



Jugowice, 11th–15th September 2017

NEURAL MASS WITH SHORT-TERM SYNAPTIC PLASTICITY (STP) AS A MODEL OF A WINNER-TAKE-ALL COMPETITION IN SENSORY SYSTEMS

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ABSTRACT

In this work, we propose a population model to characterize the binary decision making as an outcome of a winner-take-all competition between two neuronal populations communicating through plastic synapses. In particular, we study the impact of the inputs stimulating the neuronal populations on the time-course and efficiency of the decision making process. Furthermore, we demonstrate that background input and anatomical strength of connections can induce distinct, context dependent modes of activity. We obtain a range of results that may provide with new insights into the neuronal mechanisms of decisions and actions.

INTRODUCTION

Decision making – from simple perceptual choices such as the Necker cube phenomenon [1] to complex choices such as choosing the best vacation destination – is one of the basic functionalities of the human brain. While making a decision, one needs to evaluate the options, and withdraw all but one of them. This evaluation process can be time- and energy-costly to the brain [2], and has at least two tangential aspects. Firstly, decision making requires evaluating utility of the alternatives (for instance, choosing between an apple and an orange on the basis of factors such as their taste, smell, nutritious value, appearance, price etc.). Secondly, in more basic, perceptual decision making, a subject needs to disambiguate the sensory stimuli, which are often noisy. In laboratory conditions, this phenomenon is investigated with the use of two-alternative forced choice experiments. In a famous example, Michael Shadlen trained rhesus monkeys to distinguish between the dots moving on the screen towards either right or left direction [4]. This experiment was then modeled by Wang et al. [3] by a spiking neuronal network model with a slow reverberation mechanism. Wang's model is an example of a winner-take-all mechanism, which is a first line of choice to model sensory decision making in the cortical networks.

Our model also represents the winner-take-all family of models. Unlike Wang, we do not simulate stochastic spiking neuronal networks in our study though, but we represent the competing populations as a neuronal mass model and take an analytic approach instead.

MODEL DESCRIPTION

In our model, we consider two populations of neurons (1 and 2, Fig. 1). Neurons from the first population affect neurons of the second population with a synaptic weight $w_1(t)$, whereas neurons belonging to the second population interact with neurons in the first population with a synaptic weight $w_2(t)$. Synaptic weights $w_1(t)$ and $w_2(t)$ ($0 < w_1 < 1, 0 < w_2 < 1$) indicate the strength of the connections between two nodes that, from the biological standpoint, correspond to the influence the firing of the neuron from the first cluster has on the neuron from the second one. Due to the presence of plasticity at the synapses, the values of synaptic weights can vary over time. In the winner-takes-all model, the two neuronal populations constantly compete: one of them can gain in the firing rate on the cost of the other (depicted by $r_1(t)$ and $r_2(t)$). In general, the two competing neuronal populations are not an isolated system and are embedded in a bigger cortical network. Therefore, one can assume that stimuli represent the background activity within the system and are higher than zero even in the absence of the experiment-related stimulus. Therefore, both populations receive a constant external input I , representing the background neuronal activity. In addition to that, population 1 receives an input σ relating to the sensory stimulus.

The network is then supposed to *make a decision*, i.e., to correctly decode which population received the stimulus σ . The decision rule in this model is very simple, as this is a winner-take-all mechanism: if $r_1(t) > r_2(t)$, the network chooses the population 1 as the origin of the stimulus, and if $r_2(t) > r_1(t)$, the network chooses the population 2. If $r_1(t) = r_2(t)$, we interpret this as a lack of decision.

