

EFFECTS OF AVERAGING ON SODE MODELS OF DYNAMIC CELL PROCESSES

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Lucrarea studiază efectele medierii directe și ciclice asupra unui sistem neliniar de ecuații diferențiale de tip Van der Pohl, care modelează reacții chimice în procesele metabolice ale celulei. Se pune în evidență natura ciclică a sistemelor original și mediat. Rezultatele obținute sunt ilustrate prin simulări realizate cu ajutorul pachetului software Maple 9.5.

The paper studies the effects of cyclic averaging on the Van der Pohl SODE which models complex chemical reactions in metabolic cell processes. The obtained results are illustrated by Maple 9.5 computer simulations and the cyclic nature of both the original and mediated SODE is emphasized.

Keywords: dynamical system, averaging, periodicity, numerical simulation.

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Introduction

A classical example of oscillating systems of differential equations with applications in biology is the Van der Pohl dynamical system ([1], [2], [3])

$$\begin{cases} \dot{x} = y \\ \dot{y} = a(1 - x^2)y - x, \end{cases} \quad (1)$$

where a is a small real parameter. This represents a simplified model for chemical reactions in metabolic systems. In the following we shall describe the SODE averaging method and apply it to our system in both direct and trigonometric form. We shall conclude that the resulting systems lead to identical paths, and emphasize the presence of the limit cycles for both the original and the averaged systems.

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1. The averaging method - preliminaries

We consider in general a SODE of the form ([4], [5])

$$\dot{X}(t) = A(t) \cdot X(t) + \varepsilon \cdot f(X(t), t), \quad (2)$$

where $X(t) \in M_{n \times 1}(\mathbb{R})$, with the initial condition $X(0) = X_0$, time $t \in \mathbb{R}$, $A(t) \in M_{n \times n}(\mathbb{R})$, $f(X(t), t)$ is an $n \times 1$ matrix of smooth functions of t and X , and ε is a sufficiently small parameter, $\varepsilon < 1$.

We say that the equation (2) is *perturbed* by the parameter ε . Then for $\varepsilon = 0$ one obtains the non-perturbed linear SODE

$$\dot{X}(t) = A(t) \cdot X(t) \quad (3)$$

whose general solution has the form

$$X(t) = \phi(t) \cdot X_0, \quad (4)$$

where via a coordinate-change adjustment one can assume that the matrix function $\phi(t) \in M_{n \times n}(\mathbb{R})$ satisfies $\phi(0) = I_n$. In order to find the solution of the SODE (2), we apply the Lagrange process, by replacing X_0 with $Y(t)$, which will provide the solutions

$$X(t) = \phi(t) \cdot Y(t). \quad (5)$$

Replacing (5) in (2), it follows that

$$\dot{\phi}(t) \cdot Y(t) + \phi(t) \cdot \dot{Y}(t) = A(t) \cdot \phi(t) \cdot Y(t) + \varepsilon \cdot f(\phi(t) \cdot Y(t), t). \quad (6)$$

Since the matrix $\phi(t)$ satisfies the SODE (3), we have $\dot{\phi}(t) = A(t) \cdot \phi(t)$, which leads to

$$\dot{\phi}(t) \cdot Y(t) = A(t) \cdot \phi(t) \cdot Y(t). \quad (7)$$

From the relations (6) and (7), we obtain the nonlinear SODE

$$\phi(t) \cdot \dot{Y}(t) = \varepsilon \cdot f(\phi(t) \cdot Y(t), t),$$

which rewrites, taking into account the invertibility of the matrix $\phi(t)$,

$$\dot{Y}(t) = \varepsilon \cdot \phi^{-1}(t) \cdot f(\phi(t) \cdot Y(t), t). \quad (8)$$

By denoting

$$F(Y(t), t) = \phi^{-1}(t) \cdot f(\phi(t) \cdot Y(t), t),$$

the system (8) becomes

$$\dot{Y}(t) = \varepsilon \cdot F(Y, t), \quad (9)$$

where, as initially stated, $\varepsilon \ll 1$. This yields that $\dot{Y}(t)$ is very small (since it depends on the parameter ε), which implies a very small variation of $Y(t)$ in a certain amount of time T - which can be taken as the period, in the case of periodic motions. Then, assuming Y constant for $t \in [0, T]$ and averaging over the interval $[0, T]$, from (9), we infer the autonomous SODE

$$\dot{\tilde{Y}} = \varepsilon \cdot \tilde{F}(\tilde{Y}), \quad (10)$$

where $\tilde{F}(\tilde{Y}) = \frac{1}{T} \cdot \int_0^T F(\tilde{Y}, t) dt$. This new system is *autonomous*, and is generally much easier to integrate than (9).

