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NONLINEAR DYNAMICS OF THE BOMBARDIER BEETLE

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ABSTRACT

This work investigates the dynamics by which the bombardier beetle releases a pulsed jet of fluid as a defense mechanism. A mathematical model is proposed which takes the form of a pair of piecewise continuous differential equations with dependent variables as fluid pressure and quantity of reactant. The model is shown to exhibit an *effective equilibrium point* (EEP). Conditions for the existence, classification and stability of an EEP are derived and these are applied to the model of the bombardier beetle.

INTRODUCTION

The bombardier beetle (genus Brachinus) possesses a unique defensive mechanism. When disturbed, the beetle fends off an attacker by squirting it with a very hot caustic spray. These discharges, which are both visible and audible, are emitted from the tip of the beetle's abdomen, and are able to be aimed over a wide range of directions.

These remarkable insects, first identified more than a century ago, have been examined in detail by Eisner, Aneshansley, and colleagues (Aneshansley et al.,1969), (Eisner and Aneshansley,1979), (Dean et al.,1990). The irritating 100 deg C benzoquinone spray discharged by the beetle is formed at the moment of ejection, as follows: An inner reservoir compartment contains hydroquinones and hydrogen peroxide which are forced by muscular contraction into a smaller reaction chamber that contains a mixture of enzymes. In this second chamber, an exothermic reaction produces benzoquinones, oxygen, and water. When this reaction occurs, the vaporized liquid increases the pressure in the reaction chamber, closes a one-way valve between the two chambers and expels most of the contents of the reaction chamber through a slit to the ambient atmosphere. Then the pressure drops in the emptied reaction chamber and the process repeats at intervals of approximately 0.001 to 0.002 seconds.

(Deinert et al.,1997), in a class project, modelled this cycle as a three-part, sequential process:
1) The fluid from the reservoir fills the reaction chamber.
2) The biochemical reaction increases the pressure within the chamber and closes the one-way valve through which the fluid had entered the chamber, and
3) The contents are expelled from the reaction chamber under this increased pressure.
Their model predicted a pulse rate of between 360 and 560 pulses per second, which is well within the experimental results.

The task of the present paper is to model the pulsed discharge behavior within the context of nonlinear dynamics. We examine the existence, classification and stability of effective equilibrium points and discuss the qualitative aspects of the resulting oscillatory behavior.

MODEL

Our model consists of three compartments, the reservoir, the reaction chamber, and the ambient atmosphere. We imagine that the reactant is forced to flow from the reservoir to the reaction chamber if the pressure in the reservoir is larger than the pressure in the reaction chamber. Once in the reaction chamber, the reactant undergoes an exothermic chemical reaction which increases the pressure in the reaction chamber while simultaneously using up some reactant. As the pressure in the reaction chamber increases, it eventually becomes larger than the pressure in the reservoir and the flow of reactant into the reaction chamber ceases. We assume the existence of a flap or door which prevents backflow from the reaction chamber into the reservoir. The chemicals in the reaction chamber are assumed to flow out of the beetle's abdomen into the ambient atmosphere as a function of the excess of reaction chamber pressure above atmospheric pressure.

These statements may be expressed in the form of a mathematical model by using two variables to represent the state of the system:

$p(t)$ = pressure in the reaction chamber at time t, and
$r(t)$ = quantity of reactant in the reaction chamber at time t.

In addition, we assume that
p_{res} = pressure in the reservoir, and
p_a = pressure in the ambient atmosphere
are constant in time.

The governing differential equations are of the form:

$$\frac{dr}{dt} = f_1(p_{res} - p) - f_2(r) - f_3(p - p_a) \tag{1}$$

$$\frac{dp}{dt} = f_4(r) - f_5(p - p_a) \tag{2}$$

where the f_1 term is the rate at which reactant is supplied from the reservoir, the f_2 term is the rate at which reactant is used up in the reaction, the f_3 term is the rate at which reactant is lost due to ejection of material, the f_4 term is the rate at which pressure is increased due to the reaction, and the f_5 term is the rate at which pressure is decreased due to ejection of material. We assume that f_1 is a discontinuous function, representing the sudden closing of the flap or door which prevents backflow from the reaction chamber into the reservoir. This term may be modeled as $f_1(p_{res} - p) = k_1 H(p_{res} - p)$, where $H(\cdot)$ is the Heaviside step function and makes this term vanish if $p > p_{res}$. The other functions f_i are assumed to be continuous.

