A bifurcation approach to bistability and stabilization in human visual perception

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RUNNING HEAD: [Bifurcation in visual perception]

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Abstract: We discuss a computational model that describes the stabilization of percept choices under intermittent viewing of an ambiguous visual stimulus at long stimulus intervals (Toff). Unlike previous studies we incorporate the time that the stimulus is on (Ton) and Toff explicitly as parameters of the mathematical model of the perceptual choices. These parameters are then used as two bifurcation parameters of the problem. Using the new GUI environment of the MATLAB software package MatCont we elucidate the bifurcations of periodic orbits responsible for switching between alternating and repetitive sequences. We show that the stability borders in the parameter plane of the alternating and repeating sequences consist of curves of limit point and period-doubling bifurcations of periodic orbits. The stability regions overlap resulting in a wedge with bistability of both sequences. We conclude by comparing our results with the results obtained by direct numerical simulation in a grid of (Toff,Ton) values in the 2007 paper of Noest, van Ee, Nijs and van Wezel.

KEYWORDS: [bifurcation software, MatCont, ambiguous visual stimulus, percept switching]

INTRODUCTION

We consider continuous dynamical systems of the form

$$\frac{dx}{dt} = f(x, \alpha), \qquad x, f \in R^n, \alpha \in R^m \tag{1}$$

with state vector x, parameter vector α, and f a sufficiently smooth function. Such dynamical systems appear in all branches of quantitative science. It is well known that the behavior of the solutions to Eq. 1 may qualitatively (not only quantitatively) depend on the parameter α. As an example, we will study a perception problem with an ambiguous visual stimulus as considered in e.g. (Aks and Sprott, 2003; Gregson, 2004; Klink, van Wezel & van EE, 2012; Steward and Peregoy, 1983; Ta′eed, Ta′eed & Wright,1988; Tong, Meng & Blake, 2006). For ambiguous stimuli different percepts may exist depending on the parameters of the problem and under certain circumstances several percepts may coexist. We specifically focus on the phenomenon that intermittent stimulation with ambiguous stimuli leads to stabilized percepts when the time between subsequent stimuli (Toff) is long enough (Klink, van EE, Nijs, Brouwer, Noest, & van Wezel, 2008; Maier, Wilke, Logothetis & Leopold, 2003; Noest, van EE, Nijs, & van Wezel, 2007; Pearson and Clifford, 2004). When Toff is short, then the percept constantly switches from one to the other percept, i.e. the percept alternates. In our analysis of the model, we obtain precise values for Toff for this repetition or alternation of percepts to happen. We also find an intermediate range of Toff-values (we call this the wedge of bistability) in which both behaviors are possible, depending on the initial values.

To understand this phenomenon, it is important to know for which parameter values the behavior of Eq. 1 changes qualitatively and what new phenomena then appear. This is the subject of bifurcation theory, see e.g. Kuznetsov (2004). In practice the application of this theory to specific situations can only be performed by numerical methods, except in simple artificial cases.

The numerical bifurcation analysis of (1) requires a dedicated software package. For this purpose, MatCont (Govaerts, Kuznetsov, Meijer, Al-Hdaibat, De Witte, Dhooge, Mestrom, Neirynck, Riet & Sautois, 2019) was developed as a MATLAB continuation toolbox. It is a successor package to LINBLF (Khibnik, 1990) and CONTENT (Kuznetsov and Levitin, 1997). MatCont is built upon an underlying command line package ClMatCont. The new GUI environment MatCont7.1 is freely available from www.sourceforge.net/p/matcont. The kernel of this software is a numerical continuation code that allows to study the variation of a dynamical object (e.g. a periodic orbit) under variation of a parameter. The functionalities of MatCont with respect to bifurcation techniques are unrivalled. For example, no other software computes the normal form coefficients of codimension 2 bifurcations of limit cycles or allows to start curves of codimension 1 bifurcations of periodic orbits from codimension 2 bifurcation points of equilibria.

Though originally mainly used in mathematics, (bio)chemistry, physics and engineering, MatCont is nowadays also used in many life science applications. Among the citing applications we mention Saccharomyces Cerevisiae fermentation processes (Lakshmi, 2012), pattern storage in neural networks (Fasoli, Cathani & Panzeri, 2018) and modeling of innate immunity responses to sepsis (Wu, Shi, Zhenzhen, Ben-Arieh & Simpson, 2016). Many other examples can be found in the Web of Science by searching for papers that cite Dhooge et al. (2003), or Dhooge et al. (2008). This paper aims to demonstrate the use in the aforementioned perception problem.

