ON-CENTER/OFF-SURROUND NEURAL NETWORK MODEL FOR OLFACTORY ATTENTION

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Abstract: Our research group has found behavioral evidence that an attention function exists in the olfactory system similarly to in the visual and auditory systems. In this paper we propose a neural network model that accounts for olfactory attention based on macroscopic neural connections. Specifically, on-center/off-surround connections were assumed to be involved in the attention process in accordance with our hypothesis of an attention window that extracts local activity. The model employs glomerular activity patterns as its input, and compares them with stored patterns focusing on their local activity. The model also can shift and change the attention window with respect to learning. From the simulation results, we confirmed that the model can account for the results of a behavioral experiment on olfactory attention in mice.

1 INTRODUCTION

Attention is an important cognitive function for filtering out irrelevant information and extracting useful information from a noisy environment. Attention thus enables efficient information processing in the case of limited computational capacity (Dayan et al., 2000). The mechanisms of visual and auditory attention have been studied over previous decades (Broadbent, 1958) from the behavioral level to the neural level. These studies suggest that selective attention can be caused by modulation of the amplitude of neural activity evoked by stimuli (Hillyard et al., 1998). As physiological mechanisms have been gradually elucidated, their mathematical models have begun to be applied to robotics (Vijayakumar et al., 2001; Ruesch et al., 2008). In contrast to these developments for visual and auditory systems, to the best of our knowledge, the existence of an attention mechanism in olfactory systems has only recently begun to be investigated.

As natural odors are generally composed of a complex mixture of volatile compounds (odorants), of which more than 400,000 types (Mori et al., 2006) exist, focusing on part of them should be an efficient means of recognizing odor. To determine whether an attention function also exists in the olfactory system, our research group performed an odor discrimination experiment on mice (Takiguchi et al., 2008). The experiment provided evidence that mice can memorize and discriminate odors by focusing on a subset of odorants comprising an odor. Furthermore, when a difficult discrimination task was presented, the mice slowly modified the attention subset through their learning experience. As visual and auditory systems can quickly switch their attention to different ob-

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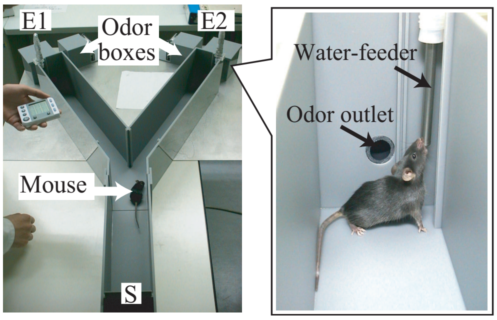


Figure 1: Y-maze.

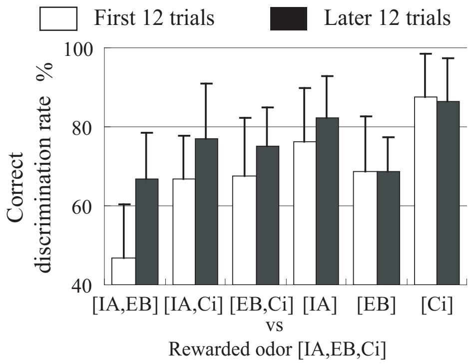


Figure 2: Results of odor discrimination experiment.

jects, from this viewpoint the attention function in the olfactory system is different from that in the visual and auditory systems.

Although an attention function was found at the behavioral level, its mechanism at the neural level is not clear. As current technology does not allow the exhaustive measurement and interpretating of neural activity, building a mathematical model is a perspective approach to this problem. Most previous olfactory models were built with the aim of accounting for neural dynamics (Cleland and Sethupathy, 2006) and background segmentation (Li and Hertz, 2000); however, a model to account for the attention mechanism has not yet been proposed. Against this background, we previously proposed an attention model that could predict perceptual similarity between odors (Soh et al., 2009); however, several assumptions employed in the model were not realistic, and the model could not explain shifts and changes in attention. In this paper, we propose an olfactory attention model taking the macroscopic neural connections in the olfactory system into account. The model employs neural activity evoked on the glomeruli as its input and predicts the odor discrimination ability of mice resulting from their attention function. In addition, we demonstrate that the discrimination ability predicted by the model has a similar tendency to that observed in experiments.

2 EXPERIMENT ON OLFACTORY ATTENTION

To elucidate the attention mechanism in the olfactory system, our research group performed an odor discrimination experiment on mice (Takiguchi et al., 2008) using different mixtures of three types of odorant: isoamyl acetate (IA), ethyl butyrate (EB), and Citral (Ci). In the experiment, the subject mice were prompted to discriminate between a water-rewarded odor [IA, Ci, EB] and odors composed of different combinations. In this section we review the procedure and experimental results.

