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Bistability and Stabilization of Human Visual Perception under Ambiguous Stimulation

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Abstract: *We discuss a computational model that describes stabilization of percept choices under intermittent viewing of an ambiguous visual stimulus at long stimulus intervals. Let T_{off} and T_{on} be the time that the stimulus is off and on, respectively. The behavior was studied by direct numerical simulation in a grid of (T_{off}, T_{on}) values in a 2007 paper of Noest, van Ee, Nijs, and van Wezel. They found that both alternating and repetitive sequences of percepts can appear stably, sometimes even for the same values of T_{off} and T_{on}. Longer T_{off}, however, always leads to a situation where, after transients, only repetitive sequences of percepts exist. We incorporate T_{off} and T_{on} explicitly as bifurcation parameters of an extended mathematical model of the perceptual choices. We elucidate the bifurcations of periodic orbits responsible for switching between alternating and repetitive sequences. We show that the stability borders of the alternating and repeating sequences in the (T_{off}, T_{on}) -parameter plane 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 modeling results with the experimental results obtained by Noest, van Ee, Nijs, and van Wezel.*

Key Words: ambiguous visual stimulus, percept switching, periodic orbit, bifurcation

INTRODUCTION

Neural mechanisms in our brain have evolved to efficiently process visual stimuli that we encounter in our daily life, such that it leads to useful behavior (Gibson, 1979). With optical illusions and ambiguous stimuli these basic neural mechanisms can be probed and studying these illusions can help us better understand brain functioning and perception (e.g. Aks & Sprott, 2003; Gregson,

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2004; Klink, van Wezel & van Ee, 2012; Stewart & Peregoy, 1983; Ta'eed, Ta'eed & Wright,1988; Tong, Meng & Blake, 2006). For ambiguous stimuli, such as, for instance, the Necker-cube (Necker, 1832), different percepts may exist depending on the problem's parameters and under certain circumstances two (or sometimes more) percepts may coexist for the same parameters.

Intermittent Stimulation of Bistable Stimuli, the Noest et al. Model

We specifically focus on the phenomenon that intermittent stimulation with ambiguous stimuli leads to stabilized percepts when the time between subsequent stimuli T_{off} 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 & Clifford, 2004). When T_{off} is short, the percept continually switches from one to the other percept, i.e., the percept alternates.

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 (for ease of applicability we use the readable notation of MATLAB):

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

with four variables, $X1$, $X2$ (neural activity of population for percept 1 and 2 respectively), and $A1$, $A2$ (adaptation term for population 1 and 2 respectively) and four fixed parameters a = 5 (adaptation strength), b = 4/15 (fixed baseline activity), g = 10/4 (cross-inhibition strength) and t = 1/50 (time constant of adaptation term).

The primes represent first-order derivatives with respect to time. The primary dynamical variables $X1, X2$ are the ``local fields" corresponding to the percept-related components of the activity of the population of 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 $X1^2/(1 + X1^2)$ for nonnegative values of $X1$. It represents the (averaged and scaled) firing rate of the neurons that contribute to the local field $X1$. The value of $S(X2)$ is defined in the same way. A different choice of the sigmoid function accompanied by a change of the system parameters α, β, γ, does not influence the qualitative behavior of Eq. 1.

Line 1 of Eq. 1 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. 1 is, of course, the dual of Line 1.

The adaptation dynamics in lines 3 and 4 of Eq. 1 is modeled by the standard "leaky integrator". From the value of τ, 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 (T_{off}, T_{on}) -space. For each point, they simulated the system with the stimulus ($Stim$ in Eq. 1) alternatingly switched off during a time T_{off} and on during a time T_{on}. The eventual behavior (after transients) varies with the choice of T_{off} and T_{on} but also depends on the initial values of the state variables.