A natural initial condition for this system could be:

$$\text{at} \quad t = 0, \quad r = 0 \quad \text{and} \quad p = p_a. \tag{3}$$

That is, there is no reactant initially in the reaction chamber, and its pressure is initially atmospheric.

As an example of the system (1),(2), we consider the following:

$$\frac{dr}{dt} = k_1 H(p_{res} - p) - k_2 r - k_3(p - p_a) \tag{4}$$

$$\frac{dp}{dt} = k_4 r - k_5(p - p_a). \tag{5}$$

where the constants k_i are nonnegative.

Fig.1 shows a simulation of eqs.(4),(5) for the initial condition (3) and the parameter values:

$$k_1 = 3, k_2 = k_3 = k_4 = k_5 = 1, p_{res} = 2, p_a = 1. \tag{6}$$

Fig.1 shows that for large time, the system approaches a point on the line of discontinuity, $p = p_{res}$. This point acts like an *effective equilibrium point.* In the rest of this paper we analyze the behavior of piecewise continuous systems in the neighborhood of such an effective equilibrium point, which we abbreviate as an EEP.

ANALYSIS

A key feature of the system (1),(2) is that the velocity component $\dot{p}$ perpendicular to the discontinuity line $p = p_{res}$ is continuous, while the velocity component $\dot{r}$ parallel to the discontinuity is discontinuous across it.

Conditions for the existence of an EEP

In order for a point Q on the line of discontinuity $p = p_{res}$ to be an EEP, we must have the following
(i) the velocity component $\dot{p}$ perpendicular to the discontinuity must be zero at Q, and
(ii) the velocity component $\dot{r}$ parallel to the discontinuity must change sign as the discontinuity is crossed.

For example, in the case of the sample system (4),(5), $\dot{p}$ vanishes along $p = p_{res}$ at

$$r = r_0 = \frac{k_5}{k_4}(p_{res} - p_a). \tag{7}$$

The point $r = r_0, p = p_{res}$ will be an EEP if $\dot{r}$ evaluated at $r = r_0, p = p_{res}^-$ has the opposite sign to itself evaluated at $r = r_0, p = p_{res}^+$, a condition which will be fulfilled if

$$k_1 > k_2 r_0 + k_3(p_{res} - p_a). \tag{8}$$

Classification of EEP's

Assuming that conditions (i) and (ii) are fulfilled by a point Q on the line of discontinuity, we proceed next to classify the resulting EEP as either saddle-like or spiral-like. By condition (i), the velocity component perpendicular to the discontinuity line must vanish at Q. This produces two generic cases: case A, in which the horizontal velocity component points to the left above Q, and to the right below Q, and case B, in which the opposite happens. See Fig.2. By condition (ii), the velocity component parallel to the discontinuity line must have opposite sign on either side of the discontinuity at Q. Here again there are two cases to consider: case C in which the vertical velocity component points up on the right side of Q, and down on the left side of Q, and case D, in which the opposite happens. See Fig.2.

Using these four cases as a guide, we may classify an EEP as follows:
Spiral-like corresponds to A-C or B-D, while
Saddle-like corresponds to A-D or B-C. See Fig.3.

As an example, consider the system (4),(5). To determine whether it is case A or case B, we set $p = p_{res}$ and $r = r_0^+$ in eq.(5) and find that $\dot{p} > 0$. This shows that the horizontal velocity component points to the right above Q on the line of discontinuity so that we are in case B. To determine whether it is case C or case D, we set $r = r_0$ and $p = p_{res}^+$ in eq.(4) and find that $\dot{r} < 0$. Thus the vertical velocity component points down to the right of Q so that we are in case D. Taken together, the B-D combination yields that we have a spiral-like EEP (Fig.3), in agreement with the simulation of Fig.1.