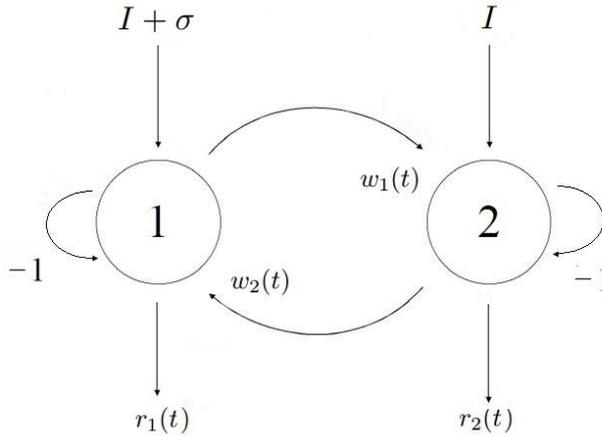


Figure 1. A simple neural-mass neuronal model of a decision making network. Neurons in the first population project to neurons in the second population with synaptic weight $w_1(t)$, while neurons in the second population project to neurons in the first population with a synaptic weight $w_2(t)$. The firing rates in the populations are denoted by $r_1(t)$ and $r_2(t)$. The two neuronal populations constantly compete: one of them can gain in firing rate on the cost of the other. Both populations receive a constant, external input I which relates to a background activity in cortical networks. In addition to this, population 1 receives an external stimulus σ , representing a sensory input.

The dynamics in this network can be characterized by a bilinear population model:

$$\begin{cases} \tau_r \dot{r}_1(t) = -r_1(t) + w_2(t)r_2(t) + I + \sigma, \\ \tau_r \dot{r}_2(t) = -r_2(t) + w_1(t)r_1(t) + I, \end{cases} \quad (1)$$

where I denotes the background activity in the neuronal populations ($[1/s]$), σ denotes the sensory stimulus, and τ_r is the time scale of the firing rates ($[s]$). In the model, we also have a self-inhibition

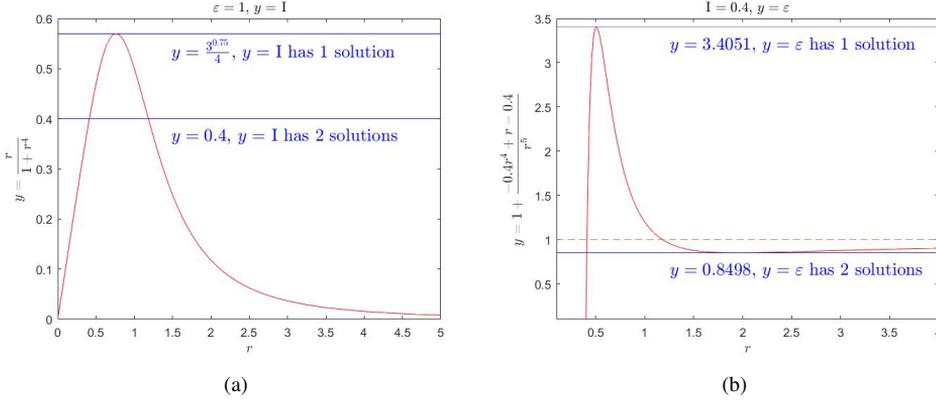


Figure 2. Existence of steady states: (a) with respect to the value of the parameter I when $\varepsilon = 1$; (b) with respect to the value of the parameter ε when $I = 0.4$.

term $-r(t)$ that represents local inhibition *within* the competing populations. Such a relaxation term is often used in modeling neuronal activity in interacting populations, i.e., see Dynamic Causal Modeling [5, 6].

The expression $w_2(t)r_2(t)$ in the first equation and $w_1(t)r_1(t)$ in the second equation reflects the positive effect of the second neuronal population on the neurons from the first cluster with connection strength w_2 , analogous to $w_1(t)r_1(t)$ in the second equation.

The short term plasticity in this system (STP, [7]) yields as follows:

$$\begin{cases} \tau_w \dot{w}_1(t) = -w_1(t) + \varepsilon f(r_1(t)r_2(t)), \\ \tau_w \dot{w}_2(t) = -w_2(t) + \varepsilon f(r_1(t)r_2(t)), \end{cases} \quad (2)$$

where $f(x) = \frac{x^2}{1+x^2}$ denotes a sigmoidal transfer function, τ_w is the time-scale of synaptic weights, and $\tau_w \ll \tau_r$. In our model, parameter ε refers to the anatomical maximum connection capacity, which can then be modulated by STP.