Bifurcation analysis usually starts with stable equilibria and periodic orbits, also referred to as limit cycles. Both can be found by time integration of the system, see the MatCont manual (Govaerts et al., 2019, §6.2 and §7.4). By numerical continuation under variation of a single system parameter, one can detect and study local codimension one bifurcations, i.e. limit points and Hopf points for equilibria, or limit points of cycles, period-doubling and Neimark-Sacker (torus) bifurcation points for periodic orbits. Further continuation of these codimension one bifurcations under variation of two system parameters leads to the detection and study of the codimension two bifurcation points; there are 5 codimension two types of bifurcations of equilibria and 11 types for periodic orbits. MatCont allows to study these bifurcations numerically and perform many related tasks, including the study of orbits homoclinic to a saddle or a saddle node as well as heteroclinic orbits. Critical normal form coefficients are computed at bifurcation points. For these coefficients, MatCont relies on symbolic derivatives or, if these are not available, on finite differences. Bifurcation curves are defined by systems of equations that include bifurcation conditions. The continuation curves can be visualized using the plot capabilities of the GUI; this can be done during and after the continuation. Special windows are provided to help with maintaining systems, diagrams and curves when generating a large amount of data.

USING MATCONT7.1

Earlier versions of MatCont and their functionalities were described in Dhooghe, Govaerts & Kuznetsov (2003) and Dhooge, Govaerts, Kuznetsov, Meijer & Sautois (2008). The inner workings and details of the functionalities of the new GUI are described in Neirynck (2019).

To start working with MatCont on a Windows 64-bit machine it suffices to download the zipped file matcont7p1.zip, to unzip it, take the MatCont directory as the MATLAB root directory and type ‘matcont’ on the MATLAB command line. The only difference for other platforms is that the seven c-files in the folder LimitCycle must be compiled to MeX files. The MeX files for Windows32 and Mac64 can also be downloaded from the folder Auxiliaries of the

MatCont webpage on Sourceforge. Of course, it is strongly recommended to read the companion readme-files of the package, and to read the tutorials. These illustrate the use of the GUI and can be used to learn to practically use MatCont. The manual Govaerts et al. (2019) is a good reference to the command line version ClMatCont.

To study a system in MatCont one has to describe it in a *system m-file*, which serves as a handle to the system. MatCont provides an interface to build such m-files, see the manual Govaerts et al. (2019), Ch. 4 or the first tutorial.

The database of MatCont consists of an archive of systems one of which is the *current system*. A system is internally characterized by the system m-file, a system mat-file and a system folder, all with the name of the system. They are all located in the subfolder **Systems** of MatCont. When a MatCont session is closed (**Select|Exit** in Fig. 1) then the session information is stored in a file *session.mat* in the **Systems** directory. This allows to restart the MATLAB session at the point where it was stopped.

The mat-file contains the information on the loaded system in a structured way that is accessible to the MatCont software. Both the m-file and the mat-file stay unchanged if the system is not changed or deleted.

The folder of each system always contains a file `session.mat' which contains the information necessary to restart the computations on that system at the stage where it was left, including the position and contents of all windows. However, computed data must be redrawn. The folder of a system also has at least one default subfolder called `Diagram'. This and other subfolders of the system folder are called *diagrams*. Each diagram contains several mat-files and each mat-file describes a computed curve with enough information to re-compute the curve. Each computed curve contains several special points, including the first point, the last point and bifurcation points, but other entities may also be defined as special points. An important example of this is the case of an orbit where a *Select Cycle* object is identified as a special point. It allows to start up the continuation of periodic orbits from an orbit computed by time integration. The user can choose the number ntst of test intervals to control the number of time intervals used in the approximation of the periodic orbit. On each interval the periodic orbit is approximated by a polynomial (default degree 4). In this paper we will always choose ntst=60.

The MatCont GUI provides a special tool called the **Data Browser** to navigate through the database and select information for further handling in MatCont via a **Select Point** button.

The Spreadsheet Viewer allows to inspect all stored data of a computed curve. It can be accessed by pressing the **View Curve** button in a Curve window that is opened in the Data Browser.