Now let us assume that we have a system (1),(2) which contains a spiral-like EEP. The question we address next is: Is it stable? In order to answer this we seek a power series solution to the ode's (1),(2). For ease of computation we introduce local coordinates x, y centered at the EEP:

$$\text{Set} \quad x = p - p_{res}, \quad y = r - r_0 \tag{9}$$

whereupon eqs.(1),(2) become:

$$\frac{dy}{dt} = f_1(-x) - f_2(y + r_0) - f_3(x + p_{res} - p_a) \tag{10}$$

$$\frac{dx}{dt} = f_4(y + r_0) - f_5(x + p_{res} - p_a) \tag{11}$$

where

$$f_4(r_0) - f_5(p_{res} - p_a) = 0. \tag{12}$$

This system may be generalized as follows:

$$\frac{dy}{dt} = \begin{cases} g(x,y) \text{ for } x \geq 0 \\ \tilde{g}(x,y) \text{ for } x < 0 \end{cases} \tag{13}$$

$$\frac{dx}{dt} = h(x,y). \tag{14}$$

In order for eqs.(13),(14) to have an EEP at the origin, we require that:

$$\text{(i)} \quad h(0,0) = 0 \tag{15}$$

$$\text{(ii)} \quad g(0^+,0) \cdot \tilde{g}(0^-,0) < 0. \tag{16}$$

We rewrite eqs.(13),(14) in the form:

$$\frac{dy}{dx} = \begin{cases} \dfrac{g}{h} \text{ for } x \geq 0 \\ \\ \dfrac{\tilde{g}}{h} \text{ for } x < 0 \end{cases} \tag{17}$$

Assuming that this system has a spiral EEP at the origin, we must be either in cases B-D or A-C of Fig.3. Assuming B-D (without loss of generality), we may determine stability by generating the Poincare map corresponding to the cut $x = 0$ by the use of power series. Let $y_0 > 0$ be an initial value of y when $x = 0$ for eq.(17) with $x \geq 0$, and let

$y_1 < 0$ be the corresponding value of y when the associated trajectory next intersects the $y-$axis, see Fig.4. Similarly, let the trajectory emanating from $y_1 < 0$ on the $y-$axis for eq.(17) with $x < 0$ next intersect the $y-$axis at $y = y_2 > 0$. Then the spiral at the origin will be stable if $y_2 < y_0$, and unstable if $y_2 > y_0$, see Fig.4. (Here we assume that y_0, y_1 and y_2 are small, limiting our stability conclusions to local behavior in a neighborhood of the EEP at the origin.)

POWER SERIES SOLUTION

Our goal is to obtain y_2 as a power series function of y_0, see Fig.4. We begin by noting that for the case $x \geq 0$, x is a single-valued function of y, but not vice versa. We therefore write

$$x = x_0 + x_1(x_0)\ y + x_2(x_0)\ y^2 + x_3(x_0)\ y^3 + x_4(x_0)\ y^4 + x_5(x_0)\ y^5 + \cdots \quad (18)$$

and substitute (18) into (17) in the form

$$\frac{dx}{dy} = \frac{h}{g} \quad \text{for } x \geq 0. \quad (19)$$

Collecting terms and equating to zero like powers of y permits us to obtain expressions for the functions $x_i(x_0)$. Here we used the computer algebra system MACSYMA.

In order to use these results to relate y_0 and y_1, we set $x = 0$ in (18). This results in a relation between x_0 and y, where y corresponds to both y_0 and y_1. We expand x_0 in the following power series in y and substitute it into $x = 0$:

$$x_0 = a_1\ y + a_2\ y^2 + a_3\ y^3 + a_4\ y^4 + a_5\ y^5 + \cdots \quad (20)$$

in which the a_i coefficients do not depend on x_0. Collecting terms we obtain expressions for the a_i, and in particular we find that

$$a_1 = 0. \quad (21)$$

Since y_0 and y_1 both correspond to the same value of x_0, we obtain the following relation between them:

$$a_2\ y_0^2 + a_3\ y_0^3 + a_4\ y_0^4 + a_5\ y_0^5 + \cdots = a_2\ y_1^2 + a_3\ y_1^3 + a_4\ y_1^4 + a_5\ y_1^5 + \cdots \quad (22)$$