Figure 1 shows three projections of the stable behavior computed by time integration for $T_{off} = 0.2\ sec, T_{on} = 0.8\ sec$ (after a transient). We note that the behavior is periodic with period 2(0.2+0.8)=2 sec, and the time evolution shows an alternating sequence, i.e., after each on/off cycle (with period 0.2+0.8=1 sec) the percept switches from one (where $X1$ dominates) to the other (where $X2$ dominates).

Figure 2 shows three projections of a stable periodic orbit computed by time integration for $T_{off} = 0.6\ sec, T_{on} = 0.8\ sec$ (after a transient). We note that the period is 0.6+0.8=1.4 sec, and the time series shows a repeating percept, i.e., during each ``on"- period, $X2$ is larger than $X1$. (For a different choice of the initial values of the state variables it could be that the percept $X1$ is larger than $X2$).

For some parameter values, there is bistability, i.e., the behavior after the transient can be stably alternating or repeating, depending on the initial values of the state variables. An important observation in Noest et al. (2007) is that for fixed T_{on}, increasing T_{off} stabilizes the behavior, 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).

Problem Description

For a better understanding, it is essential to know for which values of ($T_{off},\ T_{on}$) the behavior is eventually alternating, repeating, or could be one of the two, depending on the initial values of the state variables. Since the state space is four-dimensional, it is not feasible to perform these simulations in each point of a four-dimensional grid in each of the $128\ by\ 128$ grid points in (T_{off}, T_{on})-space. Moreover, this would not lead to a global understanding of why the behavior changes at certain parameter values. Therefore, we need a different and more global approach that focuses on the (T_{off}, T_{on})-parameter values separating the domains with alternating, repeating, and bistable behavior. We will show that bifurcation theory and methods can be applied to understand this behavior better as has been suggested by previous studies.

METHOD

Equation 1 constitutes an example of a continuous dynamical system of the general form

