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Modeling the Detection of Motion Direction Signals in the Visual Cortex of Flies

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***Abstract*— Vision motion-detection is one of the most active areas in neuroscience today. Several nonlinear differential equations are derived to model the dendrities which carry information to the tangential cells in the fly's visual cortex and to model the dynamics in the synaptic inputs. We analyze the solutions of these equations derived under both the preferred direction and the null direction of a tangential cell in the visual cortex of fly. It is found that when the parameters are within a certain range, these mathematical models can explain how the visual system of the fly encodes motion signals like the change of direction. This knowledge may be used to design an electrical circuit whose function can be expressed as the differential equations and then can be used to detect change in the motion direction.**

I. INTRODUCTION

When a moving object passes in front of fly's compound eyes, the luminance signals pass through the facets of compound eyes, then through the first layer of the visual cortex (lamina) and the second layer (medulla), then reach the third layer, lobula and lobula plate. In the third layer, there are a group of interneurons called tangential cells. These neurons are direction-sensitive. Each neuron becomes maximally active when the object moves in certain direction, i.e., each neuron has its preferred direction.

In 1961, Hassenstein and Reichardt proposed a model for motion detection called elementary motion detector (EMD). There are accumulated experimental evidences that these EMDs are carried out in the first and second layer of visual cortex and they provide inputs to the tangential cells in the third layer. The outputs of EMDs are integrated by the tangential cells.

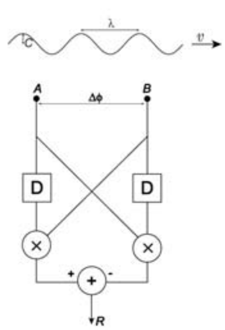

Figure 1.

A simplified version of elementary motion detector by Hassenstein and Reichardt is shown in Figure 1. A brief description about EMD based on Ron O.Dror's thesis (see [1]) is as follows:

Let the input to the visual system to be a luminance signal which varies continuously as a function of space and time. The two input channels, A and B, sample this signal at two points on the retinal field, separated by some spatial angle $\Delta\phi$. An object moving from left to right will pass first over A then over B. If the signal from A is delayed appropriately, the two signals will match. The Figture shows that the signal from A is delayed by a linear delay filter D, then multiplied with the signal form B. This delay-and-multiply operations also take place on the opposite arm. The outputs of these two multiplications are substracted to give the time dependent correlator output $R(t)$. A positive output indicates rightward image motion, a negative output indicates leftward image motion, a zero output indicates lack of motion.

We build a mathematical model for the tangential cell VS in the fly's vision system. Consider the situation when a sinuosoidal grating moves at a constant velocity along the preferred direction of VS cell (whose preferred direction is vertical motion from top to bottom). The soma of VS receive the input from its dendrity which is modelled as a "cable". At the end of the cable, the dendrity branch into many small branches. At the branch terminal sites, there are inputs from the synapses which come from the output of an array of elementary motion detectors.

First express the output of EMD in terms of the variables in the expression of luminance pattern and let the luminance pattern be a function of space (x) and time (t):

$$C\cos(2\pi f_t t - 2\pi f_s x) + K.$$

The meaning of the variables is as follows:

$$\begin{array}{lll} f_t & ---- & temporal\ frequency \\ f_s & ---- & spatial\ frequency \\ K & ---- & contant\ luminance\ level \\ C & ---- & amplitude\ of\ luminance\ signal \end{array}$$

The correlator input are given by

$$\begin{aligned} A(t) &= C\cos(2\pi f_t t) + K, \\ B(t) &= C\cos(2\pi f_t t - 2\pi f_s \Delta\phi) + K. \end{aligned}$$

The correlator output is

$$\begin{aligned} R(t) &= C^2 \times \frac{2\pi f_t \tau}{\sqrt{1+(2\pi f_t \tau)^2}} \sin(2\pi f_s \Delta\phi) \qquad (1) \\ &+ 4KC\sin(\pi f_s \Delta\phi) \times \\ &\quad \sqrt{\frac{(1+(2\pi f_t\tau)^2)^{\frac{1}{2}}-1}{2(1+(2\pi f_t \tau)^2)^{\frac{1}{2}}}} \times \\ &\quad \cos(2\pi f_t t - \pi f_s \Delta\phi - \frac{\Phi(f_t)}{2}). \end{aligned}$$

For details of the computation of correlator output, refer to Ron O.Dror's thesis (see [1]).