We seek an expression for y_1 as a power series function of y_0 in the form:

$$y_1 = -y_0 + c_2\ y_0^2 + c_3\ y_0^3 + c_4\ y_0^4 + \cdots \quad (23)$$

Substituting (23) into (22) and collecting terms, we obtain:

$$c_2 = -\frac{a_3}{a_2}, \qquad c_3 = -\left(\frac{a_3}{a_2}\right)^2, \qquad c_4 = 2\ \frac{a_3}{a_2}\frac{a_4}{a_2} - 2\left(\frac{a_3}{a_2}\right)^3 - \frac{a_5}{a_2}. \quad (24)$$

Now we repeat the calculation for $x < 0$, i.e. for the ode:

$$\frac{dx}{dy} = \frac{h}{\tilde{g}} \quad \text{for } x \geq 0. \quad (25)$$

In an analogous fashion to the foregoing procedure, we obtain the following relation between y_2 and y_1:

$$y_2 = -y_1 + \tilde{c}_2\ y_1^2 + \tilde{c}_3\ y_1^3 + \tilde{c}_4\ y_1^4 + \cdots \quad (26)$$

where the $\tilde{c}_i$'s are related to $\tilde{a}_i$'s exactly as the c_1's in eq.(24) are related to the a_i's.

Now the two calculations can be combined to give y_2 as a function of y_0. Substituting (23),(24) into (26), we obtain:

$$y_2 = y_0 + \alpha\ y_0^2 + \alpha^2\ y_0^3 + \beta\ y_0^4 + \cdots \quad (27)$$

where

$$\alpha = \frac{a_3}{a_2} - \frac{\tilde{a}_3}{\tilde{a}_2} \quad (28)$$

$$\beta = -2\left(\frac{a_3}{a_2}\frac{a_4}{a_2} - \frac{\tilde{a}_3}{\tilde{a}_2}\frac{\tilde{a}_4}{\tilde{a}_2}\right) + 2\left(\left(\frac{a_3}{a_2}\right)^3 - \left(\frac{\tilde{a}_3}{\tilde{a}_2}\right)^3\right) - 3\left(\frac{a_3}{a_2}\frac{\tilde{a}_3}{\tilde{a}_2}\right)\left(\frac{a_3}{a_2} - \frac{\tilde{a}_3}{\tilde{a}_2}\right) + \left(\frac{a_5}{a_2} - \frac{\tilde{a}_5}{\tilde{a}_2}\right) \quad (29)$$

Stability Conditions

From eq.(27) we see that the spiral EEP will be stable if

$$\alpha = \frac{a_3}{a_2} - \frac{\tilde{a}_3}{\tilde{a}_2} < 0 \qquad \text{STABLE.} \tag{30}$$

and unstable if $\alpha > 0$.

Hopf Bifurcation

Eq.(27) reveals that a non-zero fixed point $y_2 = y_0$ generically emerges from the origin as α passes through zero. This may be seen by setting $y_2 = y_0$ in (27) and solving for y_0:

$$y_0 = \sqrt{\frac{-\alpha}{\beta}} + O(\alpha) \tag{31}$$

This fixed point of the Poincare map (27) corresponds to a limit cycle of the flow (13),(14), cf.Fig.4. The existence and stability of the limit cycle depends on the sign of β. If $\beta < 0$ then the limit cycle is stable and occurs for $\alpha > 0$ (in which case the EEP at the origin is unstable.) If, however, $\beta > 0$, then the limit cycle is unstable and occurs for $\alpha < 0$ (in which case the EEP at the origin is stable.)

