Possible Stochastic Mechanism for Improving the Selectivity of Olfactory Projection Neurons

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A possible mechanism that provides increased selectivity of olfactory bulb projection neurons, as compared to that of the primary olfactory receptor neurons, has been proposed. The mechanism operates at low concentrations of the odor molecules, when the lateral inhibition mechanism becomes inefficient. The mechanism proposed is based on a threshold-type reaction to the stimuli received by a projection neuron from a few receptor neurons, the stochastic nature of these stimuli, and the existence of electrical leakage in the projection neurons. The mechanism operates at the level of the single individual projection neuron and does not require the involvement of other bulbar neurons.

Keywords: odors, olfactory bulb, olfactory receptor neurons, projection neurons, spike activity, selectivity, stochastic process.

INTRODUCTION

Primary reception of odors is provided by olfactory receptor neurons (ORNs). The ORNs are synaptically connected with mitral and tufted cells of the olfactory bulb. The latter cells, known as bulbar projection neurons (PNs), convey olfactory signals to upper brain structures (finally, to the olfactory cortex).

Communication between ORNs and PNs is of convergent nature: many ORNs synapse onto a single PN. The convergence degree depends on the animal species and can be fairly large [1]. This is one of the factors providing high sensitivity to odors [2–4].

It is known that the discriminating ability of PNs is better than that of ORNs [5, 6]. A general point of view is that the better selectivity of PN is due to the mechanism of lateral inhibition [5, 7, 8]. Such a mechanism has been well studied in the visual system, where it increases the contrast between domains of the visual field [9–11]. In the olfactory system, lateral inhibition is organized via granular cells, which are stimulated by mitral cells and inhibit other PNs [12, 13]. As a result, the system

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of PNs functions similarly to the "winner takes all" principle, and this can be the reason of PNs having better selectivity than ORNs.

In recent studies [14], it was realized that lateral inhibition in the olfactory bulb, unlike that in the retina, is organized nontopographically. Such a feature was discussed earlier [8]. If so, is lateral inhibition able to ensure the same "contrast enhancement" in olfaction as it does in vision? This question has been discussed [15], but a final answer to this question requires additional experimental studies.

Lateral inhibition of PNs happens due to the activity of inhibitory bulbar neurons. The recruitment of inhibitory neurons is necessary because there is a possibility of high odor concentrations, and such recruitment decreases with decreasing concentrations [5]. Therefore, the efficacy of lateral inhibition in improving the selectivity of PNs should decrease for low concentrations. Such a decrease has been observed [5].

In our paper, another mechanism for the selectivity gain in PNs is proposed. It is independent of lateral inhibition and could be very efficient at low odor concentrations. This mechanism can work for individual PNs without the involvement of other bulbar cells. The prerequisites of this mechanism are as follows:

(ii) a threshold-type response of PNs to the respective stimuli, and

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⁽i) existence of a leakage in the PN membrane,

(iii) the random nature of stimuli obtained by a PN from ORNs.

A similar mechanism is possible for both individual ORNs [17, 18] and "electronic nose" sensors based on adsorption-desorption of odors [19].

In this theoretical paper, a PN model is used, which has been proposed earlier [20]. The activity of a single ORN is described as a Poisson process. The communication between a set of a few ORNs and the corresponding PN is characterized by the convergence degree N and the minimal number of input spikes N_0 required for triggering that PN (firing threshold). For this system, the coefficient of selectivity gain g is defined, which shows how much the PN selectivity is improved, as compared to that of the ORN. The exact expression for g as a function of the system parameters has been found. The expression output is analyzed for different parameters. In particular, it is observed that, for physiologically relevant parameters, the PN selectivity can be several tens times better than that of ORNs due to the mechanism proposed.

METHODS

Neuronal Model with a Random Living Time of the Obtained Excitatory Impulses. A model of PN that was proposed earlier [20] has been used. In this model, an effect of the membrane leakage occurs during a random decay of individual input impulses. Before the decay, each impulse is stored unchanged, and it disappears at the decay moment. Thus, there is a finite set of possible values of depolarization. The random living time of a single obtained impulse is characterized by an exponential distribution. Therefore, the decay of total depolarization is exponential (as it should be), but the depolarization decreases by finite jumps with a height equal to the height of an input impulse. If the impulse height is small, as compared with the firing threshold, then this model describes the membrane leakage satisfactorily.

Mathematically, the model can be formulated as follows. The resting state of a neuron is characterized by zero depolarization, V = 0. When obtaining an input impulse, the depolarization advances by h, the height of the input impulse. The h is analogous to the EPSP amplitude. Between the moments of obtaining two consecutive impulses, the depolarization does not change, V(t) = const, if no decay happens. Therefore, at any time moment, the depolarization takes a value from the discrete set, $V \in \{0, h, 2h, 3h, ...\}$. The neuron is characterized by a firing threshold V_0 ; if depolarization is greater than V_0 , then the neuron generates an output spike and appears in its resting state. The triggering condition formulated in terms of V_0 can be reformulated in terms of the minimal number N_0 of input spikes capable of triggering:

$$N_0 = [V_0/h] + 1,$$

where brackets [x] denote the integer part of x.

Until now, the model described corresponds to the model known as a "perfect integrator" [21]. It has been additionally expected [20] that any impulse obtained by the neuron has a random living time. The living time is exponentially distributed with the constant μ . This means that any impulse may disappear during a small interval, [t; t + dt], with the probability μdt . If the neuron keeps k excitatory impulses at moment t, the depolarization is equal to V(t) = kh. Let us believe that stimulation is absent after t. During a short interval, [t; t + dt], any of the k impulses can decay/disappear. Let us expect that the impulses decay independently. Then the probability that depolarization decreases by h during dt is $k\mu dt$. Thus, at the end of the interval [t; t + dt], the depolarization is equal to V(t + dt) = (k - 1)hwith the probability $k\mu dt$, and to V(t + dt) = khwith the probability $1 - k\mu dt$. Averaging over many realizations, we obtain the mean value of depolarization:

$$\overline{V(t+dt)} = (k-1)hk\mu \, dt + kh(1-k\mu \, dt) = = kh(1-\mu \, dt) \approx V(t)e^{-\mu \, dt}.$$

It is clear from the latter considerations that, on average, the depolarization decreases exponentially, as it should be for electrical leakage, and the constant μ has a physical meaning of the inverse membrane relaxation time, $\mu = 1/\tau$. This model could be named, according to its authors, as the KKPT model.

A Projection Neuron that is Stimulated by Many ORNs. The communication scheme between ORNs and a PN is shown in Fig. 1. It is not necessary to take into consideration additional cells, in particular the granular ones, and additional dendrites possibly ending in other glomeruli or nearby, for investigating of how the randomness, threshold, and leakage influence the PN selectivity.