Write (1) as $R(t) = M + b\cos(\lambda t + \alpha)$, use this $R(t)$ as input to the dendritic branches.

Based on Hodgkin and Huxley's model for propagation of nerve impluse and Wilfrid Rall's model for dendrity (see [2],[3],[4],[10]), we use the following PDE to model the dynamics of motion detection.

$$\frac{\partial V_d}{\partial t} = \frac{\partial^2 V_d}{\partial x^2} - gV_d + \frac{1}{r}\int (V_{sh}(y,t) - \hat{v}(y,t))dy, \qquad (2)$$

$$C\frac{\partial V_{sh}(y,t)}{\partial t} = -C_1 \frac{V_{sh}}{w_{na}}(V_{sh} - w_{na})(\frac{V_{sh}}{w_{na}} - a) - \frac{1}{r}(V_{sh} - \hat{v}(y,t)) - C_2 z(y,t) - \int_{-\infty}^{t} F(y,t)dt, \qquad (3)$$

$$\frac{\partial z}{\partial t} = V_{sh}. \qquad (4)$$

Equation (2) describes the dynamics in the dendrity and (3) describes the dynamics in the axon terminals. Compared with Wilfrid Rall's model, we add the third term on the right hand side of equation (2) to describe the amount of current flowing into the dendritic trunk at time t. Compared with Hodgkin and Huxley's model, we add the second and the fourth terms on the right hand side of equation (3) to describe the external inputs to the axon terminals. The meaning of variables is as follows:

V_d	$----$	*voltage in dendritic trunk.*
V_{sh}	$----$	*voltage in axon terminal.*
$\hat{v}(y,t)$	$----$	*voltage in the branch terminal side at location y time t.*
z	$----$	*recovery variable.*
w_{na}	$----$	*equilibrium value of voltage related to sodium.*
F	$----$	*input to branches from EMD at location y at time t.*

Impose the boundary condition $\hat{v}(y,t) = 0$ and hold the voltage at the end of branch at zero then there is still current flowing into the branch.

We assume that on the dendritic trunk, current is only injected at the position x^*, so (2) becomes

$$\frac{\partial V_d}{\partial t} = \frac{\partial^2 V_d}{\partial x^2} - gV_d + \frac{1}{r}\int V_{sh}(y,t)dy \times \delta(x - x^*),$$

Let $g = 1, V_d = v, V_{sh} = w, \int V_{sh}(y,t)dy = g(t)$. We can write (2) as

$$\frac{\partial v}{\partial t} - \frac{\partial^2 v}{\partial x^2} + v = \frac{1}{r}g(t)\delta(x - x^*).$$

Assume that at $x = 0$, we have $\frac{\partial v}{\partial x} = 0$ (no current flows at $x = 0$). This boundary condition will be automatically satisfied if we extend the domain to $-\infty < x < \infty$ and put an image source at $x = x^*$ (for solution of this type of boundary value problem, see [5] p. 40), then we have

$$\begin{aligned} &(\partial_t - \partial_x^2 + 1)v(t,x) = Rg(t)[\delta(x - x^*) \qquad (5) \\ &+\delta(x + x^*)], \\ &v(t,x) = R\int_0^\infty g(t-t')\frac{e^{-t'}}{\sqrt{4\pi t'}} * \\ &[exp(-\frac{(x-x^*)^2}{4t'}) + exp(-\frac{(x+x^*)^2}{4t'})]dt'. \end{aligned}$$

Where $g(t) = \int w(y,t)dy,\ R = \frac{1}{r}$.

Under the assumption $\hat{v}(y,t) = 0$, (3) and (4) become

$$C\frac{\partial w}{\partial t} + C_1(\frac{w}{w_{na}})(w - w_{na})(\frac{w}{w_{na}} - a) + C_2 z + \int_{-\infty}^{t} F dt + \frac{1}{r}w = 0, \qquad (6)$$

$$\frac{dz}{dt} = w. \qquad (7)$$

Let $w = w_{na}w^*, z = w_{na}z^*$. From both sides of (6), take the derivative with respect to t, and write $w^*, z^*, \frac{F}{w_{na}}$ as $w, z, \hat{F}$ respectively. Since $C_1 >> C, C_2 \approx C$, let $C_1 = 1, \frac{C_1}{C} = \frac{1}{C} = k$, ie., let $C_1 = 1 = Ck, C_2 = C$, then we have

$$\ddot{w} + k[3w^2 - 2(a+1)w + a]\dot{w} + w = k\hat{F}.$$

This is the dynamics in the axon terminal.

