Abstract

The project is divided into 2 parts.
For the implement part, it aims to rebuild a honey bee olfactory system model which can simulate some basic cognitive behaviors found among the activities of honey bees. And then, the model is used to verify the relationship between the lateral inhibition which is a type of interaction between local interneurons in olfactory system and the cognitive behaviors. By the generalization, overshadowing experiments, the effect of lateral inhibition on the behaviors are identified. After compared with previous data, the reliability of the program based on this theory is proved.
For the research part, the parameter of time constant is researched and the different time constant is chosen to measure the effect on these behaviors. The data shows that the increase of time constant contributes to the strong generalization, which means time constant may disturb the neurons' judge on the right discrimination from the odorant mixture.
Finally, how to improve the model is described, what is more, the output of PNs in the built model will be taken as the further research object in the future to verify the classification in the more complex olfactory organization Mushroom Body.

Table of Contents

1 Introduction

It is believed that the studies on insect brains can disclose the certain cognitive abilities which were thought only belonged to vertebrates. On the one hand, the discovery of cognitive behavior in insects contradicts the statement that there are close relationship between brain size and neuronal circuits. On the other hand, the progress of understanding how it works with insect's neurons may help us do better researches on human's brain structure.

I am interested in exploring the neural network in brain of honey bee. It is well-known that there lie various kinds of associative learning involved in color and odor classification. Behind these magic cognitive abilities, there must be special communications in neural network.
In this case, I will set up and implement a model of cognition based on Linster et al.'s idea [1] to simulate the structure of honey bee olfactory system to analyze how honey bee can separate single odor from odor mixtures and the nature behind the phenomenon such as overshadowing and blocking, which are proved to occur in honey bee. Then the research on time constant will be developed and the effect will be evaluated.

1.1 Aims and Objectives

The aims of this project are to set up a neural network model of honeybee's olfactory system and use this model to research on some cognitive behaviors arising from neuronal circuits.

There are several stage objectives to meet this aim:
1. Design an artificial neural network model to simulate the neurosis in honey bee brain.
2. Adjust and choose the most suitable open parameters.
3. Analyze the output data and identify the cognitive behavior phenomenon.
4. Compare the different results when adopting different hebbian learning rules.
5. Evaluate the effect of time constant and research on the relationship between time constant and cognitive behavior.

1.2 Organization

The organization of the essay is as following:
Chapter 2: Background. In this part, the background knowledge for this project is introduced. This includes the cognitive behaviors of honey bee such as generalization and overshadowing, and some algorithms involved in the experiment such as associative learning and integrate-and-fire mode.
Chapter 3: Project design. The function of each part of the model is described and the GUI of program is shown. The designing parameters and the main algorithms are

discussed and chosen.
Chapter 4: Experiments and results. In this Chapter, several experiments about the cognitive behaviors are done and the results will be analyzed.
Chapter 5: Future work. In this part, how to improve the performance of the model is described and another classification method is presented. In the future, the model will be improved and the experiment results will be tested and compared with the present ones.
Chapter 6: Conclusion. The content of the essay will be summarized in general.

2. Background

"It is certain that there may be extraordinary activity with an extremely small absolute mass of nervous matter; thus the wonderfully diversified instincts, mental powers, and affections of ants are notorious, yet their cerebral ganglia are not so large as the quarter of a small pin's head."[2]

--- Charles Darwin

It is amazing that many insects have complex cognitive behaviors. A honeybee worker is recorded having nearly 60 behavior types[3]. All these behaviors are conducted in a tiny brain. Scientists have found that most insects with cognitive features such as numerosity, attention and catergorisation-like processes only need limited neuron numbers[3]. A honey bee, whose brain has a volume of ~1 mm^3 and fewer than 1 million neurons, shows good cognitive capacity[4]. It is said that although the honeybee's learning speed is slower than human infants, it is faster than all vertebrates that have been studied[3]. Also, it is shown from Changizi's collecting data among animalia, a honey bee can perform more kinds of behaviours than a North American moose does[3]. A mature honeybee worker has 59 distinct behavior types from Lars and Jeremy's survey, which include packing pollen, round dance, cell cleaning and so on[3].

Although the small amount of neurons, a honeybee can conduct rich activities. There must be special connectivity between neurons. Artificial neural network analyses show that the minimum number of neurons necessary to complete various complex cognitive tasks is particularly small, for instance, conducting a simple visual categorization task only needs a network of seven sensory neurons, five interneurons, and motor neurons[5].

Exploring the concrete connection and interaction of neurons in the insect neural network contributes a lot to disclose the insect behavior and know more about the human brain. This project will do the research on the cognitive behavior in honeybee using the machine learning based technique. The first part introduces the background of honeybee olfactory system and several cognitive behaviors: generalization, blocking and overshadowing. My task is to implement the cognitive model on the java platform, so the second part introduces this model proposed by Linster and Smith[1]. In order to do the further research on the higher odor structure, the hebbian learning, Pavlovian classic conditioning and some relevant models are introduced. Their theories are crucial for the research in the higher olfactory neurons.

2.1 Neuron

Scientists point out that neuron is the single most important concept in brain study. It

is special because it is the only tool to transmit electrical signals over long distance. The behavior of the organism can be divided into a great number of activities in form of neuronal circuits in neurons.

According to Eugene, a common neuron receives over 10,000 neurons inputs through the contacts on synapses, these inputs can alter the neural membrane potential by electrical currents. The great PSPs (postsynaptic potentials) produced by large currents can be amplified by the channels sensitive to voltage and contribute to the occurrence of spike. And these spikes are the important communicators for the connection of neurons. Neurons could not spike automatically, except that they are inspired by the incoming fires from other neurons[6]

When the postsynaptic potentials in a single neuron are reached a certain voltage figure which is called the firing threshold, it fires and resets membrane potential.

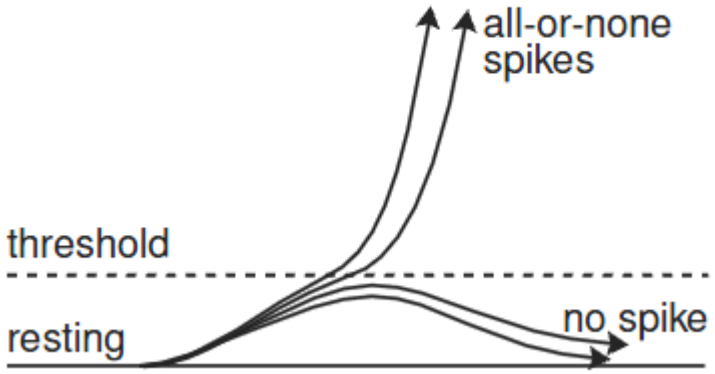

Figure 2.1: The concept of a firing threshold adopted from[4].

2.2 Olfactory System

Odor mixtures are distributed in natural environment in time and space, the olfactory system are intelligent enough to choose the essential odor signals out of noisy environment. Olfactory system contains a great many neural circuit elements which are regarded as perform essential functions and feedback and feed forward interactions among these structures[7].

The Figure 2.2 shows the main structure which process odors in an insect's olfactory system.

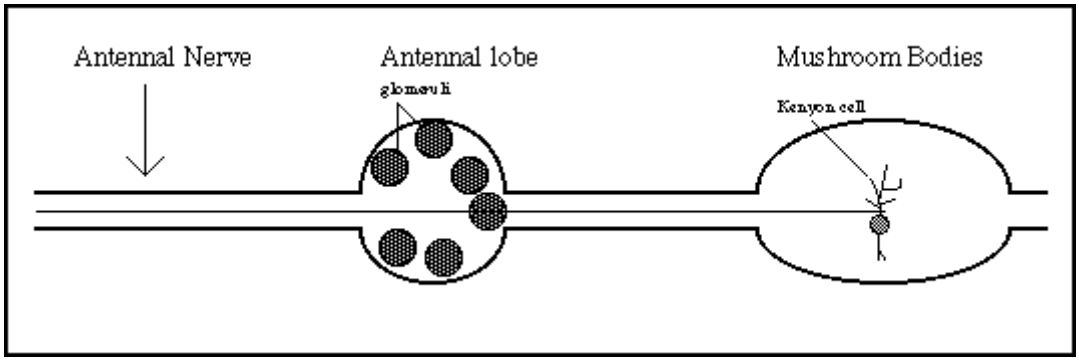

Figure 2.2: the main olfactory system in insect brain adopted from [8]

Insects such as honey bee have three essential odor-classification processing stages: The antenna, the antenna lobe(AL) and the mushroom body(MB).

