Selectivity Gain in Olfactory Projection Neurons at Low Odor Concentrations

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***Abstract*—It is known that selectivity of an olfactory projection neuron is better than that of receptor ones converging on it. Under high odor concentration, the selectivity is improved due to lateral inhibition mechanism in the olfactory bulb. This mechanism does not work at low concentrations.**

We propose an original mechanism which could improve selectivity at low concentration of odors, which is based on the stochastic nature of stimuli obtained by a projection neuron from the receptor ones. The mechanism operates at the level of communication from receptor neurons to a projection neuron, and does not require involvement of other bulbar neurons.

As a projection neuron model we use one described by the Korolyuk, Kostyuk, Pjatigoskii, Tkachenko. In this model, the membrane electrical leakage is modeled by spontaneous random decay of each input impulse, which is kept unchanged until the decay.

We analyze the neuron's triggering process due to stochastic stimulation from receptor neurons by exactly calculating the mean interspike interval for the projection neuron. This allows to compare selectivity of projection neuron with that of receptor neurons converging on it.

Exact mathematical expression is obtained for the selectivity gain in projection neurons as compared to that in the receptor ones. A possibility of high gain at low odor concentration is predicted based on the expression obtained.

The stochastic nature of communication from receptor to projection neurons causes selectivity improvement in the projection ones at low odor concentration, when the lateral inhibition mechanism in the olfactory bulb does not work.

I. INTRODUCTION

A higher selectivity of the olfactory projection neurons (PN), as compared to that of the receptor ones, has been discussed many times, see e.g. [1]. Lateral inhibition has been proposed as a sole mechanism explaining the higher selectivity of PNs [2]. This mechanism requires communication between several projection neurons which involves activity of granular cells, which are inhibitory. At low odor concentration, inhibitory activity in the olfactory bulb is either absent or quite low, see [1], which makes lateral inhibition inefficient. In our paper, a different mechanism is proposed, which is based exclusively on the electrical leakage through the PN's membrane, on the stochastic nature of the stimuli received by PNs from the receptor neurons and on the threshold-type reaction to those stimuli. This mechanism does not depend on the lateral inhibition and is capable of functioning at low odor concentrations.

II. METHODS

A. *Selectivity gain definition*

We define selectivity in a receptor neuron as follows. If two odors, O and O' are presented to a receptor neuron (RN) in two separate experiments at equal concentrations, then it may so happen that the RN's output firing rates λ_{rn}, λ'_{rn} will be different. This means that this RN is able to discriminate between these two odors. Expect $\lambda'_{rn} = \lambda_{rn} + \Delta\lambda_{rn}$, where $\Delta\lambda_{rn} > 0$. We define selectivity of that RN with respect to those two odors as $s = \Delta\lambda_{rn}/\lambda_{rn}$. A large number of RNs expressing the same receptor protein converge onto a single projection neuron. The compound stimulation rate of the PN is $\lambda_{tot} = N\lambda_{rn}$, where N — is the total number of RNs converging on a single PN (N is up to 5000 and more, [3]). If so then the PN's firing rate for those two odors will be different as well: $\lambda'_{pn} = \lambda_{pn} + \Delta\lambda_{pn}$. We define selectivity of that PN with respect to those two odors as $S = \Delta\lambda_{pn}/\lambda_{pn}$. The selectivity gain, g, can be now defined as follows: $g = S/s$. Taking into account the s and S definitions, the latter can be represented as a derivative:

$$g = \frac{\lambda_{rn}}{\lambda_{pn}} \frac{d\,\lambda_{pn}}{d\,\lambda_{rn}}. \tag{1}$$

B. *Projection neuron model*

As it can be seen from (1), in order to calculate the selectivity gain one has to know how does the λ_{pn} depend on the λ_{rn}. The required dependence can be found based on a PN's model. We choose here the KKPT model named after its authors [4]. In this model, any input impulse stays unchanged for some random period of time, after which it disappears. The living times distribution is exponential with constant μ. This model satisfactory describes the membrane electric leakage if the input impulses are small as compared to the triggering depolarization level, see Fig. 1. At the same time, this model, if stimulated with Poisson stochastic process, has purely stochastic dynamics. This is in the contrast to standard leaky integrate-and-fire model, where input is stochastic whereas depolarization decay is deterministic. Due to this mixt of two types of dynamics standard leaky integrate-and-fire model appears to be less suitable for calculations.