When the parameters satisfy certain condition, this equation has oscillating behaviour. The forcing term $k\hat{F}$ has the form $k\frac{R(t)}{w_{na}}$ where $R(t)$ is the output from the EMD.

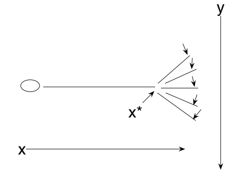

Figure 2.

$R(t) = M + b\cos(\lambda t + \alpha)$. Write $\frac{M}{w_{na}}, \frac{b}{w_{na}}$ again as M, b repectively and then (6) becomes

$$\ddot{w} + k[3w^2 - 2(a+1)w + a]\dot{w} + w = k(M + b\cos(\lambda t + \alpha)).$$

The forcing term is asymmetric, we call this oscillation an **asymmetric forced oscillation.** From the previous discussion, we know the membrane potential of the tangential cell depends on the dynamics in the axon terminals. Hence, studying this asymmetric forcing oscillation is important in understanding the dynamics of tangential cell which play an important role in the detection of motion.

II. ASYMMETRIC FORCED OSCILLATION

According to the previous discussion, when a sinsuiodal grating is moving in the preferred direction of tangential cell, we use the following equation to describe the dynamics in the axon terminal:

$$\ddot{x} + k[3x^2 - 2(a+1)x + a]\dot{x} + x = k(M + b\cos(\lambda t + \alpha)).$$

Making changes of variable and doing some arithmetic operations, we can write the above equation as an asymmetric forced van-der-pol equation:

$$\ddot{x} + k(x^2 - 1)\dot{x} + x = k(M + b\cos(\lambda t)). \qquad (8)$$

Make a change of variable to the lienard plane, and write (8) as

$$\begin{aligned} \dot{x} &= k(y - \Phi(x)) && (9) \\ \dot{y} &= -\frac{1}{k}x + R(t) && (10) \end{aligned}$$

Where $\Phi(x) = \frac{x^3}{3} - x,\ R(t) = M + b\cos(\lambda t)$.

Ploting the trajectory using the computer, we find that when M is sufficiently small and b is sufficiently large, the trajectory undergoes large amplitude oscillations and has a big "ear" and a small "ear" in the x-y plane (see Fig.3), and the system has a periodic solution. The proofs are in the appendix.

Next, consider the sinsuiodal grating moving in the null direction, the equation becomes

$$\ddot{x} + k(x^2 - 1)\dot{x} + x = -k(M + b\cos(\lambda t)).$$

In the lienard plane , we have

$$\begin{aligned} \dot{x} &= k(y - \Phi(x)) && (11) \\ \dot{y} &= -\frac{1}{k}x - R(t) && (12) \end{aligned}$$

The trajectory of (11) and (12) is just the reflection of the trajectory of (9) and (10) with respect to the origin, with "big ear" at the left bottom , "small ear" at the right top.

Ploting x as a function of t, we compare the dynamics under the preferred motion direction and the null motion

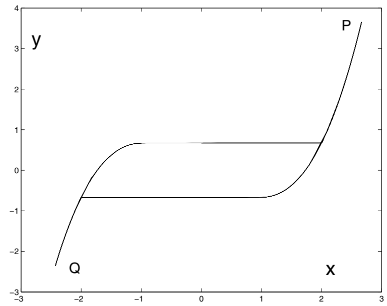

Figure 3.

direction. We find that there is a constant shift down when the direction changes from the preferred direction to the null direction. Thus, we conclude that the direction information is coded in this constant shift up and down of the voltage in the axon terminals. This is also reflected in the change of membrane potential of the tangential cell in view of equation (5). This result is obtained through mathematical modeling. We can find supporting evidence in [6] in which a similar result is obtained through biological experiments.

III. CONCLUSIONS AND FUTURE WORK

Several differential equations are used to model the dendrities which carry information to the tangential cells in the fly's vision system. We conclude that the direction information is encoded in the constant shift up or down of membrane potential of tangential cell. Research is underway to model the network of tangential cells in order to explain the mechanics underlining the "population vector" hypothesis. Therefore, we can understand how fly detect motion in an arbitrary direction.