According to Linster and Smith[1], there is great similarity between the insect's antennal lobe and vertebrate olfactory bulb in the first synaptic processing of incoming signals from primary receptor cell axons.

The antennal lobe acts a central part for odor classification. It is in charge of odor coding and short-term memory. The neural activity involved in the AL is highly organized in both time and space. Honeybees possess about 160 glomeruli[9], which is the arrangement of neural clusters and contributes to the spatial order. In every glomeruli, 3-5 projection neurons(PN) pass olfactory information to higher processing areas such as the mushroom bodies.

Mushroom bodies are crucial for odor conditioning, they are lobed neuropils that playing a key role in olfactory learning and memory. It is the higher odor-processing structure in olfactory system. According to Huerta et al., "the AL performs some preprocessing of the data to feed an adequate representation of it into the area of the insect brain that is responsible for learning odor conditioning, the MB".[10]

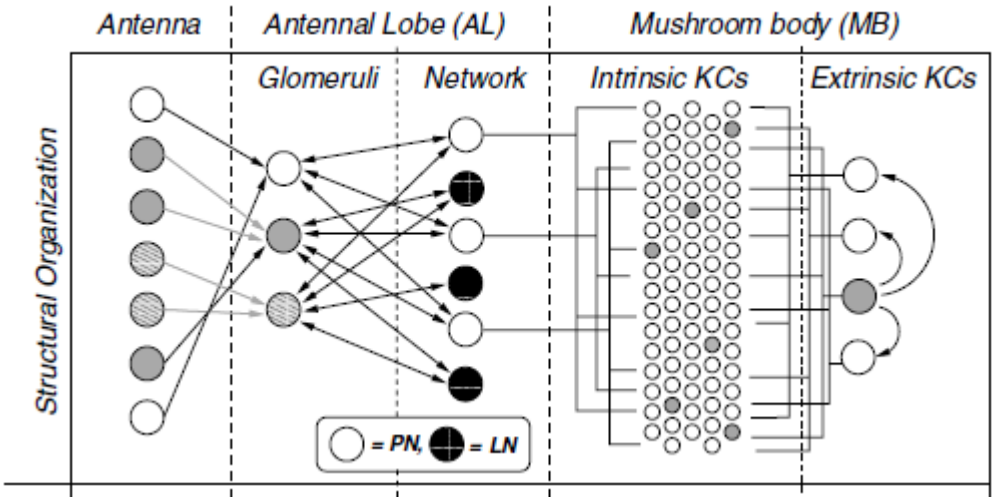

Figure 2.3: the structural organization adopted from [10]

R. Huerta et al. proposed a model is divided into two stages: a nonlinear

transformation from AL to the MB and a classification in the MB lobes[46]. They didn't address the temporal code in odor classification, though it plays a role in behavior. However, the research in the Mushroom body is important, and this part will introduce their classification idea, which will contribute a lot to my study.

Every receptor cell in the antenna expresses one kind of receptor, what is more, all olfactory receptor cells presenting the same receptor connect to the same glomerulus in the antennal lobe (AL)[11].There will be spatial code in the glomeruli derived from the encoded architecture[12].Within the layer of antennal lobe, sensory cells synapse onto output neurons carry information out of the first layer for processing in other neuropils.

The big number of antennal lobe neurons relay inhibition in themselves, while a few projection neurons pass information to other neuropils[13][14].

Because the same kinds of excitatory and inhibitory transmission conducted during different animal lineages though the special transmitters and elements are different, independent circuitry can perform quite similar or the same functions[1].

In honeybees, olfactory reward conditioning is enhanced by the biogenic amine octopamine. VUM neurons discovered have great effect on appetitive learning, showing ling-lasting excitation to the stimulation of sucrose. VUMma1 neuron, as one of these neurons, plays a more concrete role. It adjusts the reinforcing function of rewards during olfactory conditioning, since its depolarization substitutes the reward in olfactory conditioning[15]. This effect simulates a basic property of proboscis-extension response conditioning.

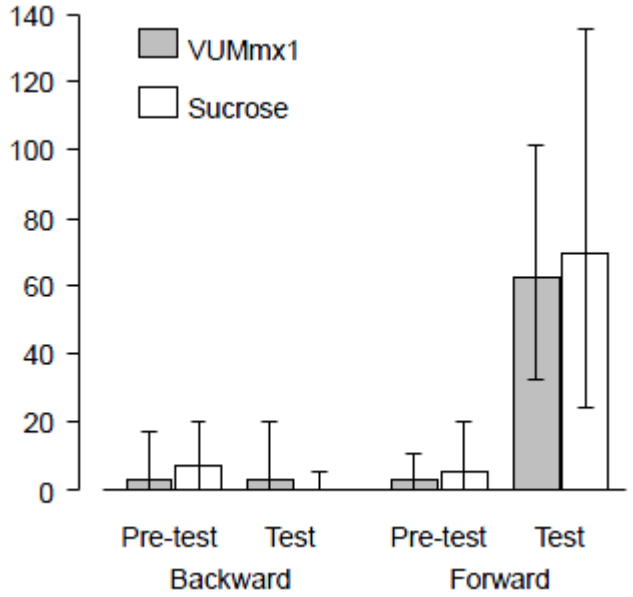

Figure 2.4: the similar between VUMmx1 response and sucrose stimuli adopted from [15]

2.2.1 VUMmx1

It is said that animals have the capacity to connect a neutral stimulus with an unconditioned stimulus which contributes a lot to associative learning in classical conditioning stage[16][17][18][19]. Consequently, information extracted from the neuron experienced unconditioned stimulus stage is demanded for grasping the global features of conditioning. Hammer had identified an interneuron which is called VUMmx1 that mediating the unconditioned stimulus during the associative learning. This special neuron pointed out has particular response features and unique morphology. Its response can last about 30 seconds which outlasts the unconditioned stimulus.[20] He also found that there are certain similarities of activity between the olfactory system and VUMmx1. The experiment of observing the VUMmx1's activity verifies his hypothesis about the close relationship between the associative strength of odors and the increase of the olfactory input to VUMmx1.
The Figure below shows that honey bees connect on kind of odor CS^+ as an indicator, after the differential conditioning, the response of VUMmx1 to the CS^+ is intensively high compared with the response to CS^-.[20]

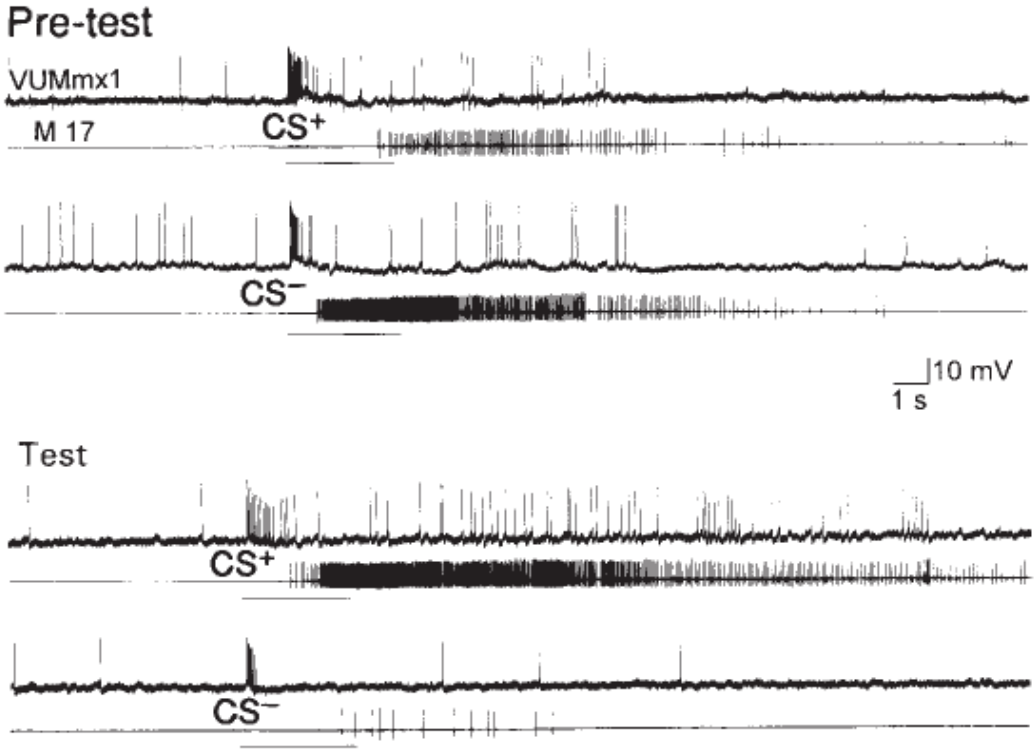

Figure 2.5: the response of VUMmx1 is in line with the odorant stimulation adopted from[20]