If one determines the solution $Y(t)$ of the SODE (9), then the solution $X(t)$ results from (5). Still, by using the presented above *averaging method*, we get the averaged solution $\tilde{Y}(t)$ of (10).

In this case, a natural question is to what extent the solution $\tilde{Y}(t)$ of the system (10) approximates the solution $Y(t)$ of the system (9).

The following theorem answers this question.

Theorem. ([4], [5]) *If the function $F(Y, t)$ and the functional determinant $\frac{DF}{DY}$ are defined, continuous and bounded by a constant $M > 0$, which is independent of the parameter $\varepsilon \ll 1$ in the domain $D(Y, \tilde{Y})$ and if $F(X, t)$ is periodic in t and has the period T , independent of the parameter ε and if \tilde{Y} takes its values in a subset which is included in the domain $D(Y, \tilde{Y})$, then the solution $Y(t)$ of the SODE (9) and the solution \tilde{Y} of the averaged system (10) satisfy the relation:*

$$\|Y(t) - \tilde{Y}(t)\| = O(\varepsilon),$$

on the time-scale $\frac{1}{\varepsilon}$, for $t \rightarrow \pm\infty$.

The method described above is called the averaging method (the general case) or *the method of direct averaging*. In the case of two-dimensional SODE which exhibits periodicity in the non-perturbed case, we often use a simpler alias of this method, which implies using polar coordinates, called *trigonometric averaging*.

2. The method of direct averaging (I)

In our case, the SODE (1) has the form (2) with $A(t) = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}$ and $f((X(t), t) = \begin{pmatrix} 0 \\ (1 - x^2)y \end{pmatrix}$. Since the complex spectrum of A is $\{\pm i\}$, the non-perturbed system $\dot{X} = AX$ exhibits periodicity. Our SODE can be re-written in the form (2)

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \underbrace{\begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}}_{A(t)} \cdot \begin{pmatrix} x \\ y \end{pmatrix} + a \cdot \underbrace{\begin{pmatrix} 0 \\ (1 - x^2)y \end{pmatrix}}_{f(X(t), t)}, \quad a = \varepsilon \ll 1. \quad (11)$$

The non-perturbed linear SODE $\dot{X}(t) = A(t) \cdot X(t)$ has the general solution

$$X(t) = \begin{pmatrix} x_0 \cos t + y_0 \sin t \\ -x_0 \sin t + y_0 \cos t \end{pmatrix} = \underbrace{\begin{pmatrix} \cos t & \sin t \\ -\sin t & \cos t \end{pmatrix}}_{\phi(t)} \underbrace{\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}}_{X_0}. \quad (12)$$

where ϕ satisfies $\phi(0) = I_n$. Following the Lagrange process, the particular solution of (1) should have the form

$$X(t) = \underbrace{\begin{pmatrix} \cos t & \sin t \\ -\sin t & \cos t \end{pmatrix}}_{\phi(t)} \cdot \underbrace{\begin{pmatrix} y_1(t) \\ y_2(t) \end{pmatrix}}_{Y(t)} = \begin{pmatrix} y_1(t) \cos t + y_2(t) \sin t \\ -y_1(t) \sin t + y_2(t) \cos t \end{pmatrix}, \quad (13)$$

which should satisfy (1), whence we get

$$\dot{Y}(t) = a \cdot F(Y(t), t), \quad (14)$$

with $F(Y(t), t)$ given by

$$\underbrace{\begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix}}_{\phi^{-1}(t)} \cdot \underbrace{\begin{pmatrix} 0 \\ (-y_1 \sin t + y_2 \cos t) \cdot [1 - (y_1 \cos t + y_2 \sin t)^2] \end{pmatrix}}_{f(\phi(t) \cdot Y(t), t)}$$

or, in detail,

$$\begin{cases} \dot{y}_1 = a(y_1 \sin^2 t - y_2 \cos t \sin t)h(t) \\ \dot{y}_2 = a(-y_1 \sin t \cos t + y_2 \cos^2 t)h(t), \end{cases} \quad (15)$$