EXAMPLE

If the foregoing method is applied to the example of eqs.(4),(5), we obtain:

$$a_2 = \frac{k_4^2}{2\left[(k_2 k_5 + k_4 k_3)(p_{res} - p_a)\right]} \tag{32}$$

$$a_3 = -\frac{k_4^3 (k_2 + k_5)}{3\left[(k_2 k_5 + k_4 k_3)(p_{res} - p_a)\right]^2} \tag{33}$$

$$\tilde{a}_2 = \frac{k_4^2}{2\left[(k_2 k_5 + k_4 k_3)(p_{res} - p_a) - k_1 k_4\right]} \tag{34}$$

$$\tilde{a}_3 = -\frac{k_4^3 (k_2 + k_5)}{3\left[(k_2 k_5 + k_4 k_3)(p_{res} - p_a) - k_1 k_4\right]^2} \tag{35}$$

Substituting (32)-(35) into the stability condition (30), we obtain:

$$\alpha = \frac{a_3}{a_2} - \frac{\tilde{a}_3}{\tilde{a}_2} = \frac{2 k_1 k_4^2 (k_2 + k_5)}{3\left[(k_2 k_5 + k_4 k_3)(p_{res} - p_a) - k_1 k_4\right]\left[(k_2 k_5 + k_4 k_3)(p_{res} - p_a)\right]} \tag{36}$$

The stabilty of the EEP is determined by the sign of α in eq.(36). Assuming that all of the parameters $k_i > 0$, and that $p_{res} > p_a$, and using the condition for the existence of an EEP, eq.(8), it follows that $\alpha < 0$, implying that whenever the EEP exists it is stable, as in the sample run of Fig.1.

If the parameters of the problem are permitted to vary in such a way that α passes through zero, then the Hopf bifurcation analysis presented above predicts that a limit cycle will generically be born out of the EEP. We have derived an expression for the parameter β in eqs.(29),(31), but it has 55 terms and is too long to give here. For the parameters in eq.(6) we find that $\alpha = -2$ and $\beta = -11/3$. Note that regardless of the sign of β, the fact that the EEP is always stable for this example shows that the associated limit cycle, if it exists for $\alpha < 0$, cannot be stable.

In this example, when the condition (8) for the existence of an EEP is not satisfied, an equilibrium point (as opposed to an EEP) appears in the region of the p-r phase plane for which $p < p_{res}$. Motions which start with the initial condition (3) end up being attracted to this equilibrium point.

CONCLUSION

Our model of the dynamics of the bombardier beetle involves a piecewise continuous system of differential equations which is characterized by the presence of an effective equilibrium point (EEP) located on the line of discontinuity. In this work we have investigated conditions for the existence, classification and stability of the associated EEP. When applied to a particular example of such a model, one that is piecewise linear (eqs.(4),(5)), our results show that the EEP is always stable (if it exists).

An open question concerning the model in eqs.(1),(2) is whether the functions f_i can be chosen so that the resulting system exhibits a stable limit cycle. This question has biological relevance because of experimental evidence obtained by biologists which indicates that the ejection stream is delivered in an oscillatory fashion. Although the stable spiral EEP behavior exhibited by the model (4),(5) does involve oscillatory behavior, it is damped. A model exhibiting the steady state periodic motion of a limit cycle might provide a more realistic representation of the dynamics of the bombardier beetle.