AN EXAMPLE FROM HUMAN PERCEPTION

In Noest et al. (2007) the authors discuss a neural explanation of the stabilization of percept choices under intermittent viewing of an ambiguous visual stimulus. They consider the following system (in the input notation of MatCont):

$$\begin{aligned} X1' &= (Stim-(1+A1)*X1+beta*A1-gamma*S(X2))/tau, \\ X2' &= \left(Stim-(1+A2)*X2+beta*A2-gamma*S(X1)\right)/tau, \qquad (2) \\ A1' &= -A1+alpha*S(X1), \\ A2' &= -A2+alpha*S(X2), \end{aligned}$$

with state variables $X1, X2, A1, A2$ and fixed parameters $alpha=5, beta=4/15, gamma=10/3$ and $tau=1/50$. The primes represent first order derivatives with respect to time. The primary dynamical variables $X1, X2$ are the `local fields', which correspond to the percept-related components of the membrane potentials of the neurons that encode the two competing percepts, indicated by 1 or 2, respectively. To each primary variable an adaptation variable is associated, called $A1$ and $A2$, respectively. In the local field interpretation these correspond to the (averaged and scaled) gating variables of the neurons. $Stim$ is the amplitude of the stimulus. $S(X1)$ is a sigmoidal function of $X1$, zero for negative values of $X1$ and equal to $X1\hat{}2/(1 + X1\hat{}2)$ for nonnegative values of $X1$. It represents the (averaged and scaled) firing rate of the neurons that contribute to the local field $X1$. $S(X2)$ is to be interpreted similarly. The precise choice of the sigmoid function does not influence the qualitative behavior of Eq. 2.

Line 1 of Eq. 2 specifies how $X1$ integrates the stimulus with its adaptation variable $A1$ and the subtractive cross-inhibition $S(X2)$. The adaptation $A1$ has two possible actions, inhibitory when $X1 > beta$, or $X1 < A1\ beta/(1 + A1)$, and excitatory in the other cases. Line 2 of Eq. 2 is of course the dual of Line 1. The adaptation dynamics in lines 3 and 4 of Eq. 2 presents the simplest possibility, a standard "leaky integrator". From the value of tau it is clear that $X1, X2$ are `fast' variables of the system while $A1, A2$ are `slow'. In (Noest et al., 2007) the authors consider a $128\ by\ 128$ grid of points in a (Toff,Ton)-space. For each point, the system is simulated with the stimulus ($Stim$ in Eq. 2) alternatingly switched off during a time span Toff and on during a time span Ton.

The eventual behavior (after transients) varies with the choice of Toff and Ton but also depends on the initial values of the state variables. It includes alternating and repeating patterns (as in Fig. 3 and Fig.4, respectively) and for some parameter values there is bistability. An important observation is that for fixed Ton the behavior can be stabilized by increasing Toff, i.e. it leads to a situation where the percept is the same whenever the stimulus switches on (but may still depend on the initial state.)

In MatCont we will approximate the intermittent stimulus presentation by a continuous system with a periodic forcing with period Toff+Ton. This involves including Toff and Ton as new parameters in the system. The first step is to introduce the system in MatCont as illustrated in

Fig. 1.

Insert Figure 1 About Here

The MatCont panels are described in Neirynck (2019, Ch. 5). The upper panel in Fig. 1 is the main MatCont panel. We note in particular the tab line at the top with the six tabs **Select**, **Type, Window/Output, Compute, Options**, and **Help**. The **Help** tab gives access to the manual. The name of the system is ‘PerceptSwitch’ and ‘SSSNN’ indicates that the derivatives of order 1, 2, 3 are to be computed by symbolic derivatives while the derivatives of order 4 and 5 are to be computed by finite differences (actually, these higher order derivatives are only used in the computation of normal form coefficients for some codimension 2 bifurcations).

The lower panel in Fig.1 is opened by clicking System|New in the main panel and it is used to introduce the ‘PerceptSwitch’ system with state variables $X1, X2, A1, A2, Y1, Y2.$ We will refer to this system of equations as Eq. 3. The auxiliary variables $S1, S2$ approximate the sigmoid functions $S(X1), S(X2)$ from Eq. 2, respectively.

The periodic forcing is implemented with new state variables $Y1, Y2.$ From their equations in Fig. 1 it follows that their stable behavior (after a transient) is a periodic orbit of the form $Y1 = cos(omega\ t + P), Y2 = sin(omega\ t + P)$ with a time shift P that depends only on the initial values of $Y1, Y2.$ The period of the orbit is $T \coloneqq Ton + Toff$, so the frequency is $omega \coloneqq 2\frac{\pi}{T}.$ We have also added an additional parameter $expp$ to the system `PerceptSwitch’ appearing in the equations for $S1, S2$ and $Stim$. By increasing its value, the smooth functions for $S1, S2$ in `PerceptSwitch’ converge to the non-analytical step sigmoid functions that are used in Noest et al. (2007). In our computations we use $expp = 60$.