Also, we try to use this mathematical model to design an electrical circuit so that the function of this electrical circuit can be expressed as the differential equations in the mathematical model. Hence we can design a motion-detector using the electrical circuit.

IV. APPENDIX

We want to show that under certain restriction of M and b, the trajectory of (9) and (10) undergoes big amplitude oscillations and has "big ear" and "small ear" as indicated in section II.

First, we prove that the trajectory is bounded , i.e., we proved that $|x| \le B, |\dot{x}| \le Bk$ if $|kM| < 2$.

To prove this, we need several lemmas, the proofs of the following lemmas (lemma 1-5) follow the same pattern as lemma 1-5 in "Forced oscillations in nonlinear systems" by M.L.Cartwright (see [8], p. 163-173) and the proof of Theorm 2 follow the pattern as lemma 4.1 in "The non-autonomous van-der-pol equation" by N.G.Lloyd (see [9], p. 215). Refer to these two papers for the meaning of symbols used in the following proofs. In this section, "A" is a constant which may be different at each occurence.

Lemma 1: If $-\frac{2}{k} < M < \frac{2}{k}$, then $|x|$ is not greater than 2 for all large t.

Proof: Suppose $x \geq 2$ for all $t > T$, we have

$$\dot{x} - Y + kF(x) + \int_T^t x dt = k \int_T^t (M + b\cos\lambda t)dt,$$
$$\int_T^t x dt = k[M(t-T) + \frac{b}{\lambda}(\sin(\lambda t) - \sin(\lambda T))]$$
$$-kF(x) - \dot{x} + Y.$$

Where $F(x) = \int_X^x f(x)dx, \quad X = x(T), Y = \dot{x}(T)$. If $x > 2$ for all $t > T$, we have

$$\begin{aligned}
2(t-T) &< \int_T^t x dt \\
&= kMt - kF(x) - \dot{x} + Y + \frac{kb}{\lambda}(\sin\lambda t \\
&- \sin\lambda T) - kMT \\
&< kMt - \dot{x} + Y + A. \\
2(t-T) - kMt &< -\dot{x} + Y + A. \\
(2 - kM)t &< -\dot{x} + Y + A + 2T.
\end{aligned}$$

Since $kM < 2$, left hand side goes to $+\infty$ as $t \to +\infty$, so we need to have $\dot{x} \to -\infty$, but then $x \to -\infty$, a contradiction.

Similarly, suppose $x < -2$ for all $t > T$, then we have

$$kMt - kF(x) - \dot{x} + Y + kM(-T) + \frac{kb}{\lambda}(\sin\lambda t$$
$$-\sin\lambda T) = \int_T^t x dt < (-2)(t-T),$$
$$-kF(x) - \dot{x} + Y < (-2 - kM)t + 2T + kMT$$
$$-\frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T),$$
$$-kF(x) - \dot{x} + Y < (-2 - kM)t + A,$$
$$-\dot{x} + Y < (-2 - kM)t + A.$$

Since $kM > -2$, let $t \to +\infty$, then right hand side goes to $-\infty$, so $\dot{x} \to +\infty$, then $x \to +\infty$, a contradiction. ■

Lemma 2: If $|x| < 2$ on an arc PQ , then $|\dot{x_Q}| < |\dot{x_P}| + B_1(k+1)$.

Proof:

$$\dot{x_Q} - \dot{x_{p_1}} + k \int_{x_{P_1}}^{x_Q} f(x)dx + \int_{P_1}^Q x dt = kM(t-T)$$
$$+\frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T),$$
$$\dot{x_Q} - \dot{x_{P_1}} = -kF(x) - \int_{P_1}^Q x dt$$
$$+kM(t-T) + \frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T).$$

$f(x) = x^2 - 1 \geq -1, F(x) \geq (-1)(x - X) \geq -4$, hence $-kF(x) \leq 4k$. $\dot{x}$ has same sign as $\dot{x_Q}$ on P_1Q, otherwise if $\dot{x}$ changes sign, then at some point we have $\dot{x} = 0$ on P_1Q, but we choose P_1 to be the last point before Q at which $|\dot{x}| \leq k+1$ or P itself whichever is the latest, so $|\dot{x}| = 0 < k+1$ on P_1Q, a contradiction.