The experiment employed a Y-maze assay, which uses a Y-shaped channel as shown in Figure 1. At the end S, there is a small chamber with a gate (starting box) separated from the channel to trap the subject. The other ends E1 and E2 have attached odor boxes, which transmit odors into the channel, and water feeders to provide the reward. During the experiment the subject mice were prohibited from drinking water except as a reward.

A trial started with setting the rewarded odor [IA, Ci, EB] and an unrewarded odor in the two odor boxes. The subject was then placed in the starting box. When the gate opened, the subject could run through the channel and choose one of the branches of the channel depending on the response to the odor. The subject was allowed to drink water from the water feeder next to the rewarded odor, otherwise it was returned to the starting box immediately. This trial was repeated 24 times in a day, referred to as one session.

After the subjects were trained to form an association between the rewarded odor [IA, Ci, EB] and water in the first several sessions, the subjects were required to discriminate between the rewarded odor and unrewarded odors. Figure 2 shows the average discrimination rate of eight subjects in the first 12 trials and the following 12 trials in a session. The discrimination rate of 46.9% against odor [IA, EB] in the first 12 trials implies that the subjects considered odor [IA, EB] as the rewarded odor, since a discrimination rate of 50% would be expected as a result of random selection. In the following 12 trials, however, the subjects became more able to discriminate between these odors since the average discrimination rate increased to 66.7%. This suggests that when the association between water and the rewarded odor [IA, Ci, EB] was made, the subjects only paid attention to the odorants IA and EB. Subsequently, the attention of the mice changed, enabling them to perform cor-

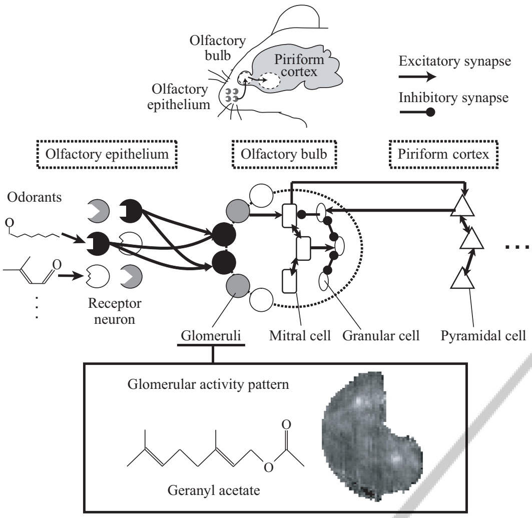


Figure 3: Structure of the olfactory system.

rect discrimination. These results thus confirmed the attention ability of the olfactory system.

Although this experiment illustrated the occurrence of incorrect discrimination caused by attention ability, considering the large number of odorants that exist, paying attention to a few important odorants comprising odors is much more efficient for identifying or discriminating between odors. Despite its importance, the mechanism of attention at the neural level has not been investigated. To explain the attention ability of the olfactory system, a window that extracts local neural activity evoked by odors was assumed (Takiguchi et al., 2008). Discrimination between odors is then performed using only the neural activity included in this window. However, this hypothesis has not been validated.

3 STRUCTURE OF THE OLFACTORY SYSTEM

As the mechanism of attention has not been elucidated in the biological field, partly because of the difficulty of exhaustively measuring and interpretation of neural activity, in this paper, we propose a possible attention model from an engineering approach based on the neural structure of the olfactory system (Mori et al., 2006; Heimer, 1968) and the above hypothesis (Takiguchi et al., 2008). In this section we briefly review the structure of the olfactory system.

Figure 3 shows the basic structure of the olfactory system of mice, which consists of three parts: receptor neurons, the olfactory bulb, and the piriform cortex. Receptor neurons are distributed on the surface of the nasal chamber, expressing a single receptor protein from among thousands of different varieties (Buck and Axel, 1991); each neuron is activated by a specific group of odorants and sends signals to the olfactory bulb.

The olfactory bulb mainly consists of glomeruli, mitral cells, and granular cells. A glomerulus is a round cluster of axon terminals accumulated from receptor neurons. The activity patterns evoked on glomeruli are odor-specific ((Mori et al., 2006; Johnson and Leon, 2000), shown in the lowest part of Figure 3). A mitral cell is an excitatory neuron that receives the output from a glomerulus. Granular cells are inhibitory neurons sending inhibitory signals to the mitral cells. Although mitral cells and granular cells appear to form complex connections, it has been suggested that they form an on-center/off-surround circuit in which neighboring mitral cells excite each other but distant cells inhibit each other (Grossberg, 1976). The mitral cells also transfer signals to the pyramidal cells in the piriform cortex, which then send signals back to the granular cells in the olfactory bulb and indirectly inhibit the mitral cells.