where $h(t) = (1 - y_1^2 \cos^2 t - 2y_1 y_2 \sin t \cos t - y_2 \sin^2 t)$. Averaging over the interval $0 \leq t \leq 2\pi$, and considering $\tilde{y}_{1,2}$ as being t -independent in the integration process, we infer

$$\begin{cases} \dot{\tilde{y}}_1 = \frac{1}{2\pi} \cdot a \int_0^{2\pi} (\tilde{y}_1 \sin^2 t - \tilde{y}_2 \cos t \sin t) \theta(t) dt \\ \dot{\tilde{y}}_2 = \frac{1}{2\pi} \cdot a \int_0^{2\pi} (-\tilde{y}_1 \sin t \cos t + \tilde{y}_2 \cos^2 t) \theta(t) dt, \end{cases} \quad (16)$$

where we denoted $\theta(t) = (1 - \tilde{y}_1^2 \cos^2 t - 2\tilde{y}_1 \tilde{y}_2 \sin t \cos t - \tilde{y}_2 \sin^2 t)$, i.e., we get the autonomous averaged system

$$\begin{cases} \dot{\tilde{y}}_1 = \frac{a}{2} \left(\tilde{y}_1 - \frac{\tilde{y}_1^3}{4} - \frac{\tilde{y}_1 \tilde{y}_2^2}{4} \right) \\ \dot{\tilde{y}}_2 = \frac{a}{2} \left(\tilde{y}_2 - \frac{\tilde{y}_2^3}{4} - \frac{\tilde{y}_2 \tilde{y}_1^2}{4} \right). \end{cases} \quad (17)$$

By division, this yields

$$\dot{\tilde{y}}_1 = \frac{\tilde{y}_1}{\tilde{y}_2} \dot{\tilde{y}}_2 \Rightarrow \tilde{y}_2 = \tilde{y}_1 \cdot k, \quad k \in \mathbb{R}, \quad (18)$$

and from the initial conditions $\tilde{y}_1(0) = x_0$ and $\tilde{y}_2(0) = y_0$, we infer $k = \frac{y_0}{x_0}$. Then the first equation in (17) leads to the ODE

$$\frac{d\tilde{y}_1}{\tilde{y}_1[\tilde{y}_1^2(1+k^2) - 4]} = -\frac{a}{8} dt, \quad (19)$$

which integrates to

$$\ln \frac{\tilde{y}_1^2(1+k^2) - 4}{\tilde{y}_1^2} = -at + C, \quad C \in \mathbb{R}. \quad (20)$$

For $t = 0$, we have $k = \frac{y_0}{x_0}$, which leads to $C = \ln |(x_0^2 + y_0^2 - 4)x_0^{-2}|$. Then from (18) and (20) we infer

$$\begin{cases} \tilde{y}_1 = \frac{2x_0}{\sqrt{x_0^2 + y_0^2 - e^{-at}(x_0^2 + y_0^2 - 4)}} \\ \tilde{y}_2 = \frac{2y_0}{\sqrt{x_0^2 + y_0^2 - e^{-at}(x_0^2 + y_0^2 - 4)}}, \end{cases} \quad (21)$$

which via (13) leads to the final solution

$$\begin{cases} \tilde{x} = \frac{2}{\sqrt{x_0^2 + y_0^2 - e^{-at}(x_0^2 + y_0^2 - 4)}} (x_0 \cos t + y_0 \sin t) \\ \tilde{y} = \frac{2}{\sqrt{x_0^2 + y_0^2 - e^{-at}(x_0^2 + y_0^2 - 4)}} (-x_0 \sin t + y_0 \cos t). \end{cases} \quad (22)$$

We notice that for arbitrary (x_0, y_0) , the solution is a spiray which approaches the circle Γ centered at the origin of radius $r = 2$, which represents in this case a *limit cycle*. In other words, we have

$$\tilde{x}^2 + \tilde{y}^2 = \frac{4(x_0^2 + y_0^2)}{x_0^2 + y_0^2 - e^{-at}(x_0^2 + y_0^2 - 4)} \quad (23)$$

which for $t \rightarrow \infty$ approaches $\Gamma : \tilde{x}^2 + \tilde{y}^2 = 4$. If the initial position (x_0, y_0) is a point on Γ , then the solution of the Cauchy problem is the limit circle itself, parametrized as:

$$\begin{cases} \tilde{x} = \frac{2}{\sqrt{4 - e^{-at}(4-4)}}(x_0 \cos t + y_0 \sin t) = x_0 \cos t + y_0 \sin t \\ \tilde{y} = \frac{2}{\sqrt{4 - e^{-at}(4-4)}}(-x_0 \sin t + y_0 \cos t) = -x_0 \sin t + y_0 \cos t. \end{cases} \quad (24)$$