It stimulates the glomeruli in the antennal lobe and also the mushroom bodies. The model to be implemented involves two key concepts which are overshadowing and blocking, which by now are the essential discovery in honeybee. Next, the explanation of both concepts will be presented.

2.3 Learning about odorant

It is well known that flower odorants are usually the complicated mixtures composed of hundreds of single odorants, and the mixture can change according to time and location, so it is hard for honey bee to identify single odorant among the blend.[21] Dionne and Dubin pointed out that many physiological processes can affect animals on discriminating single odorants from a blend.[22] The research on sensory physiology disclosed the interaction between odor molecules and reception cells can produce several effects such as mixture suppression and so on.[23]

2.3.1 Generalization

Generalization in the olfactory system has been studied to respond to a pure odorant conditioned stimulus[24]. Brian stressed animals including insects make strongly response to the conditioned stimulus and less but not as strongly to an odorant similar in structure to the conditioned stimulus. The response becomes intensively weaker when the architecture of the molecule is altered.[23]

The neuron activated by the mixture is very different from the result from a simple sum of that activated by single odorants from the mixture[25]. Actually, if there is great difference between the neural representation for the mixture and ones for the single odorants, the generalization from the blend to the single ones will be very weak. The figure below shows this particular phenomenon.

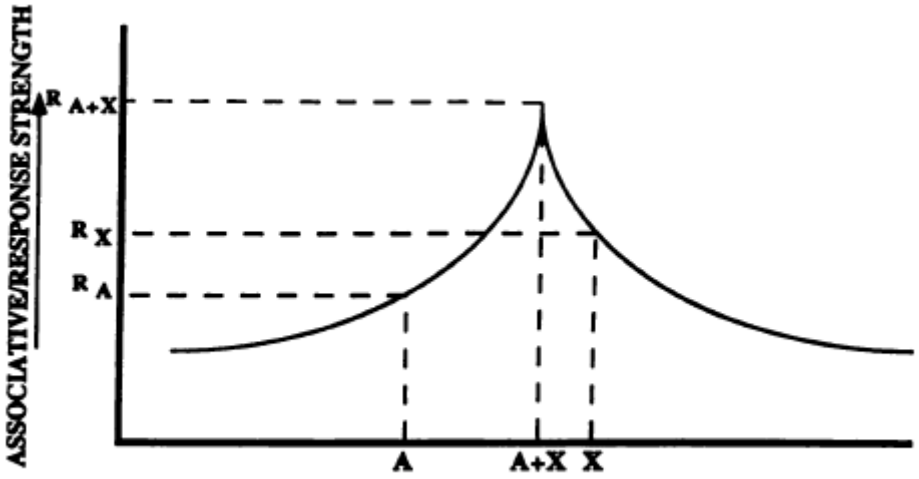

Figure 2.6: the relationship between binary mixture and generalization adopted from[23]

The farer horizontal distance A has from X, the more difference between A and X, the weaker of both R_A (the response to A) and R_X (the response to X).

2.3.2 Overshadowing

Bitterman and Menzel made the experiment to disclose the phenomenon about overshadowing[26]. They divided four equal groups of honey bee workers, during the single trial, odors were companied by sucrose reinforcement. Two groups were under mixture conditioning circumstance and others were under pure circumstance. All groups were then tested with the same pure odorant which was not reinforced. The diagram shows the probabilities of different groups respond to mixture and pure odorant of that mixture.

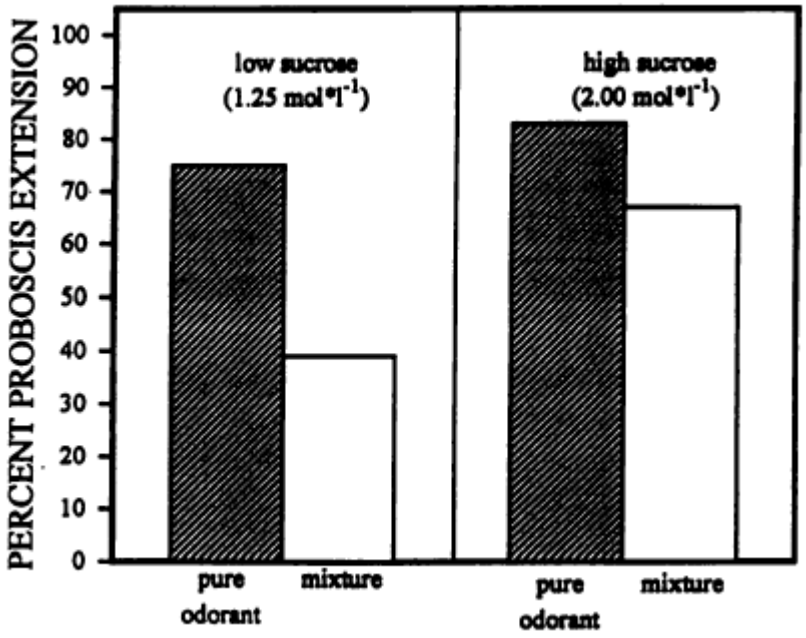

Figure 2.7: the overshadowing experiment by Bitterman and Menzel adopted from [23]

Overshadowing shows that when honey bees are conditioned to one stimulus alone, the response to that stimulus is stronger than when they are conditioned to a combination of this stimulus and another one[27]. The difference in response to an odorant is based on the difference between conditioning backgrounds and is a frequent occurrence in mixtures[1]. What is more, it can be asymmetric[28], which means one stimulus dominates the mixture and have a dominant ability to overshadow the other one in the combination.

2.3.3 Blocking

Blocking means animals are first conditioned to one stimulus A, and then they are conditioned to a mixture which contains A with the same reinforcement, the response level to another stimulus is lower when A is preconditioned and the mixture is received mixture conditioning.[1]

It is said that the overshadowing is essential as it is not enough to improve the response

to a pure odorant with the condition of spatial and temporal pairing of this odorant.

The study of blocking in honey bee is combined with control procedures. There are two control groups which are novel group and overshadowing group. The block group was first pre-trained and a single odorant A was forward-paired. The novel group is similar but novel odorant was forward-paired. And the overshadowing group was not pre-trained. All groups were equally trained to the mixture A+B in the second phase. Then the test stage came and the responses to single odorant B were tested. The result shows that in blocking group the response to odorant B is intensively lower than that in novel or overshadowing group. That means acquisition to odorant B is blocked[23].

A phenomenon is also found that when a single odor is backward-paired or unpaired, blocking did not occur [29][30]. Consequently, only forward-pairing contributes to blocking.

The first discovery on olfactory blocking in honeybee [30] show that a first odorant conditioned blocks learning a second odorant contained in a binary combination with the first one. This is contradicted by Gerber and Ullrich [31], who found that when a reduction of the intertribal interval and an absence of balance of the odorants are used, blocking did not occur. However, Hostler and Smith [32] demonstrated that blocking really occurs in the olfactory structure, although is restricted to similar odors.