BASIC PROPERTIES OF THE MODEL AND NUMERICAL EXPERIMENTS

First, we analyze the model for the basic, symmetric case when there is no sensory stimulus ($\sigma = 0$). The solutions exist and are unique as the right-hand sides of Eqs. (1)-(2) are of class \mathbf{C}^1 . Moreover, the right-hand sides fulfill the Lipschitz condition, therefore the solutions are extendable for all $t > 0$.

Existence of steady states

Steady states of Eqs. (1)-(2) for $\sigma = 0$ satisfy the following relations:

$$\begin{cases} r_1(t) = w_2(t)r_2(t) + I, \\ r_2(t) = w_1(t)r_1(t) + I, \\ w_1(t) = \varepsilon \frac{(r_1(t))^2(r_2(t))^2}{1 + (r_1(t))^2(r_2(t))^2}, \\ w_2(t) = \varepsilon \frac{(r_1(t))^2(r_2(t))^2}{1 + (r_1(t))^2(r_2(t))^2}. \end{cases} \quad (3)$$

From the symmetry of the system, $w_1 = w_2 = w$, which yields

$$\begin{cases} r_1(t) = w(t)r_2(t) + I, \\ r_2(t) = w(t)r_1(t) + I. \end{cases} \quad (4)$$

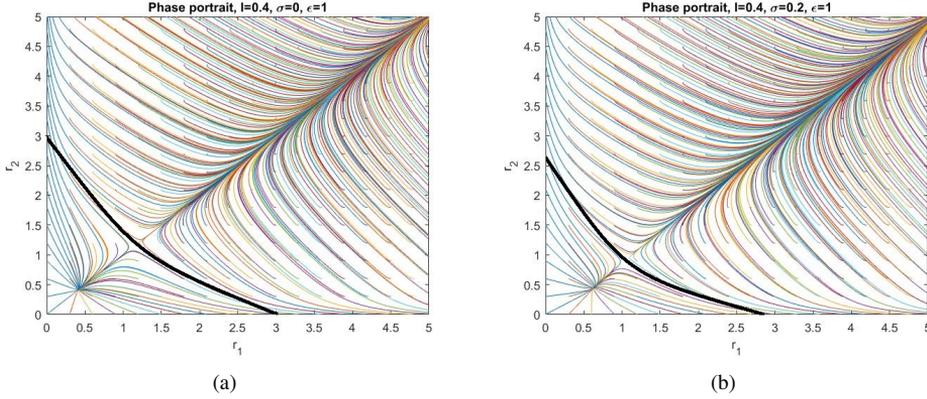


Figure 3. The influence of the stimulus on the decision making performance in the system. (a) The behavior of the system when the first and the second group of neurons are given the same input ($\sigma = 0$). In this case the decision is random (after sufficiently long period of time $r_1 = r_2$). (b) On the contrary, when the first cluster is more agitated ($\sigma > 0$), the network undertakes the first decision – the stable point (r_1, r_2) fulfills the condition $r_1 > r_2$.

Subsequently, assuming that synaptic weights are always positive ($w > 0$), we obtain $w = \varepsilon \frac{r^4}{1+r^4}$. Hence, the coordinates of a steady state satisfy the relation

$$I = r - \varepsilon \frac{r^5}{1+r^4}, \quad r > 0, \quad I > 0. \quad (5)$$

If $\varepsilon = 1$, this expression reduces to $I = \frac{r}{1+r^4}$.

Corollary 1. *If $\varepsilon = 1$, then there are: 2 steady states if $I < \frac{3^{0.75}}{4}$, 1 steady state if $I = \frac{3^{0.75}}{4}$, no steady states if $I > \frac{3^{0.75}}{4}$.*

The graphical representation of Corollary 1 is presented in Fig. 2.

Let us now assume that $I = 0.4$ (so that we have two steady states). Then, $\varepsilon = 1 + \frac{-0.4r^4 + r - 0.4}{r^5}$.

