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A neural network model of the olfactory system of mice: simulated the tendency of attention behavior

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Abstract The demands for odor processing apparatuses have been increasing in fragrance or food industries. However, odors are extremely high dimensional information composed a combination from tens thousands of different odorant molecules, and thus requires vast amounts of computation. Therefore, it is considered learning from a living nose would be an efficient approach. From the odor discrimination experiments, it was found that mice have a feature extraction ability called *Attention* by which they could focus on the important odorants for odor discrimination. In this paper we propose a neural network model approximated to actual number of neurons and the structure of olfactory system. Simulation experiments of the proposed model were implemented based on the odor discrimination experiments on the living mice. From the simulation results of the model, we confirmed not only the proposed model had ability of *Attention*, but also the tendency of *Attention* was consistent with the living mice.

Key words Olfactory system · Attention · Neural network model

1 Introduction

Recently, the demands for odor processing apparatuses have been increasing in fragrance or food industries. However, odors are extremely high dimensional information composed a combination from tens thousands of different odorant molecules. Therefore, odor information requires vast amounts of computation for discrimination or feature extraction.[1] Thus far, to reduce its dimension, the ability of most odor discriminating apparatuses were specialized for particular odor such as the electronic nose for banana ripeness developed by Llobet et al.[2] On the other hand, most animals discriminate a number of different odors for survival. Therefore, learning from the olfactory system of a living nose would be one of the most efficient and prospective approaches.[2,3]

Our research group has conducted a series of odor discrimination experiments on mice.[4] First, the mice are trained to select a rewarded odor composed of three kinds of odorants [IA, Ci, EB]. Then, they were required to discriminate the odors that contain a part of odorant in odor [IA, Ci, EB] such as [IA] or [IA, EB] etc. As a result, we observed most mice had difficulty to distinguish [IA, EB] from [IA, Ci, EB]. It implies that the mice made attention on a combination of odorants [IA] and [EB] when they learnt [IA, Ci, EB] as described in Fig. 1. This mechanism is called *Attention*. Because making attention on appropriate odorants will enable an efficient dimension reduction or feature extraction, mechanism of *Attention* is of importance to process high dimensional odor information. So far, Li et al.[5] and Cleland et al.[6] have revealed several feature extraction mechanism of olfactory system, however, mechanism of *Attention* has yet to be explored. To reveal how the olfactory system process *Attention*, the signal transduction between neurons must be measured, nevertheless it is beyond current technology to collect enough data. In this paper, we propose a neural network model constructed based on anatomical insight, and try to elucidate the mechanism of *Attention* through simulation. Further, the simulation results of the proposed model are compared with the odor discrimination experiment results of the living mice.

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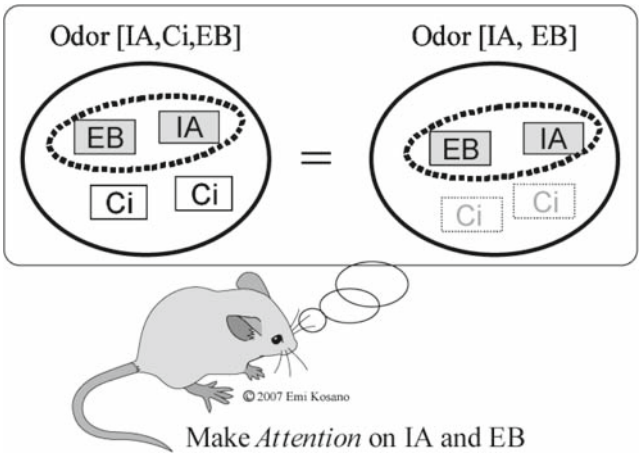

Fig. 1. The concept of *Attention*

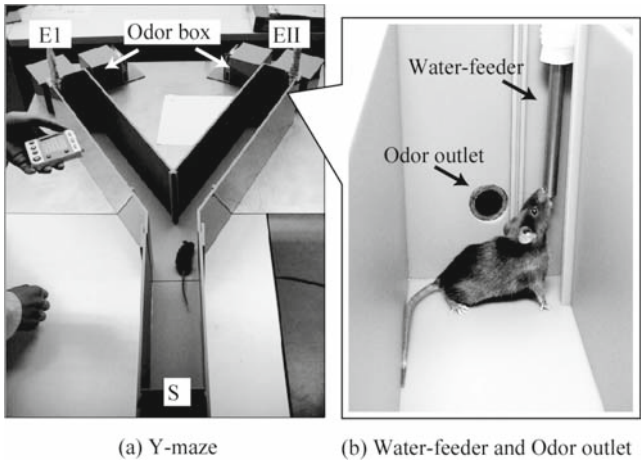

Fig. 2. Structure of Y-maze and drinking behavior of mouse (revised from the figure in the literature.[4])

