}\left(\frac{c^{\mu-1}}{L_{32}^1} - \frac{d^{\mu-1}}{L_{32}^2}\right).\end{aligned}$$

If an initial value is chosen to hold $c/d=\gamma$, then $\frac{d}{dt}(c/d)=0$ holds at all time. Therefore $\{c=\gamma d\}$ is invariant.

Next, differentiate b/d with respect to time under $c=\gamma d$:

$$\begin{aligned}\frac{d}{dt}\left(\frac{b}{d}\right) &= \frac{1}{d^2}(\dot{b}d - b\dot{d}) \\ &= \frac{1}{d}\left(\frac{I_0 bd}{S}\right)^{\mu}\left(\frac{(1+\gamma)^{\mu}d}{L_{13}} - \frac{b}{L_{32}^2}\right).\end{aligned}$$

If an initial value is chosen to hold

$$b = \frac{L_{32}^2}{L_{13}}(1+\gamma)^{\mu} d = \beta d,$$

then $\frac{d}{dt}(b/d)=0$ holds at all time. Hence (3.22) is an invariant subset. □

Proposition 13. *There are heteroclinic orbits from D to A_1 and to B.*

Proof. The system restricted on (3.22) is given by

$$\begin{cases}\dot{a} = \dfrac{I_0^{\mu}}{L_{12}}\left(\dfrac{(\beta+\gamma+1)a}{(\beta+\gamma+1)a+\beta(\gamma+1)d}\right)^{\mu} - a, \\ \dot{d} = \dfrac{I_0^{\mu}}{L_{32}^2}\left(\dfrac{\beta d}{(\beta+\gamma+1)a+\beta(\gamma+1)d}\right)^{\mu} - d.\end{cases} \tag{3.23}$$

There are equilibrium points of (3.23) corresponding A_1, B and D. These are calculaed as

$$A_1 = \left(\frac{I_0^{\mu}}{L_{12}}, 0\right), \quad B = \left(0, \frac{I_0^{\mu}}{L_{32}^2}(1+\gamma)^{-\mu}\right), \quad D = (\alpha d_D, d_D).$$

This can be easily verified by straightforward calculation.

On the phase plain, A_1 and B are stable nodes, and D is a saddle point. Any solution of (3.22) is attracted to a bounded region. In this case, limit cycle cannot exist. The ray $\{a=\alpha d\}$ is invariant and corresponds to a stable manifold of D. The unstable manifold of D intersects with this ray. Therefore, there exist heteroclinic orbits from D to A_1 and to B. □

We now make a conjecture that the complete chart is Figure 3.3, but the complete proof is not achieved so far. We have already proved that there are the connecting orbits between unstable equilibrium points and stable equilibrium points. On the other hand, it is not easy to prove the existence of the orbit connecting unstable equilibrium points to each other, although it is suggested by the simulation result as shown in Figure 3.4.

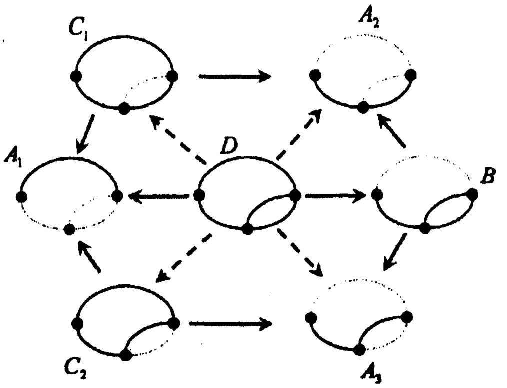

図 3.3: Connecting orbits. The broken line means the orbit to which existence is not proved.

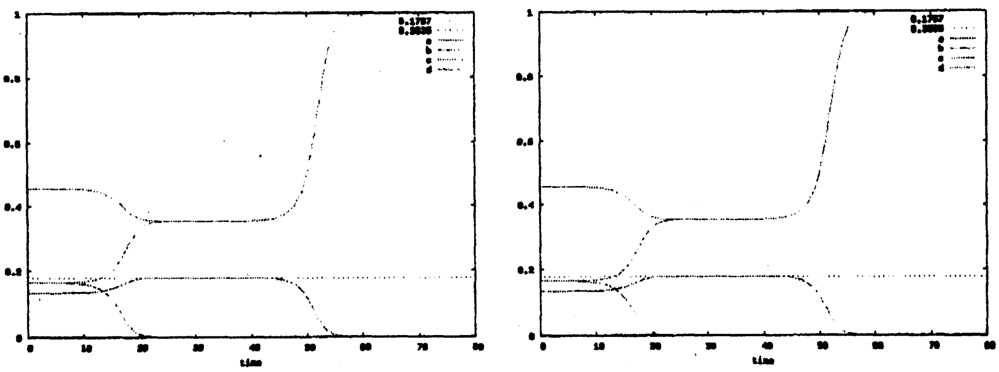

図 3.4: An orbit that leaves near D, and converges to $A_2(A_3)$ after approaching C_1(or C_2). ($L_{12} = 2.0, L_{13} = L_{32}^1 = L_{32}^2 = 1.0, I_0 = 1.0, \mu = 1.5$)

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