Suppose $\dot{x_Q} > 0$, then $\dot{x} > 0$ on P_1Q, $x - X = \int_T^t \dot{x}dt > (k+1)(t-T)$, hence $t - T < \frac{x-X}{k+1} < \frac{4}{k+1}$, so $t - T$ is at most 4. So we have

$$\begin{aligned}
\dot{x_Q} - \dot{x_{P_1}} &\leq 4k + 2(t-T) + kM(t-T) + 2\frac{kb}{\lambda} \\
&\leq 4k + 8 + 4kM + 2\frac{kb}{\lambda} \\
&\leq A(k+1).
\end{aligned}$$

If $P_1 = P$ we are done, if not, we have

$$\begin{aligned}
|\dot{x_Q}| &\leq \dot{x_{P_1}} + A(k+1) \\
&\leq k + 1 + A(k+1) \\
&< A(k+1) + |\dot{x_P}|.
\end{aligned}$$

If $\dot{x_Q} < 0, \dot{x} < 0$ on PQ, obtain the corresponding result for $-\dot{x_Q}$:

$$- \quad \dot{x_Q} + \dot{x_{P_1}} + kF(x)|_{-x_{P_1}}^{-x_Q} + \int_{P_1}^Q (-x)dt = kM(t-T)$$
$$+ \quad \frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T),$$
$$- \quad \dot{x_Q} + \dot{x_{P_1}} < kF(x) + \int_{P_1}^Q |x|dt + kM(t-T)$$
$$+ \quad \frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T).$$

$F(x) = -\int_x^X f(x)dx \leq X - x \leq 4$, note that $x < X$, we have $x - X = \int_T^t \dot{x}dt < -(k+1)(t-T)$, hence $t - T < \frac{X-x}{k+1}$, where $t - T$ is at most 4. So we have $-\dot{x_Q} < -\dot{x_{P_1}} + A(k+1)$. Done. ■

Lemma 3: If arc QR lies above $x = 2$ and begins and ends on $x = 2$, the greatest height h: $h \leq \frac{\dot{x_Q}}{3k} + \frac{2b}{3\lambda} + 1 + \frac{M}{3}(t-T)$.

Proof:

$$\begin{aligned}
\dot{x_H} = 0 &= \dot{x_Q} - k\int_1^h f(x)dx - \int_T^t x dt + k\int_T^t p dt, \\
0 &\leq \dot{x_Q} - 3k(h-1) + kM(t-T) \\
&+ \frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T), \\
(\ f(x) &= x^2 - 1 \geq 3 \ when \ x \geq 2, \int_T^t x dt > 0\ ) \\
3kh &\leq \dot{x_Q} + 3k + kM(t-T) + \frac{kb}{\lambda}(\sin\lambda t \\
&- \sin\lambda T), \\
h &\leq \frac{\dot{x_Q}}{3k} + \frac{2b}{3\lambda} + 1 + \frac{M}{3}(t-T).
\end{aligned}$$

■

Lemma 4: The time τ taken to describe QR is less than $B_3(\dot{x_Q} + k)$.

Proof: Choose any point x in the arc QR ,

$$\begin{aligned}
\dot{x} &= \dot{x_Q} - k\int_X^x f(x)dx - \int_T^t xdt + kM(t-T) \\
&+ \frac{kb}{\lambda}(\sin\lambda t - \sin\lambda T) \\
&< \dot{x_Q} - 2(t-T) + kM(t-T) + \frac{2kb}{\lambda}, \\
&\quad (\ f(x) > 0, \int_T^t x \geq 2(t-T)\ ) \\
\dot{x} &< \dot{x_Q} + (kM-2)(t-T) + \frac{2kb}{\lambda}, \\
0 &= x_R - x_Q = \int_0^\tau \dot{x}dt \\
&< \int_0^\tau (\dot{x_Q} + (kM-2)(t-T) + \frac{2kb}{\lambda})dt, \\
\tau &< 2T + \frac{4kb}{(2-kM)\lambda} + \frac{2}{2-kM}\dot{x_Q}.
\end{aligned}$$

Choose E such that $0 < E < 2$, let $kM < 2 - E$, fix E, then

$$\begin{aligned}
\tau &< 2T + \frac{4b}{E\lambda}k + \frac{2}{E}\dot{x_Q}, \\
\tau &< k(T + \frac{4b}{E\lambda}) + \frac{2}{E}\dot{x_Q}.
\end{aligned}$$

