Mechanisms for oscillations in a biological competition model

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A four-dimensional dynamical system that models perceptual bistability in the brain is analyzed. Two variables represent the activity of two competing neural populations and they evolve in fast time; other two variables are slow and they are associated with an intrinsic negative feedback to each population. The external stimulus strength I is the bifurcation parameter. We construct the normal form and prove that oscillations occur in the system through supercritical Hopf bifurcations: as I decreases from large to moderate values a limit cycle is born; then it disappears for lower values of I .

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1 Introduction

Perceptual bistability is a class of phenomena in which a deeply ambiguous stimulus gives rise to two different interpretations that alternate over time, only one being perceived at any given moment. Some classical examples of perceptual bistability are binocular rivalry, the face-and-vase figure and the moving plaid. From modeling point of view the alternation seen in experiments is an oscillation in which two populations take turn in being on and off (an anti-phase oscillation).

The goal of this paper is to analyze a system of differential equations that was proposed as model for binocular rivalry [3], [4] and determine sufficient conditions for the parameters for oscillations to exist. The system is

$$u'_1 = -u_1 + S(I - \beta u_2 - ga_1), u'_2 = -u_2 + S(I - \beta u_1 - ga_2), \tau a'_1 = -a_1 + u_1, \tau a'_2 = -a_2 + u_2 \quad (1)$$

with variables u_j ($j = 1, 2$) that measure short-time and spatially averaged firing rates of the populations, and variables a_j ($j = 1, 2$) that correspond to a slow negative feedback process such as spike frequency adaptation or synaptic depression. Positive parameters β , g and τ ($\tau \gg 1$) represent the strength of inhibition, the strength of adaptation and the time constant of adaptation respectively. I is the control parameter directly associated to the external stimulus strength (e.g. it grows with growing stimulus strength such as contrast). The system is nonlinear due to the gain function S that in neuronal models is usually defined by $S(x) = 1/(1 + e^{-r(x-\theta)})$ with positive r and real θ .

In this paper we consider functions S that satisfy the following conditions: $S : \mathbf{R} \rightarrow (0, 1)$ is a differentiable, monotonically increasing function with $S(\theta) = u_0 \in (0, 1)$, $\lim_{x \rightarrow -\infty} S(x) = 0$, $\lim_{x \rightarrow \infty} S(x) = 1$, $\lim_{x \rightarrow \pm\infty} S'(x) = 0$, $S''(x) > 0$ for $x < \theta$, $S''(x) < 0$ for $x > \theta$ and $S''(\theta) = 0$, so S' has a maximum at θ . Consequently S is invertible with $F = S^{-1} : (0, 1) \rightarrow \mathbf{R}$ monotonically increasing function such that $\lim_{u \rightarrow 0} F(u) = -\infty$, $\lim_{u \rightarrow 1} F(u) = \infty$, $F(u_0) = \theta$ and $\lim_{u \rightarrow 0} F'(u) = \lim_{u \rightarrow 1} F'(u) = \infty$, $F''(u) < 0$ for $u \in (0, u_0)$, $F''(u) > 0$ for $u \in (u_0, 1)$, $F''(u_0) = 0$. Therefore F' has a minimum value at u_0 which is $F'(u_0) = 1/S'(\theta)$. Additionally we assume that F is a $\mathcal{C}^\infty$ function on $(0, 1)$.

Since we aim to prove existence of oscillations in system (1) and use Hopf bifurcation as a tool, we start by investigating the stability of the equilibrium points. Then we continue by constructing the normal form of the Hopf bifurcation and proving that supercritical Hopf points exist.

2 Steady states and oscillations in a biological competition model

2.1 Equilibrium points and their stability

All equilibrium points of (1) satisfy $u_1 = S(I - \beta u_2 - ga_1)$, $u_2 = S(I - \beta u_1 - ga_2)$, $a_1 = u_1$ and $a_2 = u_2$ which, due to the invertibility of S , become $F(u_1) = I - \beta u_2 - ga_1$, $F(u_2) = I - \beta u_1 - ga_2$ and $a_1 = u_1$, $a_2 = u_2$.

We look for equilibrium points with equal level of activity (that is $u_1 = u_2$) and find that for any real I there exists a unique $u_I \in (0, 1)$ such that $I = F(u_I) + (\beta + g)u_I$ and $e_I = (u_I, u_I, u_I, u_I)$ equilibrium of (1). In addition we have $du_I/dI = 1/(\beta + g + F'(u_I))$ so a decrease in I leads to a decrease in u_I with $\lim_{I \rightarrow \infty} u_I = 1$ and $\lim_{I \rightarrow -\infty} u_I = 0$.