3. Trigonometric averaging (II)

We consider the SODE (1) with the initial conditions $x(0) = x_0, y(0) = y_0$, where t is the time variable and $a \ll 1$ is a small parameter. The non-perturbed system (3) obtained for $a = 0$ has the general solution (12) while the initial conditions (x_0, y_0) are written in polar coordinates

$$\begin{cases} x_0 = r_0 \cos \varphi_0 \\ y_0 = -r_0 \sin \varphi_0, \end{cases} \quad (25)$$

where r_0 is the amplitude of the movement and φ_0 is the phase shift. Then the solution of the homogeneous SODE (3) rewrites as

$$\begin{cases} x_0 = r_0 \cos(t + \varphi_0) \\ y_0 = -r_0 \sin(t + \varphi_0). \end{cases} \quad (26)$$

For $a \neq 0$, the Lagrange method aims to detect a solution of the form

$$\begin{cases} x = r(t) \cos(t + \varphi(t)) \\ y = -r(t) \sin(t + \varphi(t)); \end{cases} \quad (27)$$

which, plugged in the perturbed SODE (1) leads to

$$\begin{cases} \dot{r} \cos(t + \varphi) - r(1 + \dot{\varphi}) \sin(t + \varphi) &= -r \sin(t + \varphi) \\ -\dot{r} \sin(t + \varphi) - r(1 + \dot{\varphi}) \cos(t + \varphi) &= -r \cos(t + \varphi) - \\ &\quad -ar \sin(t + \varphi) \cdot [1 - r^2 \cos^2(t + \varphi)], \end{cases}$$

which rewrites explicitly as

$$\begin{cases} \dot{r} = ar \sin^2(t + \varphi) \cdot [1 - r^2 \cos^2(t + \varphi)] \\ \dot{\varphi} = a \sin(t + \varphi) \cos(t + \varphi) \cdot [1 - r^2 \cos^2(t + \varphi)]. \end{cases} \quad (28)$$

Averaging on the interval $0 \leq t \leq 2\pi$ and taking into account the relations

$$\begin{cases} \int_0^{2\pi} \sin^2(t + \varphi) dt = \pi, & \int_0^{2\pi} \sin^2(t + \varphi) \cos^2(t + \varphi) dt = \frac{\pi}{4} \\ \int_0^{2\pi} \sin(t + \varphi) \cos(t + \varphi) dt = \int_0^{2\pi} \sin(t + \varphi) \cos^3(t + \varphi) dt = 0, \end{cases} \quad (29)$$

the system (28) yields by integration the averaged SODE

$$\begin{cases} \dot{\tilde{r}} = \frac{1}{2\pi} \int_0^{2\pi} \dot{r} dt \\ \dot{\tilde{\varphi}} = \frac{1}{2\pi} \int_0^{2\pi} \dot{\varphi} dt. \end{cases} \Leftrightarrow \begin{cases} \dot{\tilde{r}} = \frac{a}{2} \tilde{r} - \frac{a}{8} \tilde{r}^3 \\ \dot{\tilde{\varphi}} = 0. \end{cases} \Leftrightarrow \begin{cases} \ln \frac{\tilde{r}^2 - 4}{\tilde{r}^2} = -at + K \\ \tilde{\varphi}(t) = C. \end{cases} \quad (30)$$

Using $\tilde{\varphi}(0) = \varphi_0$ and $\tilde{r}(0) = r_0$, we obtain $K = \ln \frac{r_0^2 - 4}{r_0^2}$ and $C = \varphi_0$, and then the solution rewrites

$$\begin{cases} \ln \frac{\tilde{r}^2 - 4}{r_0^2} = -at + \ln \frac{r_0^2 - 4}{r_0^2} \\ \tilde{\varphi}(t) = \varphi_0, \end{cases} \Rightarrow \begin{cases} \tilde{r}(t) = \frac{2r_0}{\sqrt{r_0^2 - e^{-at}(r_0^2 - 4)}} \\ \tilde{\varphi}(t) = \varphi_0. \end{cases} \quad (31)$$