Choose $B_3 \geq max(\frac{2}{E}, T + \frac{4b}{E\lambda})$, then $\tau < B_3\dot{x_Q} + B_3 k = B_3(\dot{x_Q} + k)$. ∎

Lemma 5: If QR is an arc above $x = 1$ begining and ending on $x = 1$, then for given $B_1 > 1$, there exists $B_4 > B_1$ such that if $\dot{x_Q} > B_4(k+1)$, then $\dot{x_R}^2 < \dot{x_Q}^2 - 8B_1 k\dot{x_Q}$.

We can prove lemma 5, only using that $p(t) = M + b\cos\lambda t \leq B$. In lemma 5, there is no need for $\int p(t)$ to be bounded, so the proof is the same as in cartwright's paper (see [8], p. 167).

With lemma 1-5 , we have the following main theorem.

Theorem 1: If $|kM| < 2$, then the trajectory is bounded, i.e. $|x| \leq B, |\dot{x}| \leq Bk$.

Then the existence of a periodic solution follows the same proof as Theorem 5 in M.L.Cartwright's paper (see [8], p.179).

Next, prove it is a big amplitude oscillation and there exists "big ear" and "small ear".

After the trajectory reaches the maximum P, we prove that it will cross -2 to reach the first minimum Q (big amplitude, see Fig.3).

$\dot{x_Q} - \dot{x_P} + kF(x)|_P^Q + \int_T^t xdt = \frac{kM}{\lambda}(\phi_Q - \phi_P) + \frac{kb}{\lambda}(\sin\phi_Q - \sin\phi_P) \Rightarrow$
$F(x_Q) - F(x_P) + k^{-1}\int_T^t xdt = \frac{M}{\lambda}(\phi_Q - \phi_P) + \frac{b}{\lambda}(\sin\phi_Q - \sin\phi_P) \Rightarrow$
$F(x_Q) = F(x_P) - k^{-1}\int_T^t xdt + \frac{M}{\lambda}(\phi_Q - \phi_P) + \frac{b}{\lambda}(\sin\phi_Q - \sin\phi_P)$

We want to show $F(x_Q) \leq F(-2)$.

At maximum or minimum point , we have $\ddot{x} + x = k(M + b\cos\phi)$, hence $\cos\phi = \frac{\ddot{x}+x}{bk} - \frac{M}{b}$. Since x is bounded, and $|\ddot{x}|$ is small at the neighborhood of P and Q, hence $|\ddot{x} + x|$ is bounded at the neighborhood of P and Q.

We have $\cos\phi = \frac{\ddot{x}+x}{bk} - \frac{M}{b} = -\frac{M}{b} + O(\frac{1}{k})$.

Let $\alpha_1 = arccos(-\frac{M}{b}), \alpha_2 = 2\pi - arccos(-\frac{M}{b})$, we have $\phi_P = \alpha_1 + O(\frac{1}{k})$ and $\phi_Q = \alpha_2 + O(\frac{1}{k})$.

$$\begin{aligned}
F(x_Q) &= F(x_P) - k^{-1}\int_T^t xdt + \frac{M}{\lambda}(\alpha_2 - \alpha_1 + O(\frac{1}{k})) \\
&+ \frac{b}{\lambda}(\sin\phi_Q - \sin\phi_P).
\end{aligned}$$

Where $\alpha_1 = arccos(-\frac{M}{b}),\ \cos\alpha_1 = -\frac{M}{b}$, $\sin\alpha_1 = \sqrt{1 - \frac{M^2}{b^2}}$ and $\alpha_2 = 2\pi - arccos(-\frac{M}{b})$, $\sin\alpha_2 = -\sin(arccos(-\frac{M}{b})) = -\sqrt{1 - \frac{M^2}{b^2}}$, $\sin\phi_P = \sqrt{1 - \frac{M^2}{b^2}} + O(\frac{1}{k}),\ \sin\phi_Q = -\sqrt{1 - \frac{M^2}{b^2}} + O(\frac{1}{k})$.