The stability properties of e_I result from the linearized system $dY/dt = \mathcal{A}Y$ with $Y = (u_1 - u_I, u_2 - u_I, a_1 - u_I, a_2 - u_I)^T$ and matrix $\mathcal{A} = (a_{ij})_{i,j=1,4}$ defined by $a_{11} = a_{22} = -1$, $a_{12} = a_{21} = -\beta/F'(u_I)$, $a_{13} = a_{24} = -g/F'(u_I)$, $a_{14} = a_{23} = a_{32} = a_{34} = a_{41} = a_{43} = 0$ and $a_{31} = a_{42} = -a_{33} = -a_{44} = 1/\tau$. Here T represents the vector transpose.

The characteristic equation of $\mathcal{A}$ is a product of two quadratic polynomials $\lambda^2 + \lambda \left(1 + \frac{1}{\tau} + \frac{\beta}{F'(u_I)}\right) + \frac{1}{\tau} \left(1 + \frac{g+\beta}{F'(u_I)}\right)$ and $\lambda^2 + \lambda \left(1 + \frac{1}{\tau} - \frac{\beta}{F'(u_I)}\right) + \frac{1}{\tau} \left(1 + \frac{g-\beta}{F'(u_I)}\right)$ so two eigenvalues of $\mathcal{A}$, say λ_1 and λ_2 have negative real part no matter the

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value of I is, while other two eigenvalues λ_3 and λ_4 change their real part sign when I is varied. Based on these observations we obtain the following result.

Theorem 2.1 *System (1) has a unique equilibrium point with $u_1 = u_2$, say $\mathbf{e}_I = (u_I, u_I, u_I, u_I)$, for any real I . The value u_I increases monotonically with I and belongs to the interval $(0, 1)$. Let us assume now that $\beta < g(\tau + 1)$.*

i) If $\beta < (1 + 1/\tau)/S'(\theta)$ then $\mathbf{e}_I$ is asymptotically stable for all $I \in \mathbf{R}$.

ii) If $\beta > (1 + 1/\tau)/S'(\theta)$ then there are exactly two values $u_{hb}^, u_{hb}^{**} \in (0, 1)$ such that $u_{hb}^* < u_0 < u_{hb}^{**}$ and $F'(u_{hb}^*) = F'(u_{hb}^{**}) = \beta/(1 + 1/\tau)$. The equilibrium point $\mathbf{e}_I$ is asymptotically stable for all $I \in (-\infty, I_{hb}^*) \cup (I_{hb}^{**}, \infty)$ and unstable for $I \in (I_{hb}^*, I_{hb}^{**})$ where $I_{hb}^* = F(u_{hb}^*) + (\beta + g)u_{hb}^*$, $I_{hb}^{**} = F(u_{hb}^{**}) + (\beta + g)u_{hb}^{**}$. At I_{hb}^* and I_{hb}^{**} the stability is lost through a pair of purely imaginary eigenvalues.*

2.2 Normal form for Hopf bifurcation

In the following we assume that both inequalities $\beta < g(\tau + 1)$ and $\beta > (1 + 1/\tau)/S'(\theta)$ are true. Let us use the notation I^* for any of the critical values I_{hb}^* and I_{hb}^{**} and similarly the notation u^* for u_{hb}^* and u_{hb}^{**} . Then the linearization matrix $\mathcal{A}$ at u^* changes such that $a_{12} = a_{21} = -(1 + \frac{1}{\tau})$ and $a_{13} = a_{24} = -\frac{g}{\beta}(1 + \frac{1}{\tau})$ and its eigenvalues are $\lambda_{1,2}$ with $Re(\lambda_{1,2}) < 0$ and $\lambda_{3,4} = \pm i\omega$ with $\omega = \frac{1}{\tau}\sqrt{g(\tau + 1)/\beta - 1}$. As I crosses I_{hb}^* and I_{hb}^{**} , the equilibrium point $\mathbf{e}_I$ becomes unstable through a pair of purely imaginary eigenvalues and we expect to find two Hopf bifurcation points.

The construction of the normal form relies on the translation of the equilibrium $\mathbf{e}_I$ to the origin for any $I \in \mathbf{R}$, that is we work with the system $v_1' = -v_1 + S(F(u_I) - \beta v_2 - gb_1) - u_I$, $v_2' = -v_2 + S(F(u_I) - \beta v_1 - gb_2) - u_I$, $\tau b_1' = -b_1 + v_1$, $\tau b_2' = -b_2 + v_2$ with $v_j = u_j - u_I$, $b_j = a_j - u_I$ ($j = 1, 2$).