$$\frac{dx}{dt} = f(x, \alpha), \quad x, f \in R^n, \in R^m, \tag{2}$$

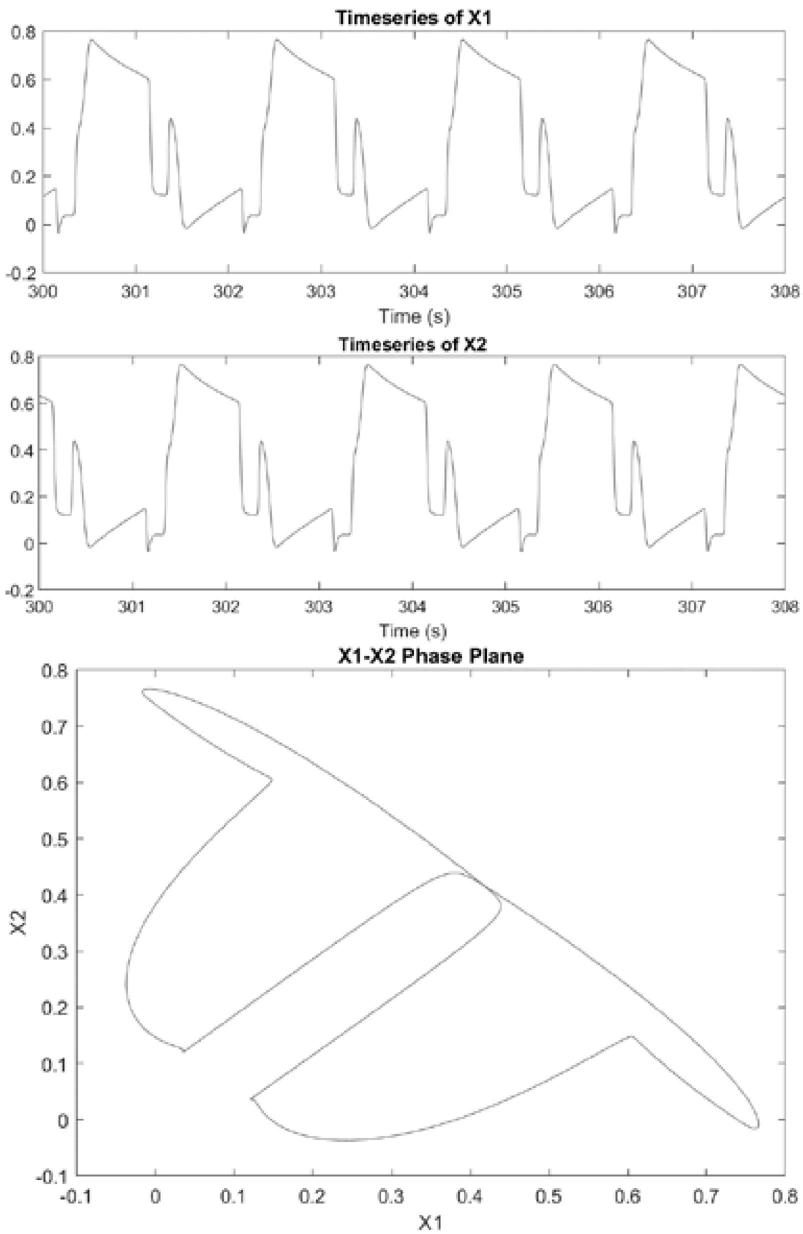

Fig. 1. Alternating stable periodic orbits computed for $Toff = 0.2, Ton = 0.8$.