$$\begin{aligned}
F(x_Q) &= F(x_P) - k^{-1}\int_T^t xdt + \frac{M}{\lambda}(\alpha_2 - \alpha_1) \\
&+ \frac{M}{\lambda}O(\frac{1}{k}) + \frac{b}{\lambda}(-2\sqrt{1 - \frac{M^2}{b^2}} + O(\frac{1}{k})) \\
&\leq F(x_P) + k^{-1}|x|(t-T) + \frac{M}{\lambda}(\alpha_2 - \alpha_1) \\
&+ \frac{M}{\lambda}O(\frac{1}{k}) - 2\sqrt{1 - \frac{M^2}{b^2}}\frac{b}{\lambda} + \frac{b}{\lambda}O(\frac{1}{k}) \\
&\leq F(x_P) + \frac{B}{k}(\frac{\alpha_2 - \alpha_1}{\lambda} + O(\frac{1}{k})) + \frac{M}{\lambda}(\alpha_2 \\
&- \alpha_1) + \frac{M}{\lambda}O(\frac{1}{k}) - 2\sqrt{1 - \frac{M^2}{b^2}}\frac{b}{\lambda} + \frac{b}{\lambda}O(\frac{1}{k}) \\
&\leq A + O(\frac{1}{k}) - 2\sqrt{1 - \frac{M^2}{b^2}}\frac{b}{\lambda}.
\end{aligned}$$

Hence when M is sufficiently small, we can choose b sufficiently large such that $F(x_Q) \leq F(-2)$. So the trajectory will cross -2 before it reach the first minimum.

Similarly we can prove that when b is sufficiently large, the first maximum after Q will cross 2, then begin another period.

Therefore we have the conclusion: When b is sufficiently large, the trajectory is big amplitude oscillation.

Next, we prove the "big/small" ear.

Want to show $|F(x_Q)| < |F(x_P)|$.

$$\begin{aligned}
|F(x_Q)| &= -F(x_Q) \\
&= -F(x_P) + k^{-1}\int_T^t xdt - \frac{M}{\lambda}(\phi_Q - \phi_P) \\
&- \frac{b}{\lambda}(\sin\phi_Q - \sin\phi_P).
\end{aligned}$$

Want to show $-F(x_P) + k^{-1}\int_T^t xdt - \frac{M}{\lambda}(\phi_Q - \phi_P) - \frac{b}{\lambda}(\sin\phi_Q - \sin\phi_P) < F(x_P)$, which is equivalent to

$$\begin{aligned}
F(x_P) &> \frac{1}{2}k^{-1}\int_T^t xdt \qquad (13) \\
&- \frac{1}{2}\frac{M}{\lambda}(\phi_Q - \phi_P) - \frac{1}{2}\frac{b}{\lambda}(\sin\phi_Q - \sin\phi_P).
\end{aligned}$$

Since $\sin\phi_Q - \sin\phi_P > -2$, if we have $F(x_P) > \frac{b}{\lambda} + \frac{1}{2}k^{-1}\int_T^t x dt$, then (13) holds.

$\int_T^t |x| dt < A(t-T) = \frac{A}{\lambda}(\phi_Q - \phi_P) = \frac{A}{\lambda}(\alpha_2 - \alpha_1) + \frac{A}{\lambda}O(\frac{1}{k})$, hence $\frac{b}{\lambda} + \frac{1}{2}k^{-1}\int_T^t x dt = \frac{b}{\lambda} + O(\frac{1}{k})$.

So we want to show $F(x_P) > \frac{b}{\lambda} + O(\frac{1}{k})$, i.e., $F(x_P) > \frac{b}{\lambda} + h$, where $h = \frac{D}{k}$, for some constant D.

Let $\hat{h}$ be a constant such that $F(\hat{x} + \hat{h}) = \frac{b}{\lambda} + h$ where $F(\hat{x}) = \frac{b}{\lambda}$. We have the following theorem

Theorem 2: Suppose trajectory will spend some time in the tube $\{x||x-\hat{x}| \leq \hat{h}\}$, then it will cross the line $x = \hat{x}+\hat{h}$. So at the maximum point P, we have $F(x_P) > \frac{b}{\lambda} + h$.

Proof: Suppose the trajectory cannot cross the line $x = \hat{x} + \hat{h}$, let x_1, x_2 be two points within the tube, trajectory first reach x_1 then reach x_2 at the phase ϕ_1, ϕ_2 respectively, choose point x_2 in the way such that the corresponding phase ϕ_2 satisfy $\sin\phi_2 - \sin\phi_1 = \frac{A}{k} < \hat{h}$.