2 The odor discrimination experiments

This section details the series of odor discrimination experiment on mice aimed to reveal *Attention*.[4]

2.1 Methods

The subject of the experiment was water-deprived C57BL/6J mouse. Figure 2 shows a Y-maze apparatus. In Fig. 2(a), E1 and E2 are the end where odors and water are presented, while S is the end where the mouse are placed at the beginning of each trial. Figure 2(b) shows a water feeder and a hole for odor emanation located at E1 and E2.

First, odor A and water are presented at either end E1 or E2 randomly so that the mouse is trained to select the end where odor A emanates. Such trials are repeated for 24 times a day until the error rate to drop below 20%. Then, the trained mice are required to discriminate the odor B of which odorants are partly common with the odor A. The odor B is presented at the opposite end to the end where odor A and water are presented. If the mouse were able to discriminate odor A form odor B, they are supposed to choose the end where water and odor A is provided.

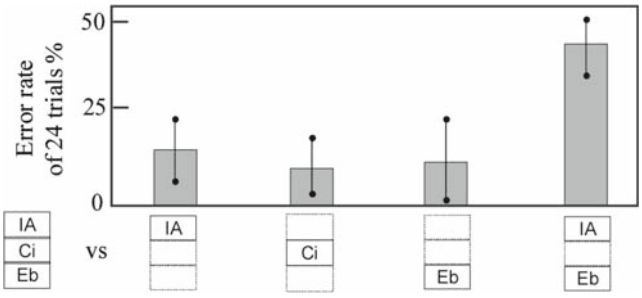

Fig. 3. Results of odor discrimination experiment. (unpublished data by Okuhara et al.)

This series of experiments was implemented on eight mice. The odor A was a mixture of three kinds of odorants, Isoamyl Acetate (IA), Citral (Ci) and Ethyl Butyl (EB), expressed as [IA, Ci, EB] by the abbreviation of each odorant. The odor Bs, such as [EB], [Ci], [IA, EB] etc., were consisted of combinations from those three odorants.

2.2 Results

Figure 3 shows the averages and standard deviations of error rates obtained from eight mice. The horizontal axis shows the odor Bs ([Ci], [EB], [IA], [EB, IA]), and the vertical axis shows the error rate.

From Fig. 3, we can find the error rates to [IA], [Ci] and [EB] are about 10 to 15%, and could be assumed that the mice were able to discriminate [IA, Ci, EB] from those odors. As in the case of [IA, EB], in contrast, the error rate is nearly 50%, which indicates the mice could not discriminate the odors because they were under an either-or situation. This result implies that the mice have made attention on the combination of odorants [IA] and [EB] when they learnt [IA, Ci, EB], and subsequently they could not find the difference between [IA, Ci, EB] and [IA, EB].[4] From the experiment, it is suggested that the mice would make attention on a part of odorants contained in an odor. This mechanism is called *Attention*.

3 A model of olfactory system of mice

In this section, a neural network model is proposed based on anatomical insights.[7,8] This section describes the basic structure of olfactory system of mice, the proposed model, and the learning algorithm.

3.1 Structure of olfactory system of mice

Figure 4 shows the basic structure of olfactory system of mice. The olfactory system is composed of three parts which

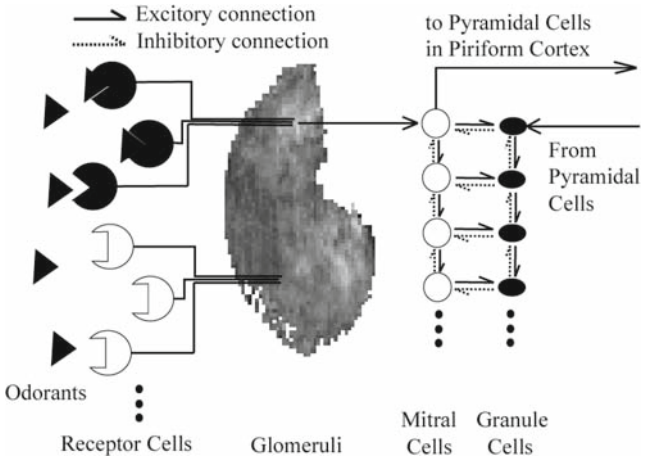

Fig. 4. Olfactory system of mice. The activity pattern of glomeruli is cited from literature[10]