Corollary 2. *If $I = 0.4$, there are: 3 steady states when $\varepsilon \in (0.8498, 1)$, 2 steady states when $\varepsilon \in \{0.8498\} \cup [1, 3.4051)$, 1 steady state when $\varepsilon \in (0, 0.8498) \cup \{3.4051\}$, no steady states when $\varepsilon > 3.4051$.*

Stability of the steady states

In this section, we focus on the stability analysis of these steady states. For this purpose, we choose a specific parameter set. However, the magnitude of the parameter ε has a significant impact on the dynamics of model as well as on the decision making performance in the system. In Fig. 4 we present the phase portraits for the symmetric case (with $\sigma = 0$) and varying values of ε , and present all four cases listed in Corollary 2.

Let us now fix $I = 0.4$, $\varepsilon = 1$ and $\tau_r = \frac{1}{3}$. Then, the coordinates $r_1^* = r_2^* = r^*$ of the two steady states take the approximate values $[r_1^*, r_2^*] = r_a^* = 0.4114655$ and $[r_1^*, r_2^*] = r_b^* = 1.1827404$.

The Jacobian matrix J of Eqs. (1)-(2) takes the following form:

$$J = \begin{bmatrix} -\frac{1}{\tau_r} & \frac{1}{\tau_r} w_2 & 0 & \frac{1}{\tau_r} r_2 \\ \frac{1}{\tau_r} w_1 & -\frac{1}{\tau_r} & \frac{1}{\tau_r} r_1 & 0 \\ \frac{1}{\tau_w} A r_2 & \frac{1}{\tau_w} A r_1 & -\frac{1}{\tau_w} & 0 \\ \frac{1}{\tau_w} A r_2 & \frac{1}{\tau_w} A r_1 & 0 & -\frac{1}{\tau_w} \end{bmatrix}, \quad A = \frac{2r_1 r_2}{(1 + (r_1 r_2)^2)^2}. \quad (6)$$

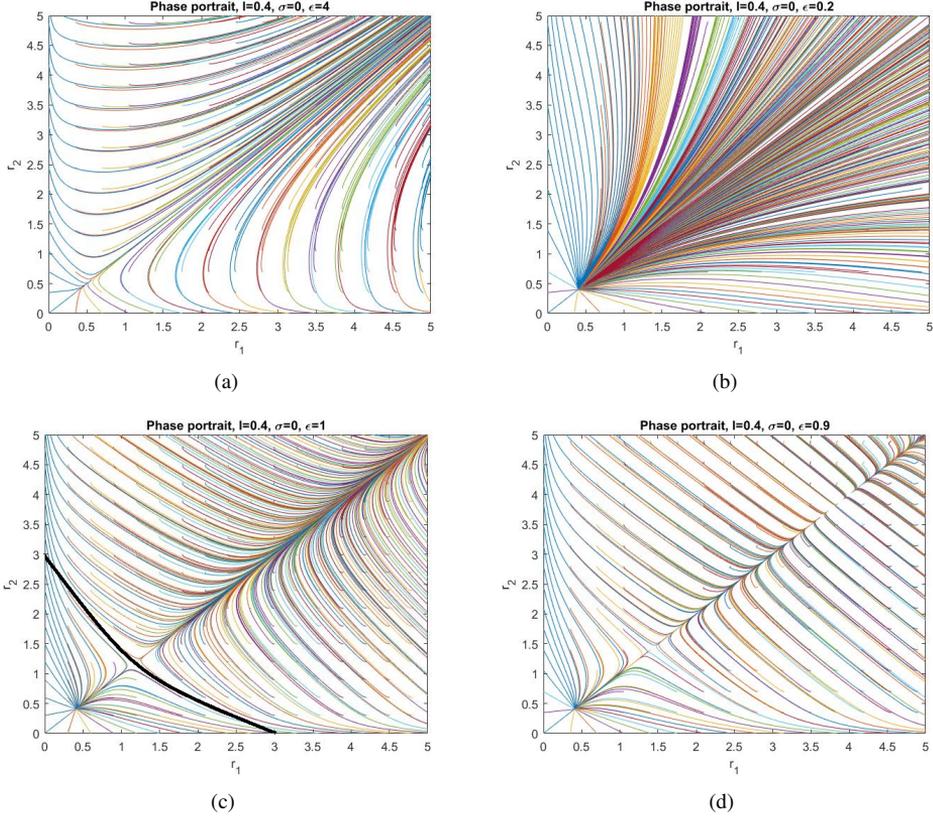


Figure 4. The influence of the magnitude of the parameter ε on the decision making performance in the system. Phase portraits for: (a) $\varepsilon = 4$ with no steady states, (b) $\varepsilon = 0.2$ with one stable steady state, (c) $\varepsilon = 1$ with two steady states, one of them stable, (d) $\varepsilon = 0.9$ with three steady states, two of them stable. The initial points (r_1, r_2) for which the solutions converge to infinity are irrelevant for us, because the model has a biological sense only for limited values of firing rates. The simulations were performed in MATLAB, thanks to the courtesy of NSG gateway [9].