Replacing in the relations (27) the averaged polar solutions (31), we get the general solution of the trigonometric averaged system (30) attached to (1):

$$\begin{cases} \tilde{x} = \frac{2r_0}{\sqrt{r_0^2 - e^{-at}(r_0^2 - 4)}} \cos(t + \varphi_0) \\ \tilde{y} = -\frac{2r_0}{\sqrt{r_0^2 - e^{-at}(r_0^2 - 4)}} \sin(t + \varphi_0). \end{cases} \quad (32)$$

Remark. Using the relations

$$\begin{cases} x_0 = r_0 \cos \varphi_0 \\ y_0 = -r_0 \sin \varphi_0 \end{cases} \quad \text{and} \quad \begin{cases} x_0^2 + y_0^2 = r_0^2 \\ \varphi_0 = -\arctan \frac{y_0}{x_0}, \end{cases}$$

we can easily infer that the solutions (22) and (32) for the SODEs obtained by the two averaging methods (the direct and the trigonometric one) coincide.

4. Maple 9.5 numerical simulations

The following Maple 9.5 code draws the trajectories of both the initial and averaged SODEs.

Maple 9.5 - Plotter of SODE and mediated counterpart

```

> restart: with(DEtools): with(plots): with(plottools):
x01:=0.25: y01:=0.5: x02:=0.25: y02:=1: x03:=0.25: y03:=1.5:
arn:=arrows=none: arm:=arrows=MEDIUM:
colb:=t=111...150, linecolor=[blue,blue,blue]:
colbr:=t=-17..17, linecolor=brown:
pl:=proc(a,arr,tim,col) DEplot({D(x)(t)=y(t),
D(y)(t)=a*(1-x(t)*x(t))*y(t)-x(t)},
[x(t),y(t)],tim,number=2,[[x(0)=x01,y(0)=y01],
[x(0)=x02,y(0)=y02], [x(0)=x03,y(0)=y03]],
stepsize=.1,col, arr, method=rkf45,scaling=constrained);
end proc:
> display(pl(0,arn,colb), pl(0,arm,colbr));
> display(pl(.25,arn,colb), pl(.25,arm,colbr));
> display(pl(1.5,arn,colb), pl(1.5,arm,colbr));
> ang:=proc(x,y) local angle: # Angle procedure
if x=0 and y=0 then angle:=0: print(Origin); end if:
if x<>0 then if x>=0 then
if y>=0 then angle:=arctan(y/x): elif y<0
then angle:=2*Pi+arctan(y/x): end if:
else angle:=Pi+arctan(y/x): end if:
elif y>0 then angle:=Pi/2: else angle:=3*Pi/2: end if: end proc:
> a:=.25: tt:=t=-17..13: # Mediated paths
pla:=proc(x,y,tim) local r,p,xt,yt: r:=sqrt(x*x+y*y): p:=-ang(x,y):
xt:=2*r*cos(t+p)/sqrt(r*r-(r*r-4)*exp(-a*t)):
yt:=-2*r*sin(t+p)/sqrt(r*r-(r*r-4)*exp(-a*t)):
plot([xt,yt,tim],-.5..2,0..2,scaling=constrained,
color=blue,thickness=3): end proc:
> plas:=proc(xs,ys) global d,p,tt: d:=pla(xs,ys,tt):
p:=point([xs,ys],symbol=circle,color=brown): end proc:
> plas(x01,y01): d1:=d: p1:=p: plas(x02,y02): d2:=d: p2:=p:
plas(x03,y03): d3:=d: p3:=p:
> dlimm:=plot([2*cos(t),2*sin(t),t=0..2*Pi],-3..3,-3..3,
scaling=constrained,color=black,thickness=3): # Med.lim.cycle
display({dlimm,d1,d2,d3,p1,p2,p3});
> a:=1.5: tt:=t=-17..2.5:
pla(x01,y01,tt): d1:=d: pla(x02,y02,tt): d2:=d:
pla(x03,y03,tt): d3:=d: display({dlimm,d1,d2,d3,p1,p2,p3});
> both:=proc(aa,tt) local dd: # Both
dd:=DEplot({D(x)(t)=y(t),D(y)(t)=aa*(1-x(t)*x(t))*y(t)-x(t)},