III. RESULTS

The pure stochastic nature of the KKPT model allows for calculating exactly the mean waiting time between two consecutive output impulses, T_o. For this purpose, e.g., formula

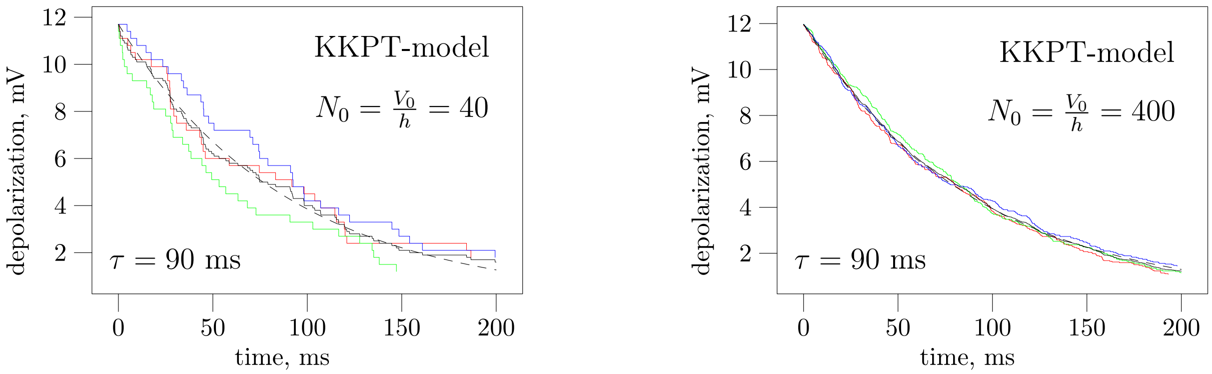

Fig. 1. Modeling deterministic exponential decay of membrane depolarization due to electric leakage with KKPT model of stochastically decaying input impulses. V_0 — is the firing threshold voltage, h — is the height of input impulse. The dashed line shows the true exponential decay. Other three curves represent realizations of stochastic decay of impulses received earlier. Here $\mu = 1/\tau$, where τ — is the PN's membrane time constant. Notice the better approximation for smaller input impulses.

(1.69) from [5] can be used. The resulting expression is as follows:

$$T_o = \frac{1}{\lambda_{tot}} \sum_{0\le l\le N_0-1} \; \sum_{0\le k\le l} \frac{l!}{k!} \left(\frac{\mu}{\lambda_{tot}}\right)^{l-k} . \qquad (2)$$

Here N_0 – is the firing threshold expresed as the minimal number of input impulses able to trigger a spike. Taking into account that $\lambda_{pn} = 1/T_o$, Eq. (1) can be rewritten as follows:

$$g = -\frac{\lambda_{in}}{T_o}\frac{d\,T_o}{d\,\lambda_{in}} . \qquad (3)$$

Using (2) in (3) one obtains after transformations:

$$g = 1 + \frac{\sum_{j=0}^{N_0-1} \frac{j}{j+1}\left(\frac{\mu}{N\lambda_{rn}}\right)^j \frac{1}{(N_0-j-1)!}}{\sum_{j=0}^{N_0-1} \frac{1}{j+1}\left(\frac{\mu}{N\lambda_{rn}}\right)^j \frac{1}{(N_0-j-1)!}} . \qquad (4)$$

This expression can be analyzed for several limiting cases. First, expect there is no leakage in the PN. This is so called “perfect integrator” case which is characterized with $\mu = 0$. In this case, $g = 1$, — no selectivity gain. Second, consider case of high odor concentration. This is characterized with $\lambda_{rn} \to \infty$. In this case, again, $g = 1$, — no selectivity gain. Third, consider case of low odor concentration. In this case λ_{rn} is small. It can be proven that

$$\lim_{\lambda_{rn}\to 0} g(\lambda_{rn}) = N_0, \qquad (5)$$

where $g(\lambda_{rn})$ is given by Eq. (4). Taking into account that $N_0 = 300$ — 500 for a PN, we see from (5) that selectivity gain in PN can be fairly large at low odor concentrations. Data taken from experimental literature and used in (4) give for g value about 30. It also can be proven that $g(\lambda_{rn})$ decreases with increasing λ_{rn}.

IV. CONCLUSIONS

In our paper, a mechanism has been proposed for improving selectivity in olfactory projection neurons as compared to the receptor neurons, which operates at low odor concentrations. This mechanism does not depend on the lateral inhibition. A coefficient of the selectivity gain, g, is defined in order to get a quantitative description. The coefficient of selectivity gain is characterized by the following. There is no selectivity gain ($g = 1$), if a secondary neuron is triggered by each single input impulse ($N_0 = 1$). This is, however, not the case for PNs, where up to several hundreds of input impulses from the receptor neurons, delivered within a narrow time window, are necessary for triggering. The selectivity gain increases with increasing triggering threshold. Also, there is no gain if the electrical leakage is absent. With decreasing odor concentration the selectivity gain due to the mechanism proposed increases. This kind of behavior has been observed experimentally when odors were applied from low concentration range, [6]. See also [7] where a similar mechanism is discussed in connection with adsorption-desorption noise.

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