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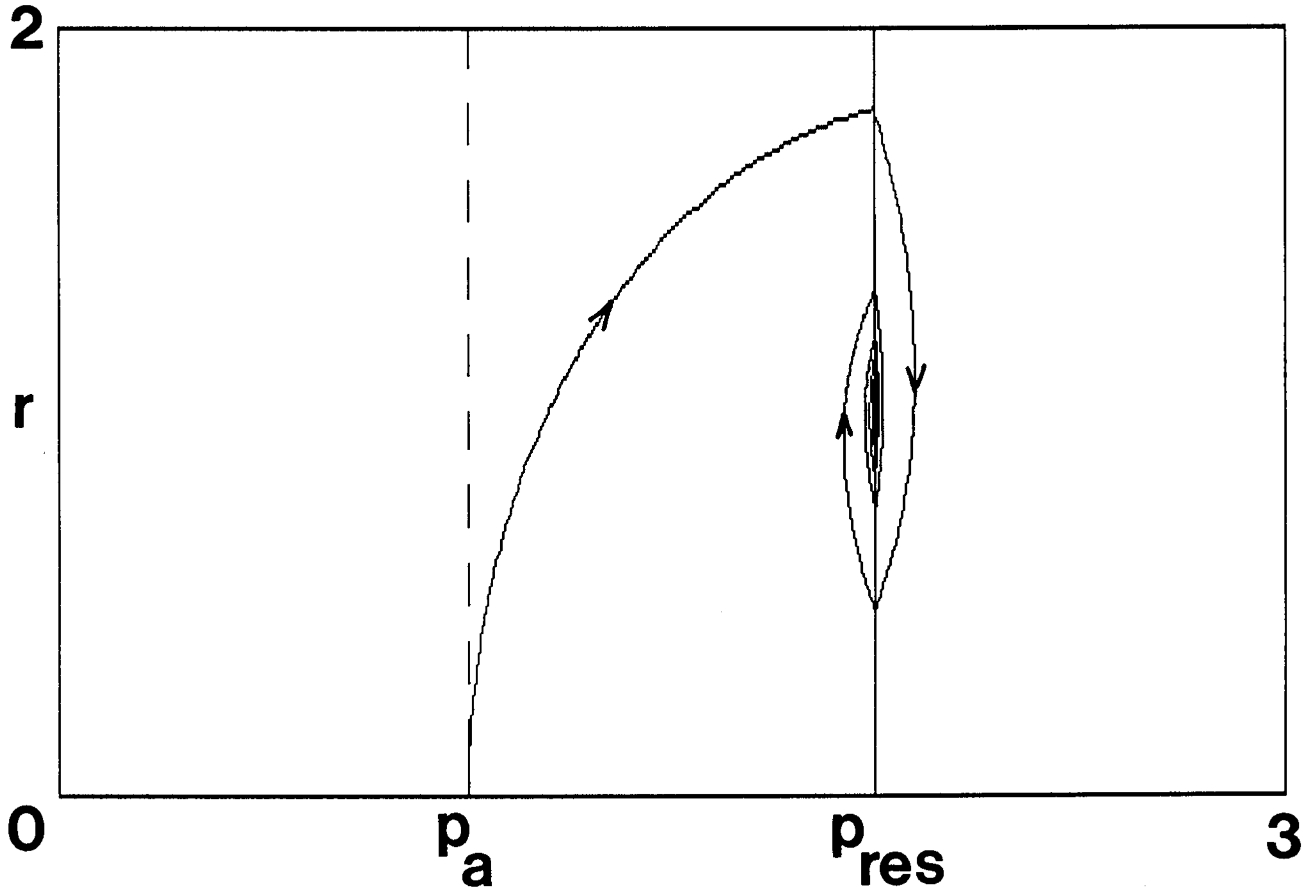
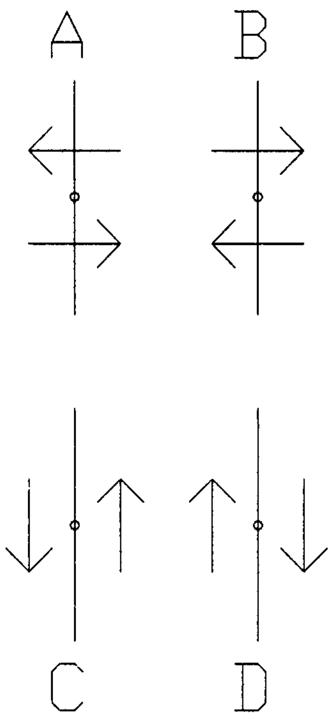


Figure 1. Results of numerical integration of eqs.(4),(5) for the initial condition (3) and the parameter values (6), displayed in the $p - r$ phase plane. The line of discontinuity of the vector field, $p = p_{res}$, is shown as a solid vertical line. The line $p = p_a$ is shown as a dashed vertical line. Note the presence of an EEP (effective equilibrium point) along the line of discontinuity $p = p_{res} = 2$, at $r = r_0 = 1$. In this case the EEP is a stable spiral.