```

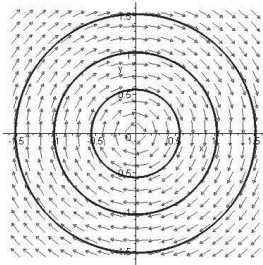
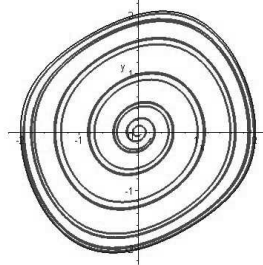
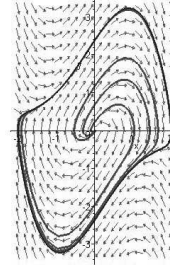


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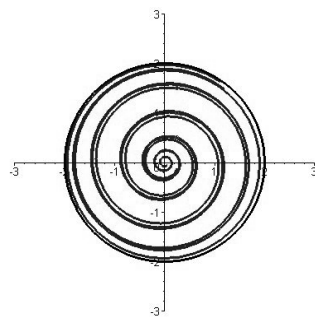
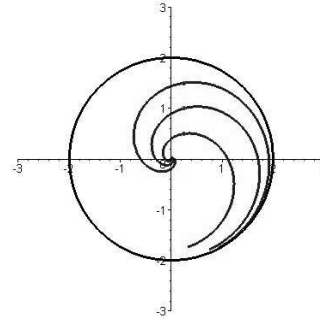
[x(t),y(t)],tt,number=2,arn,thickness=2, [[x(0)=x01,y(0)=y01],
[x(0)=x02,y(0)=y02],[x(0)=x03,y(0)=y03]],stepsize=.02,
linecolor=[red,red,red],method=rkf45,scaling=constrained):
display({dd,pla(x01,y01,tt),pla(x02,y02,tt),pla(x03,y03,tt),
p1,p2,p3}); end proc:
both(0.25,t=-.4...1.5); both(1.5,t=-.4...1.5);

```

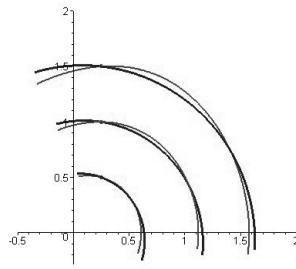
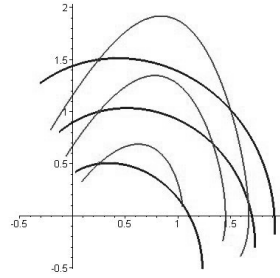
Below are displayed the trajectories of the field X which provides *the initial SODE*: in nonperturbed form (the case $a = 0$, see Fig. 1) and in perturbed form - for $a \in \{0.25; 1.5\}$ for $t \in [-17, 17]$ (Figs. 2,3).

Fig.1. $a = 0$ Fig.2. $a = 0.25$ Fig.3. $a = 1.5$

We notice that the *nonperturbed* (the case $a = 0$) initial and mediated SODEs coincide. For the *perturbed* system, the mediated SODE trajectories approaching the limit cycle can be clearly observed for $a \in \{0.25; 1.5\}$ (Figs. 4,5).

Fig.4. $a = 0.25$ Fig.5. $a = 1.5$

As well, a simultaneous plot of a sheaf of Cauchy problem solutions for the non-averaged and averaged systems in the cases $a \in \{0.25; 1.5\}$, are provided in Figs 6,7.

Fig.6. $a = 0.25$ Fig.7. $a = 1.5$

It can be seen that the deviation of the averaged (thick) trajectories (32) towards the initial (thin) trajectories of (2) are quite rough, with the degree of accuracy foreseen by the Theorem in Section 1. As well, it is essential to note that for increasing values of the parameter a , the mediated SODE trajectories diverge faster from the initial ones (see Fig. 7).

Conclusions

We have shown that both the direct and the trigonometric averaging applied to the SODE (1) leads to the same solutions. The initial SODE and the averaged systems (10) and (28) exhibit limit cycles (a circle for the averaged case). The dynamics of the systems involved is illustrated by Maple plots, which describe the behavior of solutions around the limit cycles, for different values of the parameter $a = \varepsilon \ll 1$.

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