On-center/off-surround connections in the olfactory bulb are well-known neural connections found in sensing systems and typically perform contrast enhancement. In this paper, we consider that these connections have an important role in generating a window of attention to extract neural activity.

4 PROPOSED MODEL

Since several experimental results and mathematical models have suggested that the olfactory bulb has the functions of input normalization and contrast enhancement (Grossberg, 1976; Cleland and Sethupathy, 2006), we modeled the attention function as an interaction between these two functions. However, the interconnections involved in the olfactory system can evoke complex dynamics that prevent us from analyzing attention mechanisms; we thus designed a simple model that makes it possible to focus on spatial neural activity patterns taking the macroscopic connections between neurons into account. In this section, the structure of each layer and the parameter settings of the proposed model are described.

4.1 Structure of the Proposed Model

Figure 4 shows the structure of the proposed model, which consists of three layers: the input layer, the olfactory bulb layer, and the output layer.

The input layer carries the activity patterns evoked on the glomeruli by odorants o_i mixed in an odor $O =$

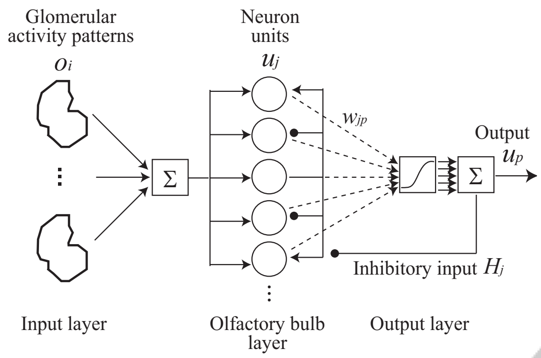


Figure 4: Structure of the proposed model.

$[o_1, o_2, ..., o_N]$. In this paper, we used the activity patterns measured from actual organisms obtained from an online database (http://gara.bio.uci.edu/). The provided activity patterns were originally in an image file format. To convert each image file into an input, the image is divided into $L = 1805$ lattice squares approximately corresponding to the number of glomeruli on a mouse's olfactory bulb. Each of the lattice squares is then converted into a value ranging from 0 to 1 depending on the color in the lattice, which corresponds to the activity strength. The activity evoked on the jth lattice square by odorant o_i is thus denoted as a_{ij}, and the activity pattern is the vector $\boldsymbol{a}_i \in \mathbb{R}^{1\times L}$.

The olfactory bulb layer consists of L neuron units. They receive inputs from the input layer as well as inhibitory inputs from the output cortex layer. To realize the functions of normalization and contrast enhancement, this layer employs a neural network model whose structure was previously proposed (Grossberg, 1976), given as

$$I_j = \sum_{i=1}^{N} a_{ij}, \quad (1)$$

$$\dot{u}_j = -Tu_j + (B - u_j)I_j - u_j\left(\sum_{j' \neq j}^{L} w_{j'j} I'_j - H_j\right), \quad (2)$$

where I_j, I'_j is the input from the input layer, which is the summation of activity strengths evoked by odorants, u_j is the activity of the jth neuron unit, T, B, and L are constant coefficients, H_j is the inhibitory input adjusted by the output layer, and $w_{j'j}$ is the weight coefficient representing the on-center/off-surround connections as follows;

$$w_{j'j} = \begin{cases} W, & d < D_e \\ -W, & D_e < d < D_i \\ 0, & d > D_i \end{cases} . \quad (3)$$

Here, W is a constant, d is the distance between the units, calculated from their corresponding locations on the glomeruli, and the coefficients D_e and D_i denote the maximum distances of the on-center excitatory connections and off-surround inhibitory connections that exist, respectively. u_j at the equilibrium point ($\dot{u}_j = 0$) is then

$$u_j = \frac{BI_j}{T + \sum_{D_e<d<D_i} WI_k - \sum_{d<D_e} WI_k - H_j}; \quad (4)$$

thus, u_j is normalized by the total input of neuron units in the region $D_e < d < D_i$ and is enhanced by those in the region $d < D_e$.

Finally, the output layer calculates the sum of the outputs from the olfactory bulb layer as follows:

$$u_p = \sum_j w_{jp} f(u_j), \quad (5)$$

$$f(x) = \frac{1}{1 + \exp[-g(x - \theta_p)]}, \quad (6)$$

where w_{jp} is the weight coefficient, and g and θ_p are the gain and threshold constants of the sigmoid function, respectively. Because the output u_p is the calculated inner product between the stored pattern and input pattern when an activity pattern is stored in w_{jp}, u_p is defined as the correspondence with the stored odor.