Let $x_1 = \hat{x} + l_1, x_2 = \hat{x} + l_2, |l_1| < \hat{h}, |l_2| < \hat{h}$.

We have

$$\begin{aligned}
&F(\hat{x} + l) = \frac{b}{\lambda} + (\hat{x}^2 - 1)l + \hat{x}l^2 + \frac{1}{3}l^3, \\
&|F(\hat{x} + l_1) - F(\hat{x} + l_2)| \\
&= |(\hat{x}^2 - 1)(l_1 - l_2) + \hat{x}(l_1^2 - l_2^2) + \frac{1}{3}(l_1^3 - l_2^3)|, \\
&\leq 2(\hat{x}^2 - 1)\hat{h} + O(\frac{1}{k^2}) + O(\frac{1}{k^3}).
\end{aligned}$$

On the other hand,

$$\begin{aligned}
F(x_2) - F(x_1) &= \frac{M}{\lambda}(\phi_2 - \phi_1) + \frac{b}{\lambda}(\sin\phi_2 - \sin\phi_1) \\
&- k^{-1}\int_{t_1}^{t_2} x dt - k^{-1}\dot{x}|_{t_1}^{t_2}, \\
&> \frac{M}{\lambda}(\phi_2 - \phi_1) + \frac{b}{\lambda}\frac{A}{k} - (\frac{C}{k} + \frac{B}{k}).
\end{aligned}$$

If $\frac{M}{\lambda}(\phi_2 - \phi_1) + \frac{b}{\lambda}\frac{A}{k} - (\frac{C}{k} + \frac{B}{k}) > 2(\hat{x}^2 - 1)\hat{h} + O(\frac{1}{k^2}) + O(\frac{1}{k^3})$ then we have a contradiction. So if $b > (\frac{C}{k} + \frac{B}{k} + 2\hat{x}^2\hat{h} - \hat{h} + O(\frac{1}{k^2}) + O(\frac{1}{k^3}) - \frac{M}{\lambda}(\phi_2 - \phi_1))\frac{k\lambda}{A}$, we have a contradiction. Thus the trajectory will cross the line $x = \hat{x} + \hat{h}$ when b is sufficiently large. ∎

Next , we impose some conditions so that the trajectory will spend some time in the tube.

We impose the initial condition $x_o > \hat{x}$. Consider the next half circle. First we need that it is big amplitude, after minimum Q ,trajectory pass 2 , then reach the first maximum R.

Then $k^{-1}\dot{x}|_Q^R + F(x)|_Q^R + k^{-1}\int_Q^R x dt = \frac{M}{\lambda}(\phi_R - \phi_Q) + \frac{b}{\lambda}(\sin\phi_R - \sin\phi_Q)$. We want that $F(x_R) = \frac{M}{\lambda}(\phi_R - \phi_Q) + \frac{b}{\lambda}(\sin\phi_R - \sin\phi_Q) - k^{-1}\int_Q^R x dt + F(x_Q) > F(2)$.

The first maximum after Q is on the slow manifold, hence $\ddot{x}$ is bounded, proceeding as before, we have

$$\begin{aligned}
\sin\phi_R &= \sqrt{1 - \frac{M^2}{b^2}} + O(\frac{1}{k}), \\
\sin\phi_Q &= -\sqrt{1 - \frac{M^2}{b^2}} + O(\frac{1}{k}), \\
\cos\phi_R &= -\frac{M}{b} + O(\frac{1}{k}).
\end{aligned}$$

We have $\sin\phi_R - \sin\phi_Q > 0$. So if b is sufficiently large, the trajectory will cross 2. Next, we prove that when b is sufficiently large, the trajectory will cross $\hat{x}$.

We need $F(x_R) = \frac{M}{\lambda}(\phi_R - \phi_Q) + \frac{b}{\lambda}(\sin\phi_R - \sin\phi_Q) - k^{-1}\int_Q^R x dt + F(x_Q) > F(\hat{x})$, i.e., $F(x_R) = \frac{M}{\lambda}(\phi_R - \phi_Q) + \frac{b}{\lambda}(\sin\phi_R - \sin\phi_Q) - k^{-1}\int_Q^R x dt + F(x_Q) > \frac{b}{\lambda}$. So we only need b greater than certain value to ensure trajectory pass $\hat{x}$, then begin another period.

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