are receptor neurons, olfactory bulb and piriform cortex. Receptor neurons that respond to specific odorants distributes on the surface of nasal, expressing only one receptor gene among a thousand different genes.[9] As the odorant molecules binded, the receptor neurons are activated and send signals to olfactory bulb. The axons from the receptors that expressing the same gene terminate at the same point on the surface of olfactory bulb.[10] The terminal of those axons form a small round cluster called glomeruli. Therefore, the 2-D map of the glomeruli distribution can be associate with the receptor genes as well as the odorants, and is called odor map.[10] The activity pattern of glomeruli shown in Fig. 4 is an example of response to the odorant [IA].[11]

Besides the glomeruli, mitral cell and granule cell are the principal neurons in the olfactory bulb, which are in charge of the feature extraction. The glomeruli are connected to the mitral cells. The mitral cells are interconnected to each other by excitatory synapse and inhibitory synapse midiated by the granule cells. The mitral cells transfer the signal to the pyramidal cells in the piriform cortex. The pyramidal cells send signal back to the granule cells in olfactory bulb and indirectly inhibit the mitral cells. The piriform cortex is divided into anterior and posterior, although division of their role is rather unclear. Generally, the piriform cortex is believed to be in charge of the identification of odors.

3.2 The model

The schematic diagram of the proposed model is shown in Fig. 5. Olfactory bulb is consisted of the *Glomeruler* layer, the *Mitral* layer, and the *Granule* layer. The *APC* layer and the *PPC* layer correspond to anterior piriform cortex and posterior piriform cortex, respectively. The number of neurons in each layer of olfactory bulb are 1805 respectively, while 1000 for the *APC* layer and 100 for the *PPC* layer. Except the *PPC* layer is consisted of liner neuron models, all layers are consisted of sigmoidal neuron models.

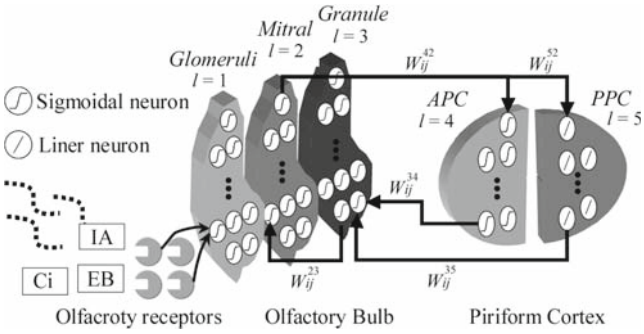

Fig. 5. Proposed model of the olfactory system

The output ${}^{l}U_i(t)$ of i_{th} sigmoidal neuron model or liner neuron model included in l_{th} layer at the time step t is given by the following equation:

$$ {}^{l}U_i(t+1) = \begin{cases} \dfrac{1}{1+\exp\{-\varepsilon_i(u_i(t)-\theta_i)\}} & (Sigmoidal\ Neuron) \\ a\,{}^{l}u_i(t) & (Liner\ Neuron) \end{cases}, \tag{1} $$

where ε_i is the gradient of sigmoid function, θ_i is the threshold value, and a is a constant gain value. The internal states ${}^{l}u_i(t)$ of the neuron model is given by the following equation:

$$ {}^{l}u_i(t) = -\alpha\,{}^{l}u_i(t-1) + \sigma_j\,{}^{lm}W_{ij}(t)\,{}^{m}U_j(t), \tag{2} $$

where α is the decay rate, $U_j(t)$ is the output of j_{th} neuron model that is connected to i_{th} neuron model, and $W_{ij}(t)$ is the connective weight between i_{th} and j_{th} neuron models included in l_{th} and m_{th} layer, respectively. The connections between the neuron models in each layer are prepared based on the structure of olfactory system described in the previous section.

It is suggested that the interconnections in piriform cortex have a role of pattern complement from retrograded input patterns.[6,7,12] For simplification, assuming no noise from input, the interconnections in piriform cortex are neglected in this model. Further, it is suggested through a simulation by Cleland et al.[6] that the interconnections in olfactory blub plays an role to normalize the amount of activity within glomeruli. In this paper, since we utilize the glomeruli activity patterns provided by Johnson et al.[10] that are already normalized to the normal distribution, the interconnections in the olfactory bulb are assumed to be able to neglected.