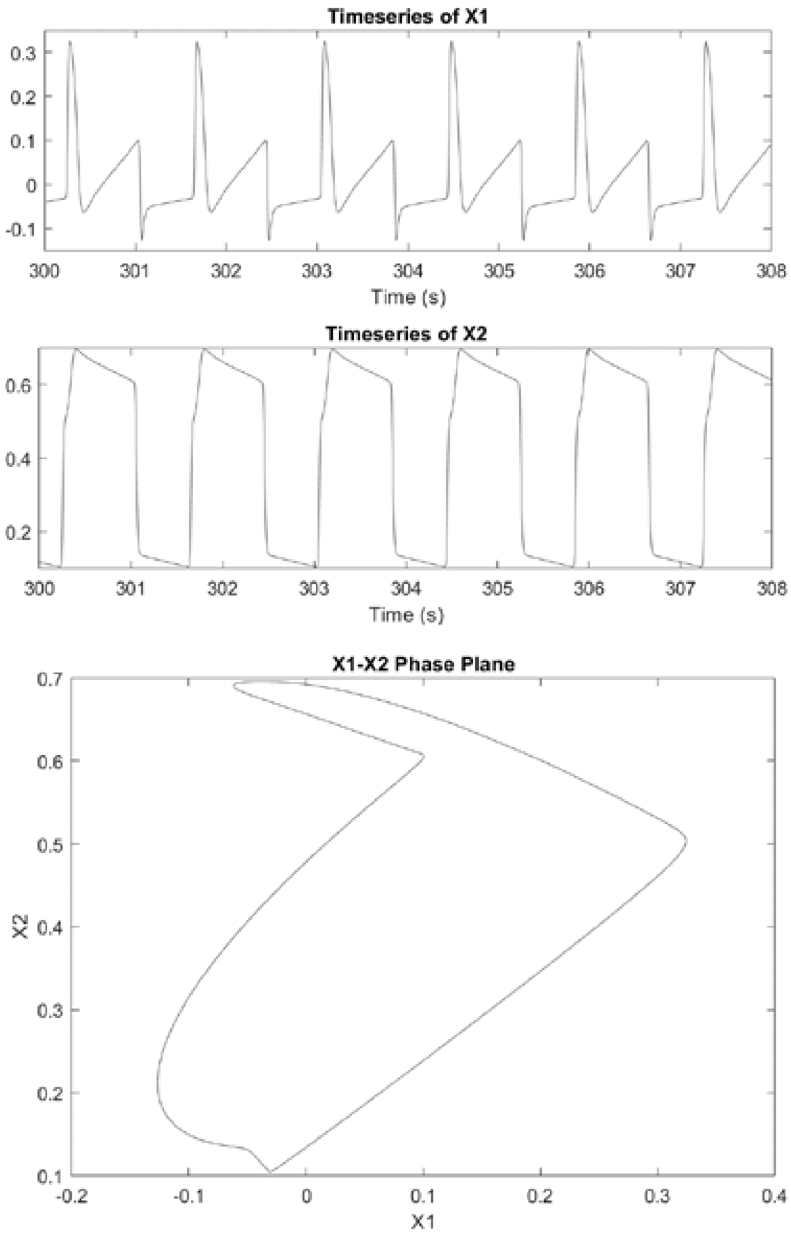

Fig. 2. Repeating stable periodic orbits computed for $Toff = 0.6, Ton = 0.8$.

with state vector x, parameter vector α, and f a sufficiently smooth function (in Eq. 1 n = m = 4). The behavior of the solutions to such systems may qualitatively (not only quantitatively) depend on the parameter α, which we can be elucidated using bifurcation theory, an advanced topic in mathematical analysis, see, e.g., Kuznetsov (2004). In practice, applying bifurcation theory to specific situations requires numerical methods, except in simple artificial cases.

MatCont Software

The numerical bifurcation analysis of Eq. 2 requires a dedicated software package. For this purpose, we developed MatCont (Govaerts et al., 2019) as a MATLAB continuation toolbox. It is a successor package to LINBLF (Khibnik, 1990) and CONTENT (Kuznetsov & Levitin, 1997). Earlier versions of MatCont and their functionalities were described in Dhooge, Govaerts & Kuznetsov (2003), and Dhooge, Govaerts, Kuznetsov, Meijer & Sautois (2008). The inner workings and details of the functionalities of the new GUI (from MatCont7.1 on) are described in Neirynck (2019).

The MatCont GUI environment is freely available from www.sourceforge.net/p/matcont. The kernel of this software is a numerical continuation code that allows studying the variation of a dynamical object (e.g., a periodic orbit) under variation of one or more parameters.

Bifurcation analysis usually starts with stable equilibria and periodic orbits, also referred to as limit cycles. One can find both by time integration of the system, see the MatCont manual (Govaerts et al., 2019, §6.2 and §7.4). Using numerical continuation varying a single system parameter, one can detect and study local codimension-1 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-1 bifurcations under variation of two system parameters leads to the detection and study of the codimension-2 bifurcation points; there are 5 codimension-2 types of bifurcations of equilibria and 11 types for periodic orbits. With MatCont, one can study these bifurcations numerically and perform many related tasks. Bifurcation curves are defined by systems of equations that include bifurcation conditions.

Each computed curve contains several special points, including the first point, the last point, and bifurcation points, but one may also define other entities as special points. A notable example of this is the case of an orbit where we identify a *Select Cycle* object as a special point. It allows us 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.

RESULTS

Our approach is to approximate the intermittent stimulus application by a continuous system with a periodic forcing with period $T_{off} + T_{on}$. Therefore, we include T_{off} and T_{on} as new parameters in the system. The new system has six state variables $X1, X2, A1, A2, Y1, Y2$, and seven parameters, namely α, β, γ, τ, T_{off}, T_{on}, expp. For ease of applicability, we use the readable notation of Matlab in such a way that the text can be copied directly into MatCont:

$$
\begin{aligned}
&S1 = (\mathrm{X1^\wedge 2})/(1 + \mathrm{X1^\wedge 2})/(1 + \exp(-\mathrm{expp} * \mathrm{X1})),\\
&S2 = (\mathrm{X2^\wedge 2})/(1 + \mathrm{X2^\wedge 2})/(1 + \exp(-\mathrm{expp} * \mathrm{X2})),\\
&omega = 2 * pi/(Toff + Ton),\\
&Stim = 1/(1 + \exp\,(-expp * (Y1 - \cos\,(2 * pi * Ton/2/(Toff + \mathrm{Ton}))\,))),\\
&X1' = (Stim - (1 + A1) * X1 + beta * A1 - gamma * S2)/tau,\\
&X2' = (Stim - (1 + A2) * X2 + beta * A2 - gamma * S1)/tau, \qquad\qquad (3)\\
&A1' = -A1 + alpha * S1,\\
&A2' = -A2 + alpha * S2,\\
&Y1' = -omega * Y2 + Y1 * (1 - Y1^\wedge 2 - Y2^\wedge 2),\\
&Y2' = omega * Y1 + Y2 * (1 - Y1^\wedge 2 - Y2^\wedge 2),
\end{aligned}
$$