2.4 Model Architecture

The model described here is supposed by Linster and Smith [1] which identifies the relationship between lateral inhibition and overshadowing, blocking.

In the model, all the synaptic interactions are in the high synaptic density areas [33]. These glomeruli are identifiable morphological neuropilar subnits [1]. The number of glomeruli is decreased to 15 and every glomerulus receives input from the same receptor cell type.

90% of antennal lobe neurons are constituted by local interneurons(LN), the most of which are possibly inhibitory[34]. Receptor cells are hypothesized to synapse primarily with LNs. 80% of LNs show a high density of branching in one special glomerulus that are called Hetero-LNs[35]. In the model, only the Hetero LNs are involved. And similar to the LNs, there are two categories in the projection neurons: Uni-PN and Pluri-PN. The previous one has dendrites invading only one glomerulus while the latter one is pluri-glomeruluar. In this model, Uni-PNs sum the synaptic activity to one glomerulus[1].Three types of activity are integrated by each glomerulus, input from one kind of receptor cell, associated inhibitory interneuron providing with local inhibition and the lateral inhibition[1]. Release of spontaneous activity of PNs by inhibition of presynaptic inhibitory local interneurons is adopted as the neural mechanism. Figure 2.8 below shows the model architecture[1], receptor axons(RC)

synapse with local interneurons(LN) in GLOM. LN receive connections from RC in a single PN, which send lateral inhibitory connections to neighboring glomeruli[1].

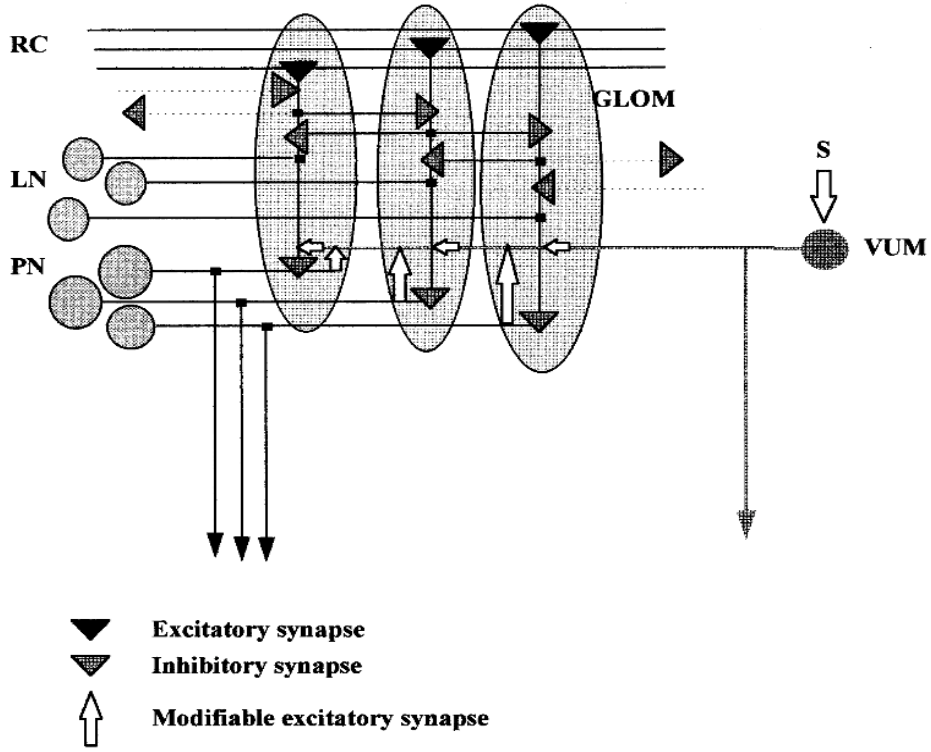

Figure 2.8: neuron interaction and connection adopted from [1]

2.4.1 Odor processing

Local interneurons(LNs) which receive the activation from receptor cells inhibit LNs in the three golmeruli next to it on the each side. And the intensity of inhibition is graded with the increase of the distance. The inhibited LNs then do not impose the inhibition on the corresponding PNs, and the PNs increase their spike probability[1].
Activated PNs often respond in form of different response patterns during the stimulus. Therefore, an across-PN pattern of activation and inhibition marks a special odor input[1].

Figure 3 describes the overlap in the model[1]. Each circle is a glomerulus, O1, O2, O3 represent odor components, when two glomeruli which two components affect on are far from each other, the value of overlap is low. In contrast, when the nearby glomeruli are stimulated, the overlap is very large.

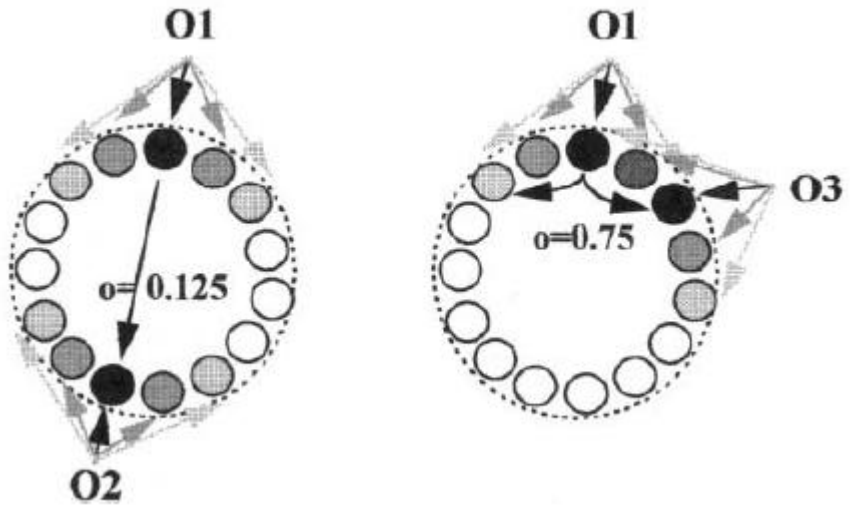

Figure 2.9: Overlapping in the antennal lobe adopted from [1]

2.4.2 Associative learning

Associative learning is a type of unsupervised learning. Unlike supervised learning of which the output is a regression during the process and can finally predict a classification, in unsupervised learning, all the observations are assumed to be caused by latent variables, it is trying to find relationship only with the help of the raw data.

2.4.2.1 Association

An association is a relationship between the input and output of a system, when input is a pattern, the system will respond with another pattern. When both patterns are linked by an association, the input one is referred to as the stimulus. Similarly, the output pattern is regarded as the response.

A number of researchers have contributed to the development of associative learning. In particular, Tuevo Kohonen, James Anderson and Stephen Grossberg are prominent. Anderson and Kohonen independently developed the linear associator network in the late 1960s and early 70s. Grossberg introduced nonlinear continuous-time associative networks during the same time period[36].

2.4.2.2 Associative network

A simple associative network is presented below:

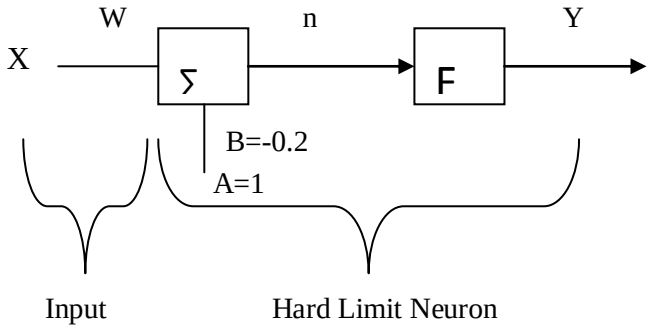

Figure 2.10: a simple associative network

The neuron's output Y is determined from factor X according to:

$$Y=F(W*X+A*B)=F(W*X-0.2)$$

If X is supposed to be either 0 or 1, presenting a stimulus is absent or present, then Y is limited to the same value by the function, which is the response of network.

$$X=\begin{cases}1, & \text{stimulus}\\ 0, & \text{no stimulus}\end{cases} \qquad Y=\begin{cases}1, & \text{response}\\ 0, & \text{no response}\end{cases}$$

The presence of an association between X=1 and Y=1 is dictated by the value of W. The network will only make response when W>-B.