The first 3 figures on the left side of Fig. 6 shows the activity patterns of glomeruli to monomolecular odorants that are normalized to normal distribution provided by Johnson et al.[10] The activity patterns are divided into 1805 lattices, and the activity of each lattice is inputted to the corresponding neuron model in the *Glomeruler* layer. The internal state of the i_{th} neuron model in the *Glomeruler* layer is given by the following equation:

$$ u_i(t) = P_i^o, \tag{3} $$

where O is the set whose elements are the odorants that consist the inputted odor, and P_i^o is the activity of i_{th} lattice

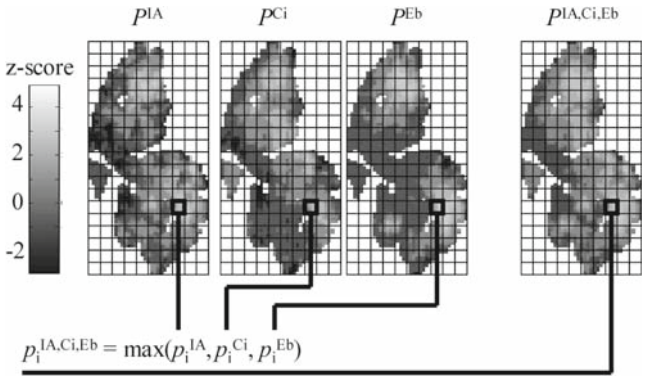

Fig. 6. Activity patterns of *Glomeruler* layer

to the odorant set O. If only one odorant consists the odorant set O, then the corresponding monomolecular activity pattern directly becomes the input to *Glemeruler* layer. Otherwise, for odorant mixture, the activity pattern is given by the following equation where the activity patterns for component odorants are combined as described in Fig. 6:

$$P_i^O = \max_{x \in O} P_i^x, \tag{4}$$

where P_i^x is the activity of i_{th} latice to monomolecular odorant x.

3.3 The learning algorithm

As most computational functions of the olfactory system have not been revealed clearly, in this paper, the modulation of synapse plasticity or the signal transduction between the neurons are hypothesized based on related studies[14] and the experimental results of odor discrimination on the mice[4] described in Section 2. Considering the experiment required the mice to discriminate an rewarded odor A and unrewarded odor B, the learning algorithm for the proposed model consists of the following three phases. In the 1st phase, the connective weights ${}^{42}W_{ij}(t)$ from the *Mitral* layer to the *APC* layer are modulated to learn the relationship between the inputted odors and the reward odor.

The output of each neuron model in the *Mitral* layer for odor A is assumed to be ${}^2U_i^{\text{A}}$, while for odor B, ${}^2U_i^{\text{B}}$. In addition, considering the odors are identified in the *APC* layer, the output which indicates the rewarded odor is set to be ${}^4U_j^{\text{A}}$, while for unrewarded odor, ${}^4U_j^{\text{B}}$.

To covert the input patterns ${}^2U_i^{\text{A}}$ and ${}^2U_i^{\text{B}}$ to ${}^4U_j^{\text{A}}$ and ${}^4U_j^{\text{B}}$ respectively, ${}^{42}W_{ij}(t)$ is modulated by the following equation:

$${}^{42}W_{ij}(t+1) = \begin{cases} \alpha_{ma}\,{}^{42}W_{ij}(t) + \beta_{ma}\,{}^2U_i^A(t)\,{}^4U_i^A(t) & (\text{Odor } A) \\ \alpha_{ma}\,{}^{42}W_{ij}(t) + \beta_{ma}\,{}^2U_i^B(t)\,{}^4U_i^B(t) & (\text{Odor } B) \end{cases}, \tag{5}$$

where α_{ma} is the forgetting term and β_{ma} the learning rate.

The 2nd phase is to calculate the difference between odor A and odor B by modulation of connective weights ${}^{34}W_{ij}(t)$ from the *APC* layer to the *Granule* layer.

$${}^{34}W_{ij}(t+1) = \begin{cases} \alpha_{ag}\,{}^{34}W_{ij}(t) + \beta_{ag}\,{}^4U_i^A(t)\,{}^3U_i^B(t) & (\text{Odor } A) \\ \alpha_{ag}\,{}^{34}W_{ij}(t) + \beta_{ag}\,{}^4U_i^B(t)\,{}^3U_i^A(t) & (\text{Odor } B) \end{cases}, \tag{6}$$