The MatCont panels are described in Neirynck (2019, Ch. 5). To introduce Eq. 3 in MatCont, one starts by clicking Select/System/New in the main MatCont panel. Then Eq. 3 can be copied directly into the big input field in the System window. The system will be called ``PerceptSwitch", and we let the Matlab symbolic toolbox compute the derivatives of order 1 to 3.

The auxiliary variables $S1, S2$ in Eq. 3 approximate the sigmoid functions $S(X1), S(X2)$ from Eq. 1, respectively. The new state variables $Y1, Y2$ implement the periodic forcing. Their equations in Eq. 3 are decoupled from the other state variables, and one quickly sees 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 $T \coloneqq T_{off} + T_{on}$, so the angular velocity is $\omega \coloneqq 2\frac{\pi}{T}$. We have also introduced an additional parameter $expp$ to the system ``PerceptSwitch" in the equations for $S1, S2$, and $Stim$. By increasing its value, the smooth functions for $S1, S2$, and $Stim$ in Eq. 3 converge to the non-analytical step sigmoid functions as 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 T_{off} and close to one during a time T_{on}, see Fig. 3 for this behavior (after a transient). The stimulus term $Stim$ thus acts as an on/off switch for the periodic forcing of subsystem Eq. 1 in Eq. 3.

With this setup, we can approximate in MatCont the computations in Noest et al. (2007) without having to integrate the system in Eq. 1 intermittently over time intervals T_{off} and T_{on} with Stim=0 and Stim=1, respectively. Instead, we compute orbits of ``PerceptSwitch" to reproduce (after a transient) Fig.1 and Fig.2. With the choice $expp = 60$, the final behavior for (T_{off}, T_{on}) = (0.2,0.8) is visually indistinguishable from the one in Fig.1, and for (T_{off}, T_{on}) = (0.6,0.8) it is indistinguishable from the one in Fig. 2.

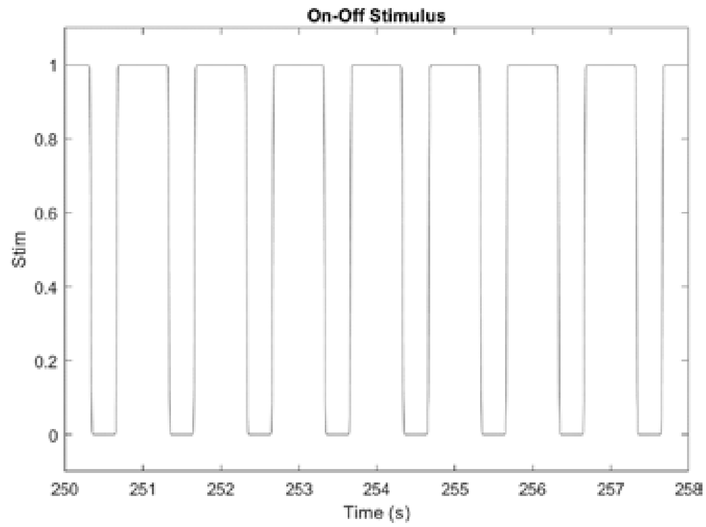

Fig. 3. The time evolution of Stim for $Toff = 0.4, Ton = 0.8$ after a transient.

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 (T_{off}, T_{on})-plane where a particular type of behavior exists directly as curves of codimension-1 bifurcations of periodic orbits.