When $Y1, Y2$ evolve along the unit circle, then $Stim$ is alternatingly close to zero during a time span $Toff$ and close to one during a time span Ton. This behavior (after a transient) is shown in Fig. 2. The stimulus term $Stim$ thus acts as an on/off switch for the periodic forcing of the subsystem in Eq. 2.

Insert Figure 2 About Here

We can now approximate in MatCont the computations in Noest et al. (2007) without having to integrate the system in Eq. 1 intermittently over time intervals Toff and Ton with Stim=0 and Stim=1, respectively.

Fig. 3 shows three projections of a stable periodic orbit computed by time integration for $Toff = 0.2, Ton = 0.8$ (after a transient, starting from values of $(Y1, Y2)$ which are not both zero). We note that the period is 2*(0.2+0.8)=2 and the time evolution shows an alternating sequence, i.e. after each on/off cycle (with period 1) the percept switches from one to the other.

Fig. 4 shows three projections of a stable periodic orbit computed by time integration for $Toff = 0.6, Ton = 0.8$ (after a transient, starting from values of $(Y1, Y2)$ which are not both zero). We note that the period is 0.6+0.8=1.4 and the time series show a repeating percept, i.e. during each `on' period we see that $X2$ is larger than $X1$. (for a different choice of the initial values of the state variables it could be the percept $X1$ that is larger than $X2$)

Insert Figure 3 About Here

Insert Figure 4 About Here

MatCont allows us to study the transition changes based on the theory and numerics of codimension 1 and codimension 2 bifurcations of periodic orbits (Kuznetsov 2004; De Witte & Della Rossa & Govaerts & Kuznetsov 2013). We will not need to repeat computations on a grid. Instead we will compute boundaries of regions in the (Toff,Ton)-plane where a particular sequence exists directly as curves of codimension 1 bifurcations of periodic orbits.

To study the stability regions of repeating and alternating periodic orbits we use the Select Cycle functionality mentioned above. We start the continuation of limit cycles from the stable limit cycles in Fig. 3 and Fig. 4 under variation of $Toff$. By using the branch switching functionalities of MatCont we then construct the bifurcation diagram in $(Toff,Ton)$–space in Fig.5 as follows. The first step is to continue the (alternating) periodic orbit starting from the one presented in Fig. 3 for increasing values of Toff. MatCont detects a LPC (limit point of cycles) when the continuation path meets the right green boundary curve of the wedge. A special phenomenon here is that the LPC points are also detected as branch points of cycles (BPC); this is due to the fact that the `PerceptSwitch' system is periodically forced, see also De Witte (2013), section 6.3; this phenomenon can be ignored for our purposes.

From the detected LPC point we start the continuation of LPC points forward and backward to trace the right (green) boundary curve. To the right of this curve there are no alternating periodic orbits.

Next, starting from the (repeating) periodic orbit at (0.6,0.8) presented in Fig. 4 and decreasing Toff, MatCont detects another LPC when the continuation path meets the left boundary of the wedge. From the detected LPC point we can start the continuation of LPC points forward and backward (i.e. trace the green part of the left boundary of the wedge) until it detects an LPPD point (a codimension-2 bifurcation of limit cycles). The lower (blue) part of the left boundary of the wedge can be traced similarly by starting from a stable repeating orbit at (0.4,0.4). Decreasing Toff we encounter a period doubling bifurcation of limit cycles. Continuation starting from the PD point results in the (blue) period-doubling bifurcation curve containing a generalized period-doubling point (GPD, another codimension-2 bifurcation of limit cycles). The LPPD point is situated at (0.41416,0.60659), the GPD point at (0.29837,0.34146). Interestingly, the stability regions of alternating and repeating orbits overlap in the wedge shown in Fig. 5.

Insert Figure 5 About Here

To conclude, we note that the overlap of our Fig. 5 with Fig. 3(c) in Noest et al. (2007) is the region of the (Toff, Ton)-plane where Ton is between 0.5 and 0.9. In Noest et al. (2007) the zones with alternating percepts (blue) or repeating percepts (red) only are clear. There is a small intermediate zone though with ill-defined behavior and seemingly irregular boundaries. This can be expected if both the alternating and repeating percepts are stable there, so that for the same initial values of the state variables slightly different values for Toff and Ton can lead to different percept sequences.

In our Fig. 5 the situation is clearer. The curves of codimension-1 bifurcations divide the (Toff,Ton)-space into three regions. In the leftmost region, the only stable limit cycle exhibits the two percepts alternatingly. In the rightmost region, only the repeating percepts are stable. Finally, in the inner region (in the wedge) both types of stable limit cycles coexist. On the boundaries, stable limit cycles lose their stability either by a limit point of cycles bifurcation or by a period doubling bifurcation.

