

DISCRIMINATING ABILITY IMPROVEMENT IN SENSORY SYSTEMS DUE TO COOPERATIVITY

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Natural sensory systems have a remarkable discriminating ability (selectivity), which is hardly explainable based on primary reception mechanisms, specific for each sensory modality. For example, response characteristics of cone photoreceptor cells to the light of different wavelength are wide, suggesting poor color discrimination at this stage of visual perception. At the same time, color discrimination at the level of visual cortex can be much more precise [10]. The same is with spatial grating discrimination known as hyperacuity of vision [7].

In the auditory system, the primary sound reception is realized by means of tectorial membrane, which has low quality factor, Q , for mechanical oscillations [5], which does not allow to expect sharp tuning at the primary stage. But the sound frequency discrimination at behavioral level can be very high in some cases.

In the olfactory system, the odor quality discrimination in the olfactory bulb is better than that in the primary receptor neurons [2].

One more example is the weak electric fish [1]. This fish has sensory system for registering oscillating electric potential. The frequency of oscillations has behavioral meaning as well as its amplitude. It is established that the frequency tuning is better at behavioral level as compared to the primary level realized by means of electroreceptive cells.

All sensory systems, if taken between a primary reception point and corresponding area in the sensory cortex, have two features in common. First, they are convergent. This means that many outputs from first-order neurons converge onto a single secondary neuron. For example, up to 1000 olfactory receptor neurons converge onto a single secondary cell in some insects [4]. The second feature is the threshold, which is raised by the secondary neuron. Due to the threshold the inputs from first-order neurons must cooperate one or another way for triggering further stages of neural processing. The cooperativity may be the reason for sharp selectivity, as it has been shown for chemical systems in which cooperativity emerges due to autocatalysis [8].

Cooperative mechanism of this same type can be found in a single chemoreceptor neuron as well. Its process exposed to odor (cilia) has a large number (N) of identical receptor proteins, which can bind odors selectively. The number N can be as large as 5000 in mice [6]. In the framework of simplified model, if N_0 receptor proteins are bound with odor, where $1 \leq N_0 \leq N$, the neuron fires a spike. If $N_0 \gg 1$, both convergence and threshold are present in a single chemoreceptor neuron.

For uniformity, we say that the first-order stage of perception is active if either a receptor protein is bound with odor (in case of chemoreceptor neuron), or a spike is coming from a first-order neuron to the secondary one (in case of further processing stages of sensory signal).

Table 1: Numerical example of improved selectivity. The firing rates R_1 , R_2 are calculated based on spike duration 1 ms (refraction time included).

| N | N_0 | p_1 | p_2 | μ | ν | R_1 | R_2 |
|------|-------|-------|-------|-------|-------|--------|---------|
| 5000 | 200 | 0.038 | 0.032 | 0.176 | 5.545 | 248 Hz | 0.97 Hz |

The input synaptic activities to secondary neurons are stochastic due to irregular firing of first-order neurons. The process of binding-releasing of odors by receptor proteins is a stochastic one due to thermal fluctuations.

We say that the first-order stage discriminates two stimuli, if the probabilities p_1 , p_2 for this stage to be active are different for those stimuli. The quality of discrimination can be characterized by the following expression:

$$\mu = \ln(p_1/p_2). \quad (1)$$

Expect for definiteness that

$$\mu > 0. \quad (2)$$

Every time when the number of active inputs attains the firing threshold, N_0 , the neuron fires a spike. The firing rates, R_1 , R_2 , will be different for the two above mentioned stimuli due to differences in the stimulation rates caused by discrimination at the first-order level. The first-order level here is either odor binding-releasing (for chemoreceptor neuron), or firing of first-order neurons (for secondary neurons of any modality).

Thus, there will be a discrimination at the secondary level, the quality of which can be characterized by the following expression:

$$\nu = \ln(R_1/R_2). \quad (3)$$

Our purpose is to estimate ν based on given μ , N , N_0 .

The evolution in time of the number of active inputs can be characterized by the set of transition probabilities [3]: $p(n, t|n', t')$, $t' \leq t$, $0 \leq n \leq N$, $0 \leq n' \leq N$, $p(n, t|n', t) = \delta_{nn'}$, which are subjected to the backward Master equation:

$$\begin{aligned} \frac{\partial p(n, t|n', t')}{\partial t'} &= r^-(n')(p(n, t|n', t') - p(n, t|n' - 1, t')) \\ &+ r^+(n')(p(n, t|n', t') - p(n, t|n' + 1, t')), \quad n, n' \in \{0, 1, \dots, N\}. \end{aligned}$$

In case of chemoreceptor neuron $r^+(n) = k_+(N - n)[O]$, $r^-(n) = k_-n$, where k_+ , k_- are the binding and releasing rate constants, and $[O]$ is the odor concentration.

The following estimate has been obtained, based on this equation and first passage technique (see [9]):

$$\nu > \mu \cdot N \frac{p_0 - p_1}{1 - p_1}. \quad (4)$$

where $p_0 = N_0/N$. Interesting that this estimate is similar to Eq. (9) in [8], where selectivity is estimated for a cooperative chemical system. The estimate (4) allows one to

expect that the secondary discriminating ability could be much higher than the primary one. The sufficient condition for this is as follows:

$$N(p_0 - p_1)/(1 - p_1) \gg 1. \quad (5)$$

The last condition implies that

$$p_1 < N_0/N, \quad (6)$$

which means that the stimulation should not be intensive. One numerical example of the improved selectivity in chemoreceptor neuron is given in the Table 1.

Conclusion: The discriminating ability in any sensory tract taken as a whole can be improved as compared to the discriminating ability of the primary reception stage in this tract. The improvement is due to cooperative character of signal processing. The cooperativity arises due to convergent wiring and thresholds, which must be overcome for passing the signal from previous stages of processing to the next ones. The hierarchical structure of any sensory tract allows for its discriminating ability to be improved at each stage of the hierarchy.

References

- [1] Bastian, J., 1994. Electrosensory organisms. *Physics Today* 47(2), 30–37.
- [2] Duchamp-Viret, P., Duchamp, A., Sicard, G., 1990. Olfactory discrimination over a wide concentration range. Comparison of receptor cell and bulb neuron abilities. *Brain Research* 517, 256–262.
- [3] Gnedenko, B.V., 1962. *The Theory of Probability*. Chelsea, New York.
- [4] Kaissling, K.-E., 1996. Peripheral mechanisms of pheromone reception in moths. *Chem.Senses* 21, 257–268.
- [5] Neely, S.T. Kim, D.O. 1983. An active cochlear model showing sharp tuning and high sensitivity. *Hearing Res.* 9, 123–130.
- [6] Ressler, K.J., Sullivan, S.L., Buck, L.B. 1994. Information coding in the olfactory system: evidence for a stereotyped and highly organized epitope map in the olfactory bulb. *Cell* 79, 1245–1255.
- [7] Smallman, H.S., MacLeod, D.I.A., He, S., Kentridge, R.W., 1996. Fine grain of the neural representation of human spatial vision. *J.Neurosci.* 16(5), 1848–1855.
- [8] Vidybida, A.K., 1991. Selectivity and sensitivity improvement in cooperative system with a threshold in the presence of thermal noise. *Journ. theor. Biol.* 152(2), 159–165.
- [9] Vidybida, A.K., 2000. Selectivity of chemoreceptor neuron. *BioSystems* 58, 125–132.
- [10] Wehrhahn, C., 2000. Is chromatic induction retinal or cortical? Lecture delivered to NATO ASI “Modulation of Neuronal Signaling: Implications for Visual Perception”, Nida, Lithuania, July 12–21.