In the same way as Eq. 5, α_{ag} is the forgetting term, and β_{ag} the learning rate. When odor A is inputted, the outputs of the *APC* layer ${}^4U_j^{\text{A}}$ are converted to the outputs of the *Granule* layer ${}^2U_i^{\text{B}}$ through ${}^{34}W_{ij}(t)$. Similarly, when odor B is inputted, the outputs of the *APC* layer ${}^4U_j^{\text{B}}$ are converted to the outputs of the *Granule* layer ${}^2U_i^{\text{A}}$ through ${}^{34}W_{ij}(t)$. Then, the outputs of the *Granule* layer inhibits the neuron models in the *Mitral* layers through ${}^{32}W_{ij} = -\delta_{ij}$. Consequently, the neuron models in the *Mitral* layer output a activity pattern either ${}^2U_i^{\text{A}} - {}^2U_i^{\text{B}}$ or ${}^2U_i^{\text{B}} - {}^2U_i^{\text{A}}$ which represents the difference between two odors.

The 3rd phase extracts the most effective neurons for discrimination. After learning phase 2, it is considered that the neuron models of the *Mitral* layer with the strongest outputs emphasize the difference between odor A an odor B. In the proposed model, we assume the connective weights between the *Mitral* layer and the *PPC* layer form a competitive system, and the corresponding connective weights are determined according to the competitive system proposed by Amari et al.;[14] these connective weights include self-feedback connective weights ${}^{22}W_{ij}$ in the *Mitral* layer, feed-forward connective weights ${}^{25}W_{ij}$ from the *Mitral* layer to the *PPC* layer, and the feedback connective weights from the *PPC* layer to the *Granule* layer. The competitive system extracts a neuron having the greatest ouput within a certain neuron group in the *Mitral* layer. In the proposed model, the neurons in the *Mitral* are randomly divided into 100 groups. Consequently, after the 3rd learning phase, at most 100 neurons should be extracted.

Finally, it is expected that the proposed model could extract the information that expresses the difference between odors, and have importance for odor discrimination.

4 Simulation

In this section, the computer simulations with the proposed model are described. The simulation condition was determined according to the odor discrimination experiment of the living mice. Then, the computer simulation results are compared to that of the living mice described in Section 2.

4.1 Learning of the reward odor

Following the odor discrimination experiment of the living mice, odor[IA, Ci, EB] and [Air] are inputted to the proposed model alternatively, and the connective weights are adjusted following the learning algorithm described in Section 3.3. The initial values of the connective weights are determined by uniform random values.

Figure 7 (a), (b) shows the outputs of the *Glomeruler* layer when odor [IA, EB, Ci] and odor [Air] are inputted respectively. In this simulation, it is assumed that the output of odor [Air] for the *Glomeruler* layer to be a constant

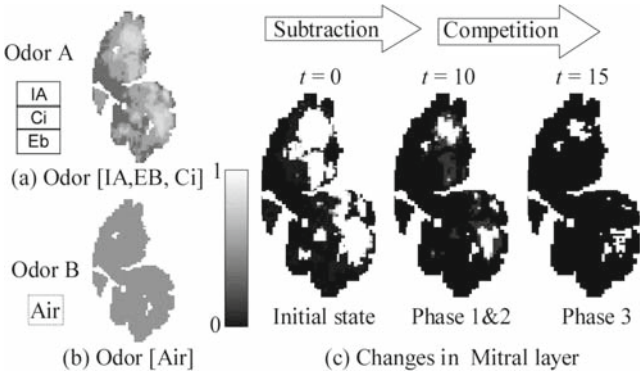

Fig. 7. The changes in states of the *Mitral* layer

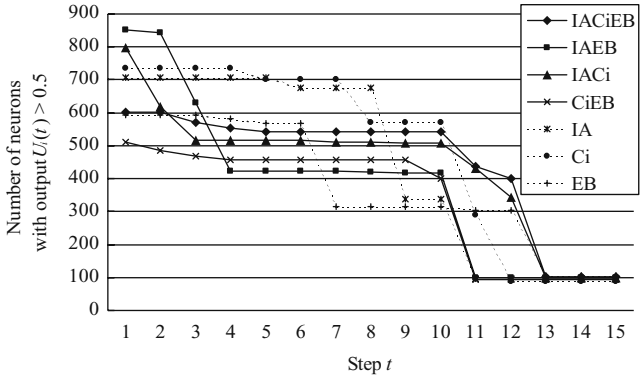

Fig. 8. Decrease in activation of *Mitral* layer

noise. Figure 7 (c) shows the outputs of the *Mitral* layer when odor [IA, EB, Ci] is inputted at the time step *t*. The activity distribution of the neuron models corresponds to the color bar where whiter dot denotes the neuron that has higher activity.