Though the irregular zone in Noest et al. (2007) has no precise boundaries, it can be checked easily that it lies in our wedge of bistability. For example, for $Ton = 1/\sqrt{2}$ the irregular zone lies near Toff=0.4583 while the left LPC is found for Toff=0.43936 and the right one for Toff=0.48481.

Our methods are equally applicable to other perceptual models with time-dependent stimuli, e.g. Jayasuriya and Kilpatrick (2012), though their model does not exhibit stabilization.

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CAPTIONS

Caption 1:

The MatCont Main panel and the introduction of the PerceptSwitch system in MatCont.

Caption 2:

The time evolution of Stim for $Toff = 0.4, Ton = 0.8$ after a transient

Caption 3:

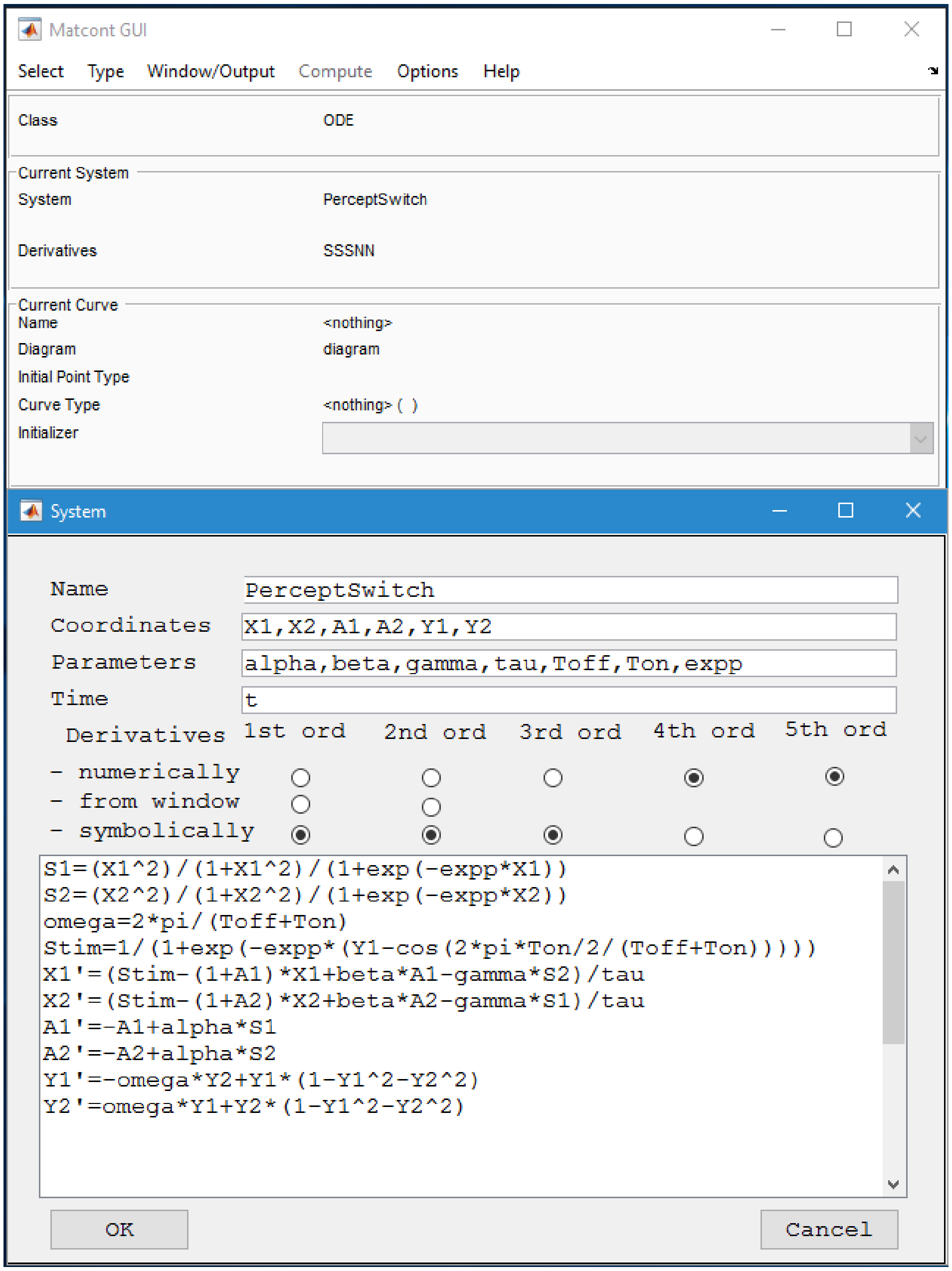
Alternating stable periodic orbits computed for $Toff = 0.2, Ton = 0.8$.