4.2 Proposed Attention Process

To implement the hypothesis that a window extracts a local activity pattern for attention, the weight coefficient w_{jp} is determined as follows:

$$w_{jp} = \begin{cases} 0, & u_j(O_r) < \theta_U \\ 1/P, & u_j(O_r) \geq \theta_U \end{cases} , \quad (7)$$

where O_m represents a rewarded odor such as [IA, Ci, EB] used in the odor discrimination experiment. $u_j(O_r)$ is then the activity pattern of the olfactory bulb layer evoked by odor O_r, θ_U is the threshold constant for u_j, and P is the total number of neuron units in the olfactory bulb layer whose output is greater than θ_U. This allows the output layer to compare the activity patterns by focusing only on the part activated by odor O_r, which is expressed in the window of attention.

As observed in the odor discrimination experiment, attention can cause incorrect discrimination. In this case, the window has to be changed. To model this function, we apply the inhibitory input H_j to the olfactory bulb layer when an odor different from the rewarded odor generates a high output for u_p. The inhibitory input H_j is thus determined as follows:

$$H_j = \begin{cases} \beta u_j, & u_p < \theta_P \text{ and } u_j(O_r) \geq \theta_U \\ 0, & \text{otherwise} \end{cases} , \quad (8)$$

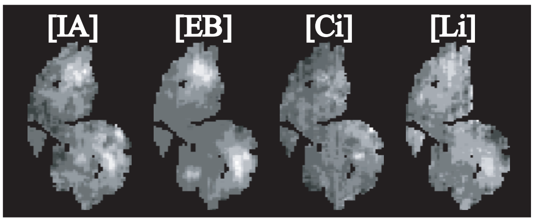


Figure 5: Glomerular activity patterns evoked by the odorants in odor discrimination experiments.

where θ_P is the threshold constant for u_p, and β is a gain coefficient used to determine the strength of H_j. This configuration generates new activity by turning off inhibition from off-surround connections, and the activity produces a new window in accordance with Equation 7.

5 SIMULATION

5.1 Simulation Procedure

The model was validated by performing two sets of discrimination experiments. First, the parameters of the model were adjusted manually in accordance with the experimental results when a combination of IA, EB, and Ci was used. The parameters were then validated by comparison with another set of experimental results using the odorants IA, linaool (Li), and Ci. Finally, the ability to change the attention window was also investigated.

As the input to the model, we used measured glomerular activity patterns evoked by the odorants in the odor discrimination experiment. These were obtained from the database website http://gara.bio.uci.edu/, where the activity patterns are provided as unrolled maps of the spherical surface of the olfactory bulb as shown in Figure 5. However, since the activity pattern for odorant Ci was not in the database, we used the activity pattern predicted from a glomerular activity prediction model (Soh et al., 2011). Figure 5 shows the activity patterns for each odorant.

A comparison between the simulation and experimental results was carried out by defining a metric corresponding to the correct discrimination rate obtained from the experiment on mice described in Section 2. As mentioned in the previous section, the output u_p represents the correspondence with the stored pattern in weight coefficient $w_j p$; we thus used the following metric to represent the correct discrimination rate:

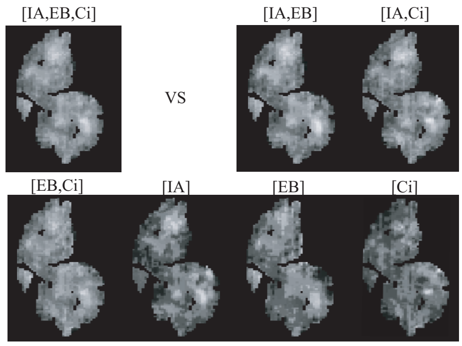


Figure 6: Activity patterns on the olfactory bulb layer for each odorant obtained by simulation.

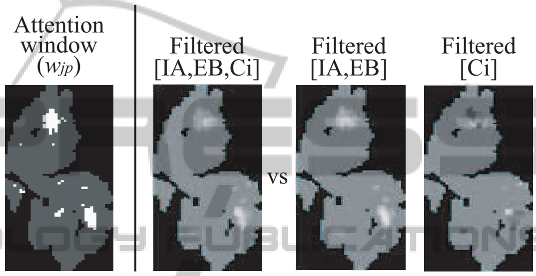


Figure 7: Attention window and activity patterns filtered by the window.

$$r = \frac{u_p(O_r)}{u_p(O_r) + u_p(O_u)}, \tag{9}$$

where $u_p(O_r)$ is the output of the rewarded odor and $u_p(O_u)$ is that of the unrewarded odor. The parameters were thus adjusted to fit r with the correct discrimination rate.