In this new system we expand near u^* the nonlinear terms with respect to u_I and then take small perturbations about the values I^* and u^* : $I - I^* = \varepsilon^2\alpha$, $V(t) = \varepsilon V_0(t) + \varepsilon^2 V_1(t) + \varepsilon^3 V_2(t) + \dots$ with α playing the role of the bifurcation parameter and $V = (v_1, v_2, b_1, b_2)^T$.

The details of the normal form constructions (see also [1] for the general method) are the following: we expand the coefficients $S^{(j)}(F(u_I))$, $j = 1, 2, 3, \dots$ with respect to ε and get $S'(F(u_I)) = (1 + \frac{1}{\tau})/\beta + \alpha A\varepsilon^2 + \mathcal{O}(\varepsilon^4)$, $S''(F(u_I)) = B + \mathcal{O}(\varepsilon^2)$ and $S'''(F(u_I)) = C + \mathcal{O}(\varepsilon^2)$ with A , B and C defined by

$$A = -\frac{F''(u^*)}{F'(u^*)^2(\beta + g + F'(u^*))}, B = -\frac{F''(u^*)}{F'(u^*)^3}, C = \frac{3F''(u^*)^2 - F'(u^*) \cdot F'''(u^*)}{F'(u^*)^5}. \quad (2)$$

Then we use the notation $U = (v_1, v_2, b_1, b_2)^T$ and $W = (w_1, w_2, c_1, c_2)^T$, $\tilde{v}_{ij} = \beta v_j + gb_i$, $\tilde{w}_{ij} = \beta w_j + gc_i$, and define the operators $L_0 U = \frac{dU}{dt} - \mathcal{A}_0 U$, $\Lambda U = -\alpha A(\tilde{v}_{12}, \tilde{v}_{21}, 0, 0)^T$, $\mathcal{B}(U, W) = \frac{B}{2}(\tilde{v}_{12}\tilde{w}_{12}, \tilde{v}_{21}\tilde{w}_{21}, 0, 0)^T$, $\mathcal{C}(U, U, U) = -\frac{C}{6}(\tilde{v}_{12}^3, \tilde{v}_{21}^3, 0, 0)^T$.

The normal form results from a process of matching coefficients for different powers of ε in the expansion $L_0 V = \Lambda V + \mathcal{B}(V, V) + \mathcal{C}(V, V, V) + \dots$ with V chosen above (see [2] for a more comprehensive study of the system (1)). We obtain the following result.

Theorem 2.2 *Suppose conditions $\beta < g(\tau + 1)$ and $\beta > (1 + 1/\tau)/S'(\theta)$ are true. Then in the neighborhood of I^* (with I^* either I_{hb}^* or I_{hb}^{**} , and u^* its corresponding value u_{hb}^* or u_{hb}^{**}), the dynamical system (1) has the normal form*

$$\dot{z} = A\varphi(I - I^*)z - \mathcal{L}z^2\bar{z}, \quad \mathcal{L} = 4\tau^2\omega^2 \frac{|\varphi|^2}{|\psi|^2} \varphi\psi \left(\frac{\beta + g}{2} + i\beta\omega\tau \right) B^2 + 2\tau^2\omega^2 |\varphi|^2 \varphi \left(\frac{2(\beta + g)}{1 + (\frac{g}{\beta} + 1)(1 + \frac{1}{\tau})} B^2 - C \right)$$

with $\varphi = \frac{\beta}{2} + i\frac{g-\beta}{2\tau\omega}$, $\psi = 2 - \frac{3g}{\beta} + \frac{1}{\tau} \left(5 - \frac{3g}{\beta} \right) - 4i\omega(\tau + 1)$, $\omega = \frac{1}{\tau}\sqrt{g(\tau + 1)/\beta - 1}$ and A , B , C as in (2).

If u^* satisfies the condition

$$F'(u^*)F'''(u^*) > 2F''(u^*)^2 \quad (3)$$

for the gain function S (here $F = S^{-1}$), then $Re(\mathcal{L}) > 0$. Therefore I^* is a supercritical Hopf bifurcation point for system (1) and stable oscillations exist; the stable limit cycle occurs to the left of I_{hb}^{**} ($I < I_{hb}^{**}$) and to the right of I_{hb}^* ($I > I_{hb}^*$).

We mention that at least for the particular case of gain function $S(x) = 1/(1 + e^{-r(x-\theta)})$, the inequality (3) is true. Moreover it is true not only for u^* but for all $u \in (0, 1)$.

Acknowledgements This work was supported by the Romanian Research Council grant CNCSIS -AT 55/2006-2007.

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