2.4.2.3 Pavlovian Classical conditioning

Classical conditioning is a form of associative learning that was first supposed by Ivan Pavlov. The presentations of a neutral stimulus and a stimulus of some significance induce the classical conditioning. The neutral stimulus which is any event that does not contribute to an overt behavioral response is referred as a conditioned stimulus(CS), while presentation of the stimulus evokes an innate is called the unconditioned stimulus(CS). [37]

Based on Figure 2.11, the simple model about classical conditioning is presented below:

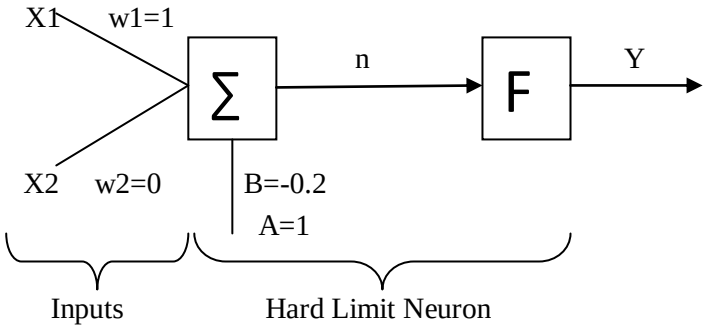

Figure 2.11: classic conditioning model

$$Y=F(W1*X1+W2*X2+A*B)=F(W1*X1+W2*X2-0.2)$$

X1 stands for a mixture of odors o1+o2, X2 presents a type of odor o2, and the inputs of

the unconditioned and conditioned in this network are:

$$X1=\begin{cases}1, & O1+O2 \text{ detected}\\ 0, & O1+O2 \text{ not detected}\end{cases} \qquad X2=\begin{cases}1, & O2 \text{ detected}\\ 0, & O2 \text{ not detected}\end{cases}$$

The network is to associate the compound, but not the O2 with a response separating o1 from O2. The values of weight during the input stage should satisfy that: X1=1, X2=0. The new equation is that:

$$Y=F(X1-0.2)$$

In this case, the network will respond only if X1=1, not considering whether the odor O2 is received or not.

2.4.3 Unsupervised Hebb Rule

"Hebbian theory describes a basic mechanism for synaptic plasticity wherein an increase in synaptic efficacy arises from the presynaptic cell's repeated and persistent stimulation of the postsynaptic cell."[38]

It has been the fundamental basis for the traditional view that when analyzed from a holistic level, engrams are neuronal nets or neural networks.[38]

Hebb's principle can be regarded as a method to determine the value of weights between model neurons. The weight between two neurons increases if the two neurons activate at the same time. On the contrary, it reduces if they activate separately. There are strong positive weights between the nodes which tend to be either positive or negative simultaneous while strong negative weights will arise from those to be opposite.

A basic description of Hebbian learning is described as below:

$$W_{ij}=X_iX_j$$

W_{ij} is the weight of the connection between neuron I and j, the X is the input of neuron. Weights updated after every training process.

The network in figure 6 can explain the Hebb rule well. If odor compound o1+o2 stimulus occurs simultaneously with o2 output, the network should strengthen their connection.
The unsupervised Hebb rule increases the weight W_{ij} between a neuron's input p_j and output a_i:

$$W_{ij}(q)= W_{ij}(q-1)+ka_i(q)P_j(q)$$

The learning rate k shows how many times a stimulus and response have to occur together before an association is made.

Rules that satisfy the condition are called local learning rules.

The vector form is as below:

$$W(q)=W(q-1)+ka(q)P^{T}(q)$$

Learning is conducted in response in the training sequence:

$$\mathbf{P}(1),\mathbf{p}(2),\ldots,\mathbf{p}(Q)$$

At the each process, the output **a** is calculated in response to the input **p**, and the weights **W** are updated.

Previous studies have shown that networks of spiking neurons with biological feature can process information fast in the way of encoding information instead of using firing probability as the code. In most of neural network structures, there are two ways of activation in single unit that are binary variable in the form of 0 or 1 and continuous function in the form of any values between 0 and 1. Continuous activation functions have close relationship with firing rates of biological neurons[39].

However, S.J.Thorpe proposed that firing rate codes could not be fully used because the speed of neural computation is so fast that it could not leave enough time for individual units to produce single spike.[40] Some solutions were raised, for example, analog-to-delay convertors are applied and the strength of a neuron's input could decide whether a spike occurs. Moreover, the neurons fire in order was used instead of computing the latency figures.

Manuel,Simon and Emmanuel had then raised a Hebbian reinforcement learning scheme to change the weights of relative neurons to solve the classification problem. The core part of their integrate and fire model is described as below[39]:

$$V(t+1)=\begin{cases}(1-\alpha)V(t)+f[u(t)] & \text{when } V(t)<k\\ V_0 & \text{when } V(t)\geq k\end{cases}$$

In this equation, V_0 is the neuron ground potential, k is the firing threshold, f is the integrating function computing the value of input u(t).

The whole network structure is composed of preprocessing layer and decision neurons. The first layer receives the constant activation, after the output of the increasing sigmoidal function, the output values of each neurons of the first layer are passed to decision neurons. The latency λ is introduced and the expression is[39]:

$$\lambda=\frac{k-V_0}{f(u)}$$

The idea of processing the input signals in time order is convenient since it is complex to compute λ between the spiking time intervals.

According to Hebbian learning, when the signal passed from neuron is in the firing state, the synaptic weights are increased.

Here is Manuel et al's formula[39]:

$$W_{ij}(t+1)=W_{ij}(t)+\gamma X_i(t)(\sum_{k=0}^{k=t}\alpha^k u_{ij}(t-k)-W_{ij}(t))$$

Where γ is the learning rate and the value is restricted between 0 and 1. The synaptic weights will not be modified when other patterns are involved. The synaptic weights are computed according the random recurrence[39]:

$$W_{ij}(k)=W_{ij}(k-1)+\gamma[\beta^{r_j(k)}-W_{ij}(k-1)]$$

r_j marks the rank of the activity of neuron j at the step k. $\beta^{r_j(k)}$ is the random variable whose mean is $m_{i,j}$ and standard deviation $\sigma_{i,j}$. $W_{ij}(k)$ is a Markov chain. It is important to note that when γ is small, the weights in the stationary law is in almost Gaussian form, therefore, the learning rate can adjust the range of fluctuation.

2.4.4 Integrate-and-fire models

In 1907, Lapicque researched one of the earliest neuron models[41].
The described graph is as below:

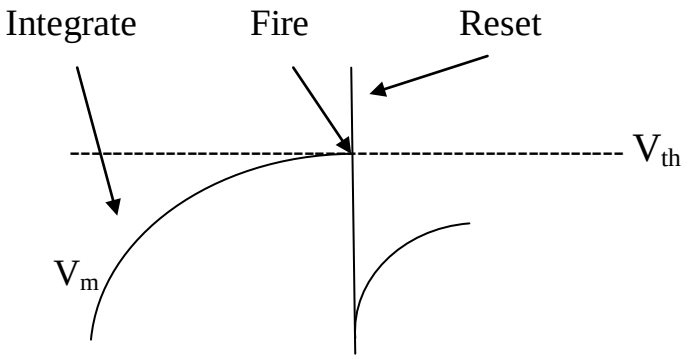

Figure 2.12: an integrate-and-fire model

The model is represented in the below equation:

$$I(t)=C_m\frac{dV_m}{dt}$$

It is derived from the law of capacitance, which is shown below:

$$Q=CV$$

The membrane potential increases with time and stops when it reaches the threshold V_{th}. A fire then occurs and the resting potential is recovered. The spiking rate increases linearly with the increase of input current.
The circuit diagram is as below.
$I_{in}(t)$ is the input current which is changed with time.

$$I_c=C_m\frac{dV_m}{dt} \quad \text{and } V_m=V_{rst} \text{ when } V_m=V_{th}$$

V_{rst} is reset potential and V_{th} is the threshold potential.