Due to the fact that $\tau_w \ll \tau_r$, we choose $\tau_w = 0.01\tau_r$. Now, from the symmetry $r_1 = r_2 = r$, $w_1 = w_2 = w$, yielding

$$\det(J - \lambda \mathbb{I}) = \det \begin{bmatrix} -\frac{1}{\tau_r} - \lambda & \frac{1}{\tau_r} w & 0 & \frac{1}{\tau_r} r \\ \frac{1}{\tau_r} w & -\frac{1}{\tau_r} - \lambda & \frac{1}{\tau_r} r & 0 \\ \frac{100}{\tau_r} Ar & \frac{100}{\tau_r} Ar & -\frac{100}{\tau_r} - \lambda & 0 \\ \frac{100}{\tau_r} Ar & \frac{100}{\tau_r} Ar & 0 & -\frac{100}{\tau_r} - \lambda \end{bmatrix} =$$

$$= \left(\lambda + \frac{100}{\tau_r} \right) \left(\lambda + \frac{1}{\tau_r} w + \frac{1}{\tau_r} \right) \left(\left(\lambda + \frac{100}{\tau_r} \right) \left(\lambda - \frac{1}{\tau_r} w + \frac{1}{\tau_r} \right) - \frac{200}{\tau_r^2} Ar^2 \right) \quad (7)$$

The roots of Polynomial (7) satisfy:

$$\begin{aligned}\lambda_1 &= -\frac{100}{\tau_r} < 0, \\ \lambda_2 &= -\frac{1}{\tau_r}(w + 1) < 0, \\ \lambda_3 &= \frac{1}{2\tau_r}((w - 101) - ((w - 101)^2 + 400(w - 1 + 2Ar^2))^{0.5}) < 0, \\ \lambda_4 &= \frac{1}{2\tau_r}((w - 101) + ((w - 101)^2 + 400(w - 1 + 2Ar^2))^{0.5}).\end{aligned}$$

Taking into account the assumptions made at the beginning, substituting each of the previously received steady states, we obtain that the steady state r_a^* is stable ($\lambda_4 < 0$) and r_b^* is unstable ($\lambda_4 > 0$).

Note that when the system is symmetric ($\sigma = 0$), then in the steady state, $r_1^* = r_2^*$ (Fig. 3(a)), therefore according to our decision rule, the network cannot take a decision. Otherwise, if $\sigma > 0$, then the stable point $[r_1^*, r_2^*]$ fulfills the condition $r_1^* > r_2^*$ (Fig. 3(b)), and therefore the correct decision is made.

DISCUSSION

In this paper, we propose a population model of decision making based on a winner-take-all mechanism. In this simple model, the network needs to make a binary choice between the two options. With this model, we study the influence of a magnitude of the sensory stimulus (represented here by σ) on making perceptual choices. As mentioned before, the number of steady states and therefore the behavior of the system depends also on the value of the parameter relating to the strength of the anatomical fibres linking the populations limiting the maximal connection capacity, ε . The model has a biological sense only if it is possible to reach a stable attractor from its initial state, i.e. if the firing rates are from the beginning in the basins of attraction of stable steady points, as shown for example in the Fig. 3. This decision-making model is currently being extended by a delay parameter exhibits a rich dynamic repertoire [8]. In this paper, we demonstrate that large delays in the local inhibition can lead to the subcritical Hopf bifurcation resulting in complex impairments in the decision making process. We also demonstrate that above the Hopf bifurcation point, increasing the strength of the stimulus may lead to the change in the final decision into a wrong one.

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