5.2 Results

First, the parameters were adjusted. Similarly to in the odor discrimination experiment, odor [IA, EB, Ci] was used as the rewarded odor. As a result of simulation, the activity patterns of the olfactory bulb layer shown in Figure 6 were obtained. In addition, Figure 7 shows the attention window, represented by white spots generated by the model, and examples of activity patterns on the olfactory bulb layer filtered by the attention window. This figure demonstrates how a comparison between odors can be made by focusing on the window generated by the model.

Figure 8 shows the values of r obtained from the model with adjusted parameters and the correct discrimination rate against each odorant. This figure confirmed that r and the correct discrimination rate have a similar tendency, for example, the lowest correct discrimination rate was observed when odor [IA EB] was the unrewarded odor. These results confirmed that the model focused attention on the activity

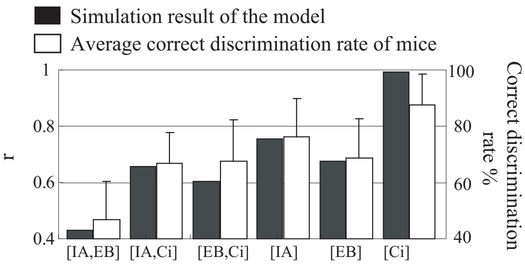


Figure 8: Comparison of attention between model and mice. (rewarded odor: IAEBCi).

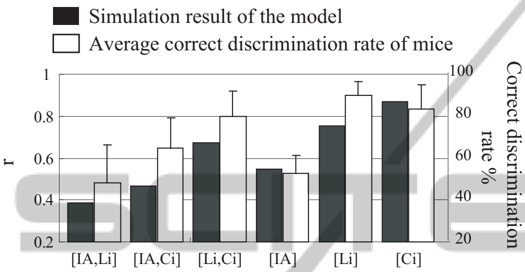


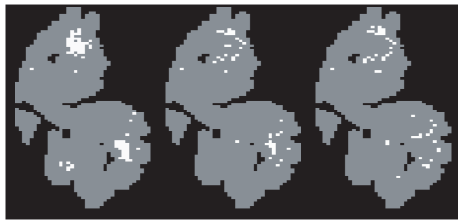
Figure 9: Comparison of attention between model and mice. (rewarded odor: IALiCi).

evoked by [IA EB], as observed in the odor discrimination experiment. The adjusted parameters were as follows.

- Olfactory bulb layer
  $T = 0.1, B = 2.0,$
  $D_e = 3.0, D_i = 10.0, W = 0.012$
- Output layer
  $g = 0.03, \theta_p = 0.7$

Using the adjusted parameters, a simulation was performed with another odor set, where odor [IA, Li, Ci] was used as the rewarded odor. Figure 9 shows the values of r obtained from the model and the correct discrimination rate of mice against each odorant. From the figure, we can confirm that the proposed model and the mice have a similar tendency that both focused attention on odorant [IA].

We then tested the ability to change the attention window by applying an inhibitory input H_j to the olfactory bulb layer. Since the discrimination ability of the mice improved in the later 12 trials as described in Section 2, we also investigated whether the value of r increases when the attention window is changed. For this simulation, we set [IA, EB, Ci] as the rewarded odor. Figure 10 shows the changes in the attention window with increasing strength of the inhibitory input (parameter β). From the figure, we can confirm that the window changed with increasing β. We also confirmed that when β was increased from 0 to 0.3, r increased from approximately 0.48 to 0.72. These results confirmed the ability to change the attention window, as observed in the odor discrimination experiment on mice.



β=0.1 β=0.2 β=0.3

Figure 10: Changes in attention window (white spots).

6 CONCLUSIONS

We proposed an attention model for the olfactory system assuming the existence of an attention window generated by normalization and contrast enhancement processes in the olfactory bulb. A possible learning mechanism was also proposed in which an inhibitory signal is applied to the olfactory bulb, which modifies the attention window. Although the model only considered the macroscopic structure of the olfactory system, a comparison with the correct discrimination rate of mice confirmed the attention ability of the model.

The correct discrimination rate can also be interpreted in terms of the perceptual characteristics of mice as the Y-maze experiment is a type of sensory evaluation assay. The proposed model can thus be applied as an artificial sensory evaluation method. As a future work we are planning to increase the odorant set to validate and improve the model. We are also considering applying the model to predict the perceptual characteristics of human olfaction.

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