Caption 4:

Repeating stable periodic orbits computed for $Toff = 0.6, Ton = 0.8$.

Caption 5:

Wedge of bistability of alternating and repeating periodic orbits. Green: Curve of limit points of cycles. Blue: Curve of period doubling bifurcations of cycles.



Class ODE

Current System

System PerceptSwitch

Derivatives SSSNN

Current Curve

Name <nothing>

Diagram diagram

Initial Point Type

Curve Type <nothing> ( )

Initializer

Name PerceptSwitch

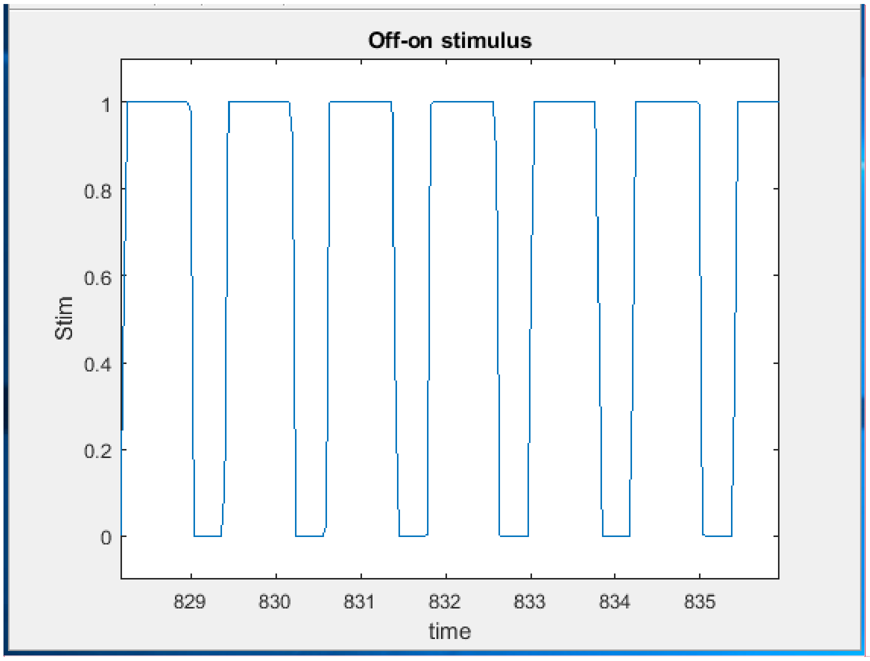
Coordinates X1,X2,A1,A2,Y1,Y2

Parameters alpha,beta,gamma,tau,Toff,Ton,expp

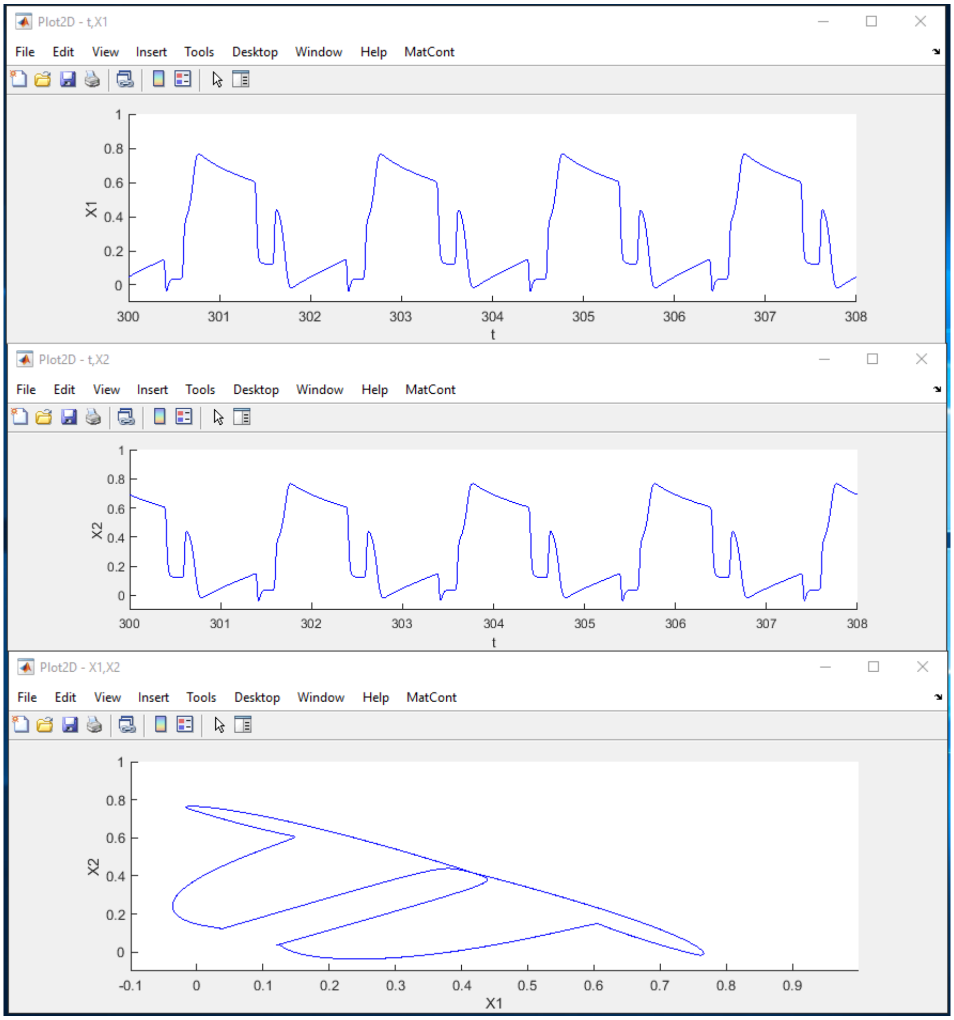
Time t

Derivatives	1st ord	2nd ord	3rd ord	4th ord	5th ord
- numerically	○	○	○	●	●
- from window	○	○			
- symbolically	●	●	●	○	○

```
S1=(X1^2)/(1+X1^2)/(1+exp(-expp*X1))
S2=(X2^2)/(1+X2^2)/(1+exp(-expp*X2))
omega=2*pi/(Toff+Ton)
Stim=1/(1+exp(-expp*(Y1-cos(2*pi*Ton/2/(Toff+Ton)))))
X1'=(Stim-(1+A1)*X1+beta*A1-gamma*S2)/tau
X2'=(Stim-(1+A2)*X2+beta*A2-gamma*S1)/tau
A1'=-A1+alpha*S1
A2'=-A2+alpha*S2
Y1'=-omega*Y2+Y1*(1-Y1^2-Y2^2)
Y2'=omega*Y1+Y2*(1-Y1^2-Y2^2)
```



Met opmerkingen [MH(1]: Zou de verticale range iets groter kunnen, bv. -0.1 tm 1.1 zodat je de kromme ook echt goed ziet?