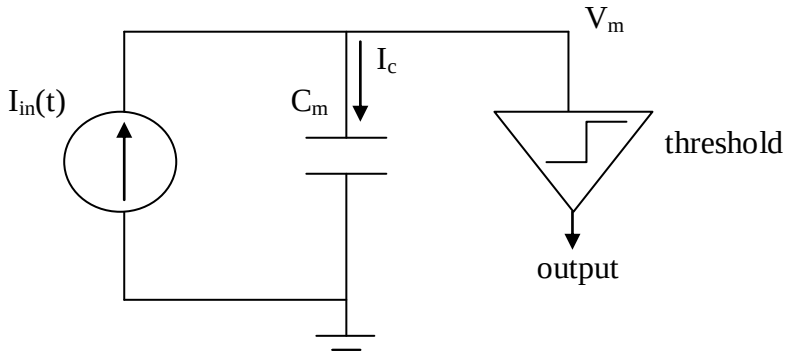

Figure 2.13: perfect integrate-and-fire current diagram

It is also called perfect integrate-and-fire model, which is not suitable for the practical neuronal behavior because it has no time-memorial function.
After leaky integrate-and-fire model was introduced, this problem is solved.
The model is described below:

$$I(t)-\frac{V_m(t)}{R_m} = C_m \frac{dV_m(t)}{dt}$$

The circuit diagram describes the equation above well:

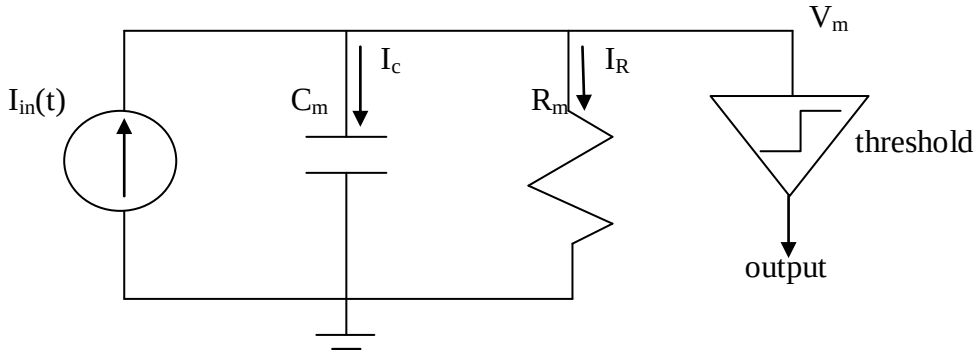

Figure 2.14: leaky integrate-and-fire current diagram

R_m is the membrane resistance.

$$I_{in}(t)=I_c+I_R=C_m \frac{dV_m(t)}{dt} + \frac{V_m(t)}{R_m}$$

After transformation,

$$R_mC_m\frac{dV_m(t)}{dt}+V_m(t)=R_mI_{in}(t)$$

Where R_mC_m is membrane time constant and it is expressed below:

$$\tau= R_mC_m$$

Then

$$\tau\frac{dV_m(t)}{dt}+V_m(t)=R_mI_{in}(t)$$

When τ is larger than the interval time between the fires of output, the leak could be ignored. Oppositely, when τ is much smaller, the input fluctuation decides whether or

not a spike occurs.

It is pointed out that $I_{in}>I_{th}$ is a necessity to produce a fire in the cell, where $I_{th}=V_{th}/R_m$. Or some change will be leaked out in potential, the spiking frequency is shown below[42]:

$$f(I)=\begin{cases} 0, & I \le I_{th} \\ (t_{ref} - R_m C_m \log(1 - \frac{V_{th}}{IR_m}))^{-1}, & I > I_{th} \end{cases}$$

2.4.5 Model parameter

When it comes to the model of honey bee olfactory system, it is essential to define which synapses should be used in Hebbian learning to reproduce the electrophysiological and the behavioral data.[1] Linster and Smith introduced an interneuron which contains properties of VUMmx1[43]. It receives sucrose-like input and has arborizations in 15 glomeruli. It is also pointed out that odor processing in the intrinsic antennal lobe circuitry should not be subject to synaptic plasticity. That means only the synapses from or onto VUM can be modified by Hebbian learning.[1]

Synaptic plasticity activated by a special stimuli from AL neurons to the VUM ones is a necessary. Learning rule 1 will be used to the simulations between VUM and PNs, while the simulations between VUM and LNs will be added when use learning rule 2.[1]

2.4.6 The process of simulation

At the beginning, the synapses are weak and their value is under the threshold of the neurons. A particular compartment in each glomerulus is the input of VUM in this glomerulus, consequently, the change of synaptic occurs during learning results from the activity rates in each glomerulus.[1]

2.4.6.1 The McCulloch-Pitts Model of Neuron

The McCulloch-Pitts neuron model is introduced by Warren McCulloch and Walter Pitts in 1943. The model adopts some features of real neurons, the inputs of which have either of two activities: excitatory to make the output fire and inhibitory not fire. The general equation is as below[44]:

$$y = f(\sum_{i=1}^{N} I_i W_i)$$

I_i (i=1,…,N) is the input and y is binary output, W_i(i=1,…,N) is weight value in the range of either (0,1) or (-1,1). The function is a linear step function, when the sum of I_iW_i above the

threshold, the output y keeps the constant value 1. The function is described below:

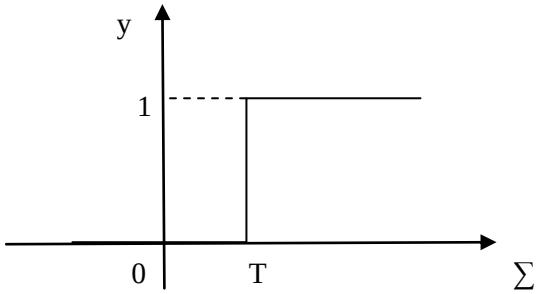

Figure 2.15 non-linear threshold function

The neuron model can be described as below network:

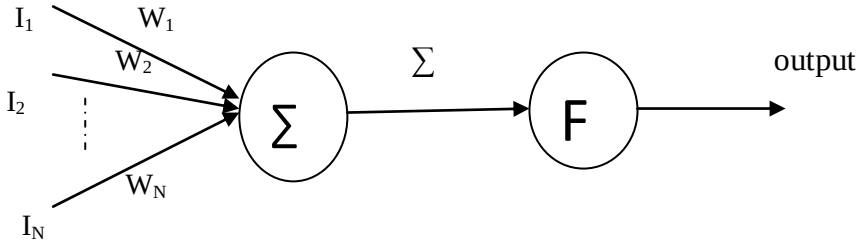

Figure 2.16: the McCulloch-Pitts Model adopted from [44]

The function below describes the activity of neurons[1]:

$$o(t) = F[\sum_{i=0}^{glom} v_i(t)]$$

The output O(t) is the instantaneous firing frequency and only has two values, 1 stands for a spike occurs at time t and 0 stands for not .

F is a non-linear threshold function, $F(X_i(t)=1)$ means that the state $X_j(t)$ of neuron j at time t is 1 is given by the function of the neuron membrane potential $V_j(t)$ at time t, the lower threshold A decides the quantity of spontaneous activity, while the upper one B determines the value of the membrane potential that the maximal spiking frequency is reached:

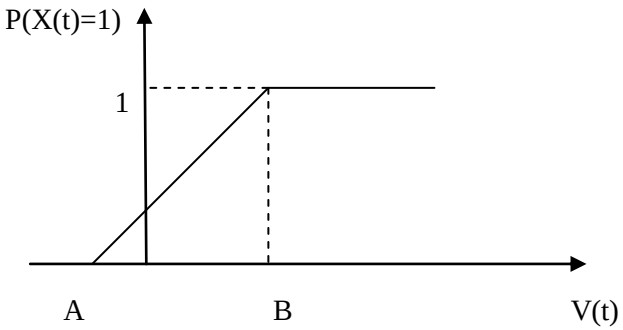

Figure 2.17: the firing frequency of VUM adopted from [1]

The membrane potential V(t) in each glomerulus satisfies the next formula[1]:

$$\tau \frac{d_{v_i}}{d_t} + v_i(t) = w_i^{PN} O_i^{PN}(t) + S(t)$$

τ is the membrane time constant of VUM, w_i^{PN} is the connection strength between PNs and VUM is glomerulus I, o_i^{PN} (t) is the output of PNs and S(t) is the sucrose input.