Figure 7 (c) indicates that the activity pattern of the *Mitral* layer is an enhanced pattern of the *Glomeruler* layer shown in Fig. 7 (a) at the initial state ($t = 0$). After the 1st and 2nd learning phase have completed ($t = 10$), the activity pattern of the *Mitral* layer reflects the difference of the patterns shown in Fig. 7 (a) and (b). When the 3rd learning phase has completed ($t = 15$), the neurons of the *Mitral* layer with the strongest outputs at $t = 10$ are extracted as a result of competition (shown in Fig. 7 (c)). Consequently, the activated region becomes narrowed but the activity has gained stronger through the proposed learning algorithm. The decrease in activation also can be observed from Fig. 8, where the number of neurons with output larger than 0.5 ($^2U_i(t) > 0.5$) are plotted along with each step.

Although, different odor can activate different number of neurons, the activation are decreased gradually through the 1st and 2nd learning phases ($t = 1$~10), and eventually about 100 neurons are chosen by the 3rd learnin phase ($t = 11$~15).

The simulation results indicate that a part of the inputted pattern on the *Glomeruler* layer has extracted by the *Mitral* layer, and thus, it can be concluded that the proposed model has an ability of feature extraction.

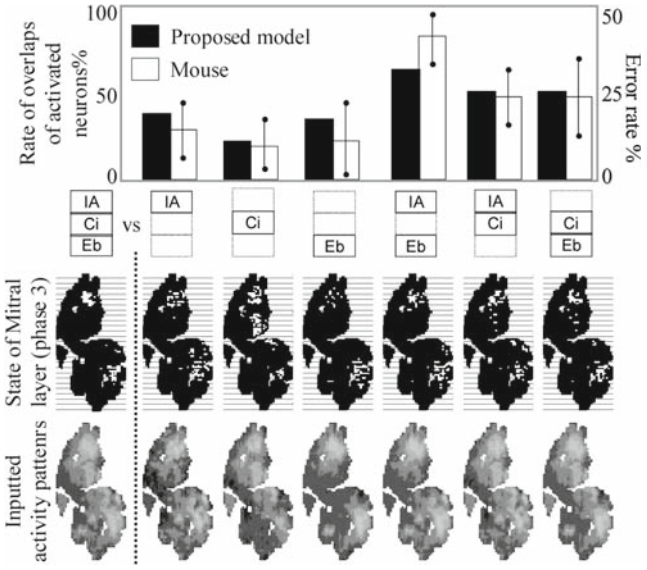

Fig. 9. Comparison to the behaivior experiments

4.2 Comparison with the behavior experiments on mice

To compare the tendency in the feature extraction of simulations and the *Attention* behavior of the living mice, the simulation results are compared to that of odor discrimination experiments on mice. First, the similar simulation as the previous section have implemented on 6 different odors [IA], [EB], [Ci], [IA, EB], [IA, Ci] and [Ci, EB]. The outputs of the *Glomeruler* layer to each odor are shown on the lower side of Fig. 9. The outputs of the *Mitral* layer after the 3rd learning phase are shown in the middle row of Fig. 9. In addition, the overlap rates of each activity pattern of the *Mitral* layer to that of odor [IA, Ci, EB] are plotted on the top of Fig. 9. The overlap rate is defined as the ratio of the region that both patterns are activated in common against to the total activated region. Further, the error rates obtained from the odor discrimination experiments on the living mice are plotted beside the overlap rates. From Fig. 9, we can find similar tendency between the error rates and the overlap rates; the higher overlap rate is, the higher the error rate. This result indicates the feature extraction by the proposed learning algorithm is consistent with *Attention* to an extent.

However, in the case of odor [Ci, EB] and [IA, Ci], the overlap rate differs significantly as compared to the error rates of the living mice. This could be caused by the initial values of the connective weights. Therefore, the simulation result might be able to be improved by taking the average of simulation results over various initial values of the connective weights.

5 Conclusion

In this paper, we proposed a neural network model of the olfactory system of mice aimed to explore the algorithm called *Attention*. The simulation results of the proposed

model have a certain consistency with that of the odor discrimination experiments on mice, which indicates that the model has ability similar to *Attention*.

Having the mice to discriminate the same odors repeatedly, we found the mice could lower the error rate and improve their discrimination ability with changing the tendecy of *Attention*. For the future work, we are planning to investigate the underlying algorithm of the experiment results and improve the proposed model.

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