We use the Select Cycle functionality mentioned above to study the stability regions of repeating and alternating periodic orbits. We start the continuation of limit cycles from the stable limit cycles in Figs. 1 and 2 varying T_{off}. Using the branch switching functionalities of MatCont, we construct the bifurcation diagram in (T_{off}, T_{on})-space in Fig. 4 as follows. The first step is to continue the (alternating) periodic orbit starting from the one presented in Fig. 1 for increasing values of T_{off}. MatCont detects an LPC (limit point of cycles) when the continuation path meets the right green boundary curve of the wedge. A particular phenomenon here is that MatCont detects the LPC points also as branch points of cycles (BPC); this is due to the periodic forcing of the ``PerceptSwitch" system, see also De Witte (2013), section 6.3; we can ignore this phenomenon for our purposes.

From the detected LPC point, we start the continuation of LPC points forward and backward to trace the right 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. 2 and decreasing T_{off}, 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 T_{off}, we encounter a period-doubling (PD) bifurcation of limit cycles. A PD (or flip) bifurcation can generically appear on one-parameter curves of periodic orbits or fixed points of maps. 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 parameter values of the LPPD point are $(0.41416{,}0.60659)$ and the GPD point is at $(0.29837{,}0.34146)$. Interestingly, the stability regions of alternating and repeating orbits overlap in the wedge shown in Fig. 4.

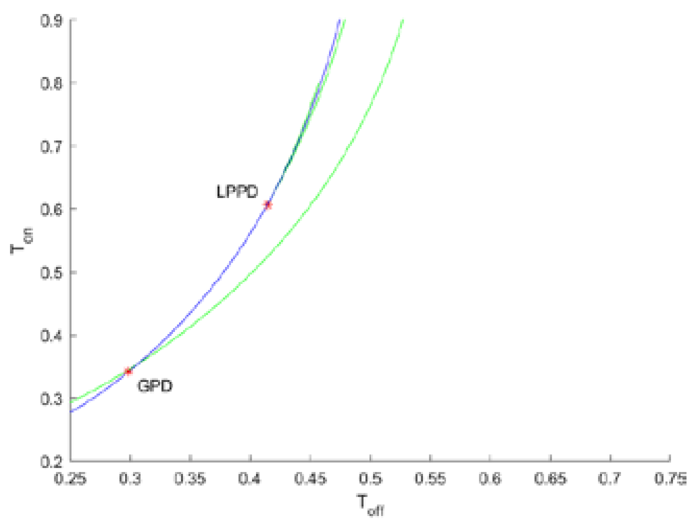

Fig. 4. The wedge of bistability of alternating and repeating periodic orbits. Green: Curve of limit points of cycles. Blue: Curve of period-doubling bifurcations of cycles.

DISCUSSION

To conclude, we note that for the experimentally relevant part of (T_{off}, T_{on})-plane with T_{on} between 0.5 and 0.9, there is considerable overlap of Fig. 4 with Fig. 3c in Noest et al. (2007). In Noest et al. (2007), the zones with alternating percepts (blue) or repeating percepts (red) are pronounced. There is a small intermediate zone, though, with ill-defined behavior and seemingly irregular boundaries, which one may expect 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 T_{off} and T_{on} can lead to different percept sequences.

The situation is presented more clearly in Fig. 4. The curves of codimension-1 bifurcations divide the (T_{off}, T_{on})-plane 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 between 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 is straightforward to check that it lies in our wedge of bistability. For example, for $T_{on} = 1/\sqrt{2}$, we find the irregular zone lies near T_{off}=0.4583, while the left LPC is at T_{off}=0.43936, and the right one is at T_{off}=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.

With the approach that we have presented in this paper, it is not clear what the underlying biological mechanisms are of the different components of the model. However, our analysis makes predictions that could be tested in future human psychophysical studies, for instance, a more detailed analysis of percepts for different $\boldsymbol{T_{on}}$ durations might reveal the more complicated boundaries that we predict from our modeling study.

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