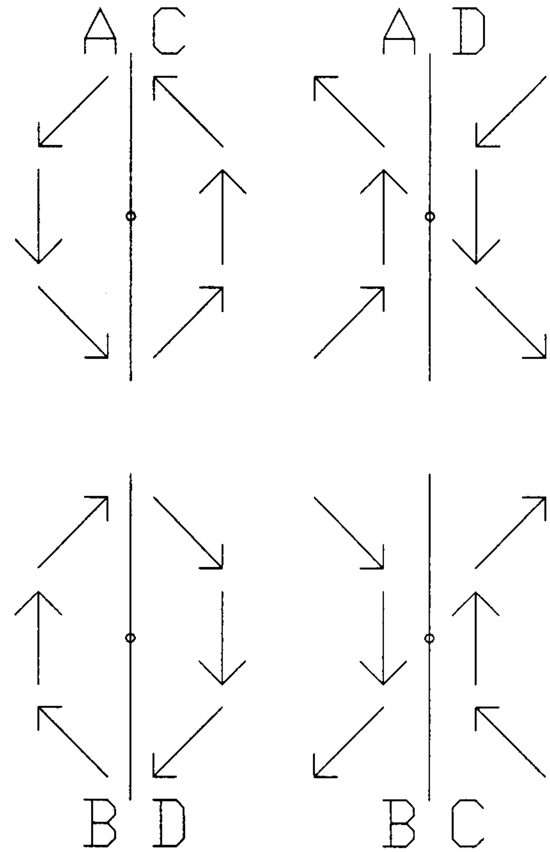


Figure 2. In order for an EEP (shown as a dot) to exist along the line of discontinuity (shown as a vertical line), (i) the horizontal velocity component, which is assumed to be continuous, must change sign at the EEP, and (ii) the vertical velocity component, which is assumed to jump as the line of discontinuity is crossed, must change sign on either side of the vertical line.

Figure 3. The four cases in Fig.2 may be organized to classify an EEP as spiral-like or saddle-like, as shown. Spiral-like corresponds to A-C or B-D, while saddle-like corresponds to A-D or B-C.

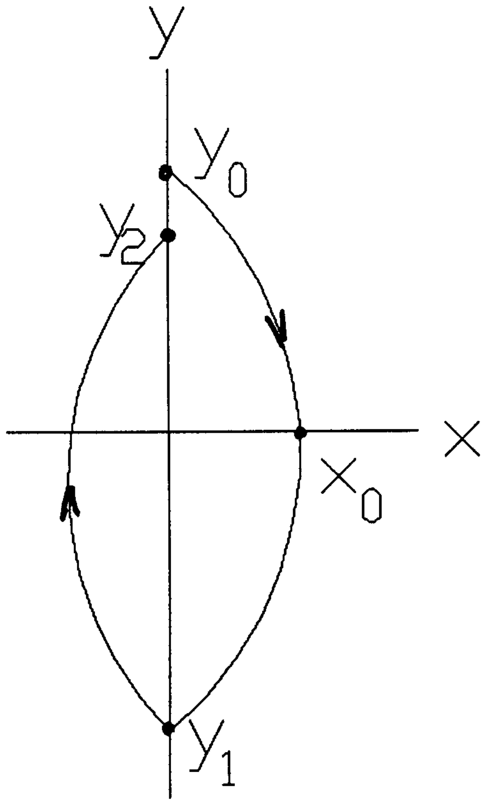


Figure 4. Geometry of the power series solution is based on a Poincare map corresponding to the cut $x = 0$. For the flow in the right half-plane $x \geq 0$, a motion starting at $y = y_0$ when $x = 0$ next cuts the y−axis at $y = y_1$. Both y_0 and y_1 share the same value of the x−intercept, $x = x_0$. For the flow in the left half-plane $x < 0$, a similar procedure relates y_2 to y_1. Combining the two halves gives y_2 as a function of y_0, yielding a determination of the stability of the EEP.