Plot2D - t,X1
File Edit View Insert Tools Desktop Window Help MatCont
X1
1
0.8
0.6
0.4
0.2
0
300 301 302 303 304 305 306 307 308
t
Plot2D - t,X2
File Edit View Insert Tools Desktop Window Help MatCont
X2
1
0.8
0.6
0.4
0.2
0
300 301 302 303 304 305 306 307 308
t
Plot2D - X1,X2
File Edit View Insert Tools Desktop Window Help MatCont
X2
1
0.8
0.6
0.4
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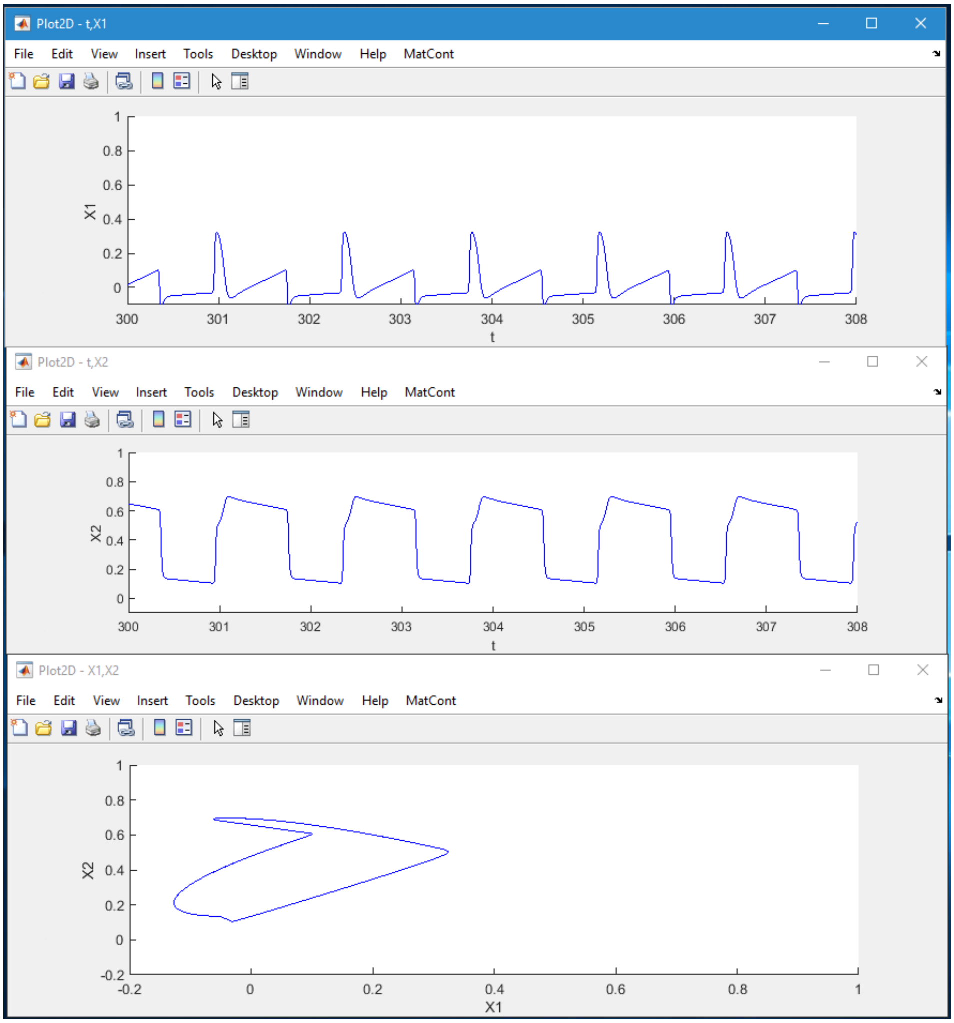
-0.1 0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
X1


Plot2D - t,X1
File Edit View Insert Tools Desktop Window Help MatCont
X1
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0.6
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300 301 302 303 304 305 306 307 308
t
Plot2D - t,X2
File Edit View Insert Tools Desktop Window Help MatCont
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Plot2D - X1,X2
File Edit View Insert Tools Desktop Window Help MatCont
X2
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0.2
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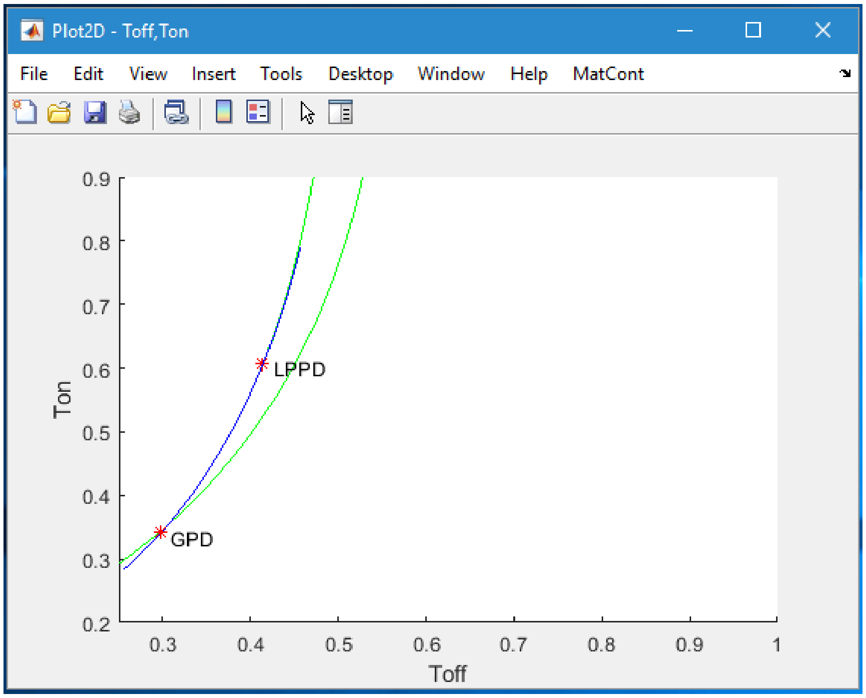
-0.2
-0.2 0 0.2 0.4 0.6 0.8 1
X1


Plot2D - Toff,Ton
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0.9
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Toff
LPPD
GPD