What is more, the sucrose-induced VUM activity synaptic changes can also occur between VUM and LN[1]:

$$w_{ji}(t+1) = w_{ji} + v_{ji} * (o_j(t) * o_i$$

The changes of synaptic strength are computed between pre and postsynaptic neural activity.

3 Project Design

3.1 Input and Output

Odor stimuli which afferent the continuous value to reception cell is regarded as project input. This is simulated in Gaussian distribution form. Each RC(reception Cell) of 15 has the maximal sensitivity to one kind of odor, and the rapidly decreasing values are received by the neighbors, for instance, if the No.8 RC has the most intensive response to one kind of odorant, the Gaussian distribution (σ=0.5) for 15 RC is shown as below:

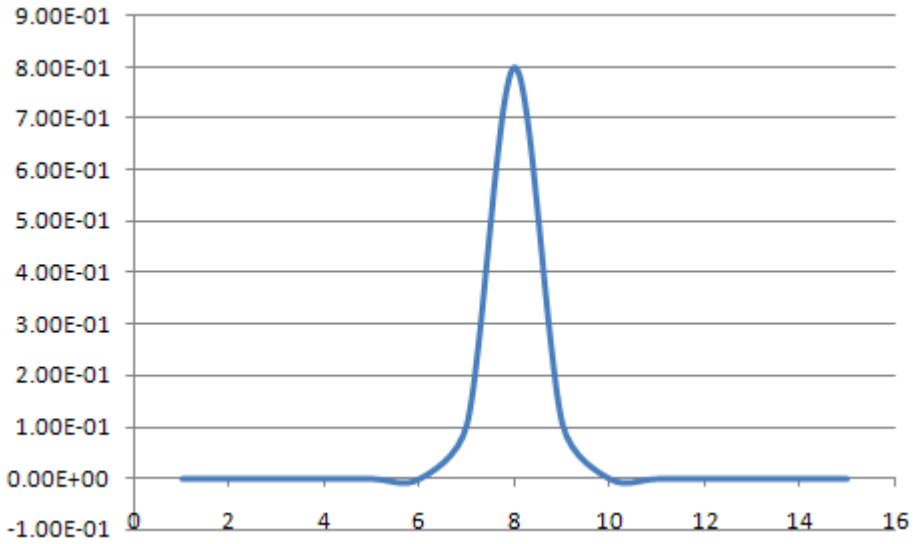

Figure 3.1: odor processing

The horizontal number stands for the RC, and the corresponding value received by RC is shown on the left.

The output of project is the activity of 15 projection neurons and the VUMmx which is an integrated interneuron. The time interval between twice stimulation is 10ms, which is identical to the time delay.

3.2 module design

The general flow chart is shown as Figure 3.2.

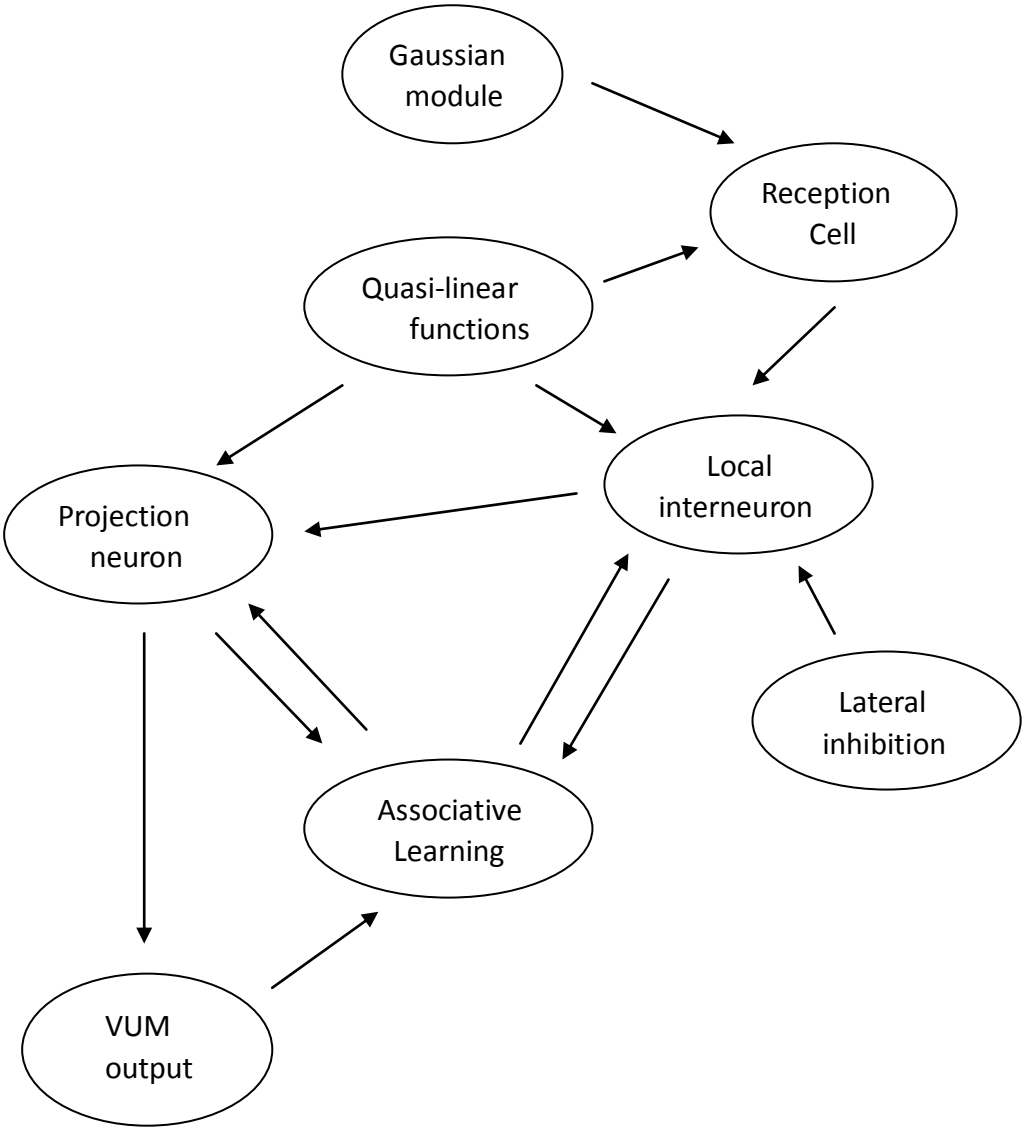

Figure 3.2: the model system

3.2.1 Gaussian Module

The Gaussian distribution formula is as below:

$$f(x)=\frac{1}{\sqrt{2\pi\sigma^2}}e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

Because each kind of RC receives different continuous values if stimulated by

different odorant, the mean of Gaussian function is taken between 1 and 15. σ is regarded as the open parameter and the value is adjusted from 0 to 1.

3.2.2 The quasi-linear function

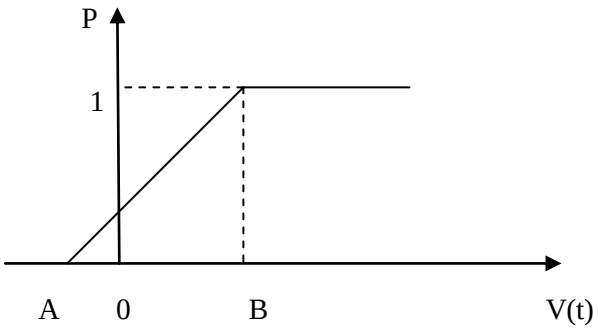

Figure 3.3: non-linear threshold function

The vertical value stands for the firing probability, the horizontal value is the membrane potential.

In the program, the values of A and B are entitled below:

	RC	LN	PN
A	-0.1	-0.2	-0.05
B	1.0	0.5	0.1

Table 3.1: threshold values

3.2.3 Reception Cell

There are 15 RC arranged in a ring, each of them receives the continuous value from odor stimulation. When the accumulation reaches on or over the minimal threshold of the quasi-linear function, the activated signal will be probably produced and passed to LN(local interneuron). The greater the membrane potential is, the more probability for RC to make the firing signals. When the membrane potential reaches the maximal threshold, the values stored in the RC will be cleared and the membrane potential will be reset.

For the single odorant from binary mixtures has different stimulation to different RC, so the relative distance between the two RCs who have most sensitivity to two odorants respectively may have the important effect on the cognitive behaviors. So the distance is considered as an essential overlapping parameter. If A stands for the RC having maximal sensitivity to one odor from binary mixture and B stands for another one, the distance is set as below:

The cells between A and B	0	1	2	3	4	5	6	7
The distance in overlap	1.0	0.875	0.75	0.625	0.5	0.375	0.25	0.125

Table 3.2: the overlapping degree

3.2.4 Local Interneuron

There are 15 kinds of LN and each receive signals from RC, at the same time, they receive the inhibit signals produced 10ms ago from the neighboring LNs in the form of negative figures and the membrane potential from the VUM neuron. The sum potential will be computed in local interneuron and decided whether firing or not by quasi-linear function. Every local neuron can input their activated signal to neighboring 3 LNs on each side. The algorithm is as below:

$$i_j(t)=W_1*R_j(t)+W_2*I_i(t-d)+W_{vum}*V(t)$$

where W_1 is the connection strength between RC and LN, W_2 is the connection strength between LN and neighbors and W_{vum} is the modifiable connection strength of the VUM branch. d is 10ms.

3.2.5 Projection Neuron

Projection neuron receives the inhibition signal from the local interneuron and fires when the membrane potential reaches the corresponding threshold. The formula is shown below:

$$X=W*I(t-d)$$

Where X is the membrane potential in PN, W is the connection strength between LN and PN.

PN also outputs the signal to the VUM branch which connects with it. It will be introduced later.

3.2.6 Lateral inhibition

Lateral inhibition has already been found in animals' olfactory bulbs. It is demonstrated by Galizia and Menzel that not only the direct neighbor can impose the inhibition, but also some indirect ones can produce this activity. The reasons are that the antennal lobe is like a ring, surrounded by all glomeruli. LN's neurites travel more likely to the central neuropil instead of the neighbors[why honey bee]. Secondly, Not all of glomeruli with quite similar response features are direct neighbours[29]. Here, one LN can impose 3 neighbors on the each side, both directly and indirectly. However, the connect strengths are different according to the distance. For the direct neighbor, the connect strength is -0.2, and -0.1 for the indirect ones.

3.2.7 The relationship of RC, LN and PN

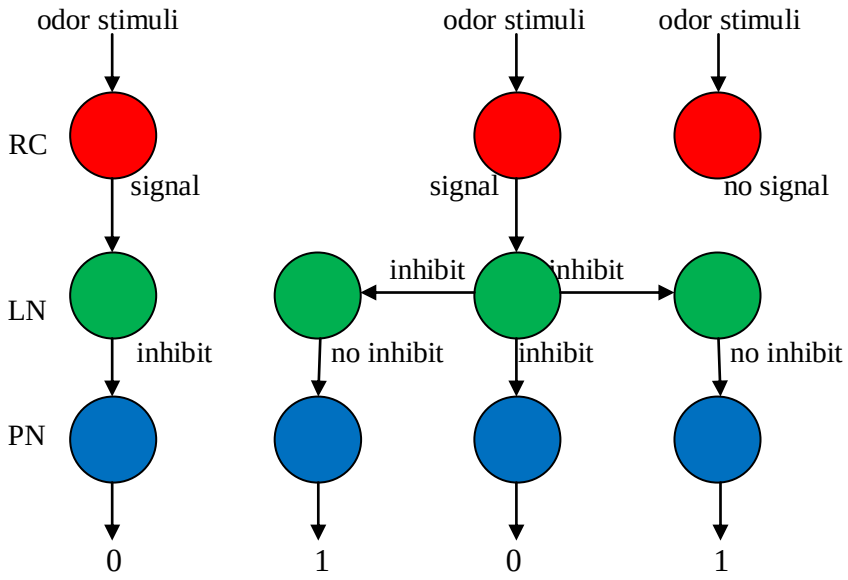

Figure 3.4 : the relationship between RC, LN and PN

It needs to know that the output of PN is uncertain. The diagram above just shows the maximal probable output of PN.

3.2.8 Associative Learning

Associative learning is used both in LN and PN modules during the training time. Synapse VUM is utilized to output the signals which is controlled by a non-linear function with the input of the total membrane potential. At this time, if PN or LN in this glomeruli also spikes, the feedback will strengthen the synaptic weight between VUM and the PN or LN. The diagram below describes this kind of activity.

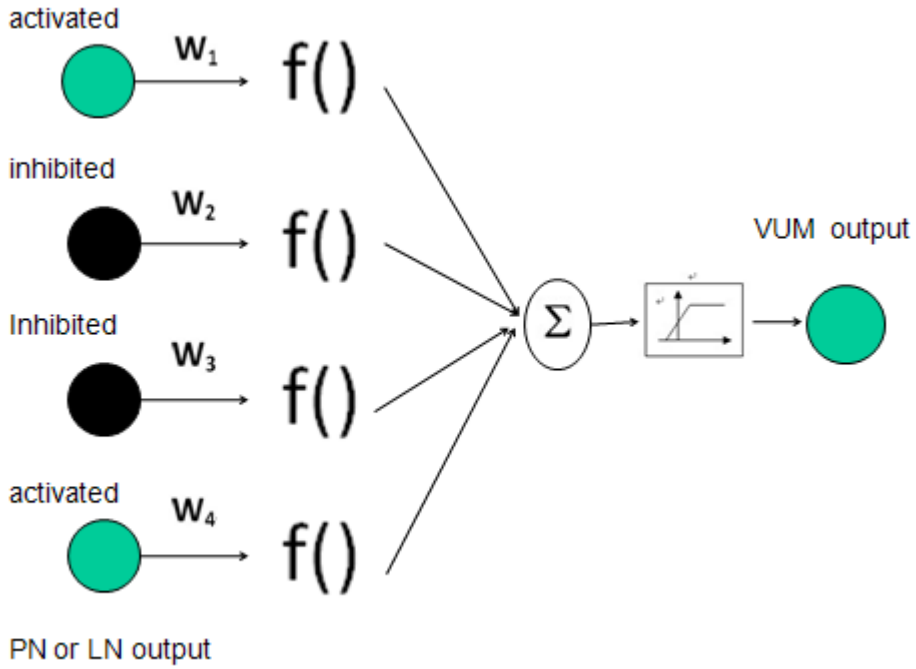

Figure 3.5: Hebbian Learning in associative learning

From the chart, it is clear that if the input and output are both firing sequentially, the connection weight between them is increased, or it is unchanged. The formula is demonstrated:

$$W_{ij}(t+1)=\begin{cases} W_{ij}(t)+r_{ij} & \text{if } O_i(t)=1 \text{ and } O_j(t)=1 \\ W_{ij}(t) & \text{othewise} \end{cases}$$

Where r_{ij} is the learning rate and the value is 0.5, $O_i(t)$ is the output of PN or LN and $O_j(t)$ is the output of VUM.

There are two kinds of learning methods that are applied in the program. One is that only the weight between PN and VUM is modifiable. In the other one, not only the weight between PN and VUM, but also the weight between LN and VUM is involved.

3.2.9 VUM output

First, the membrane potential in each glomeruli is computed first, the value is changed according to the time. The algorithm during training time is described below:

$$V_i(t)=W_i^{PN} O_i(t) + S(t) - \tau\frac{d_v}{dt}$$

Where W is the modifiable strength between PN and VUM, $O_i(t)$ is the output of PN at time t, S(t) is the external input and the value is 0.5. τ is the time constant.
Then at the time t, the output of VUM is computed in next formula:

$$O(t)=f(\sum_{0}^{14} V_i(t))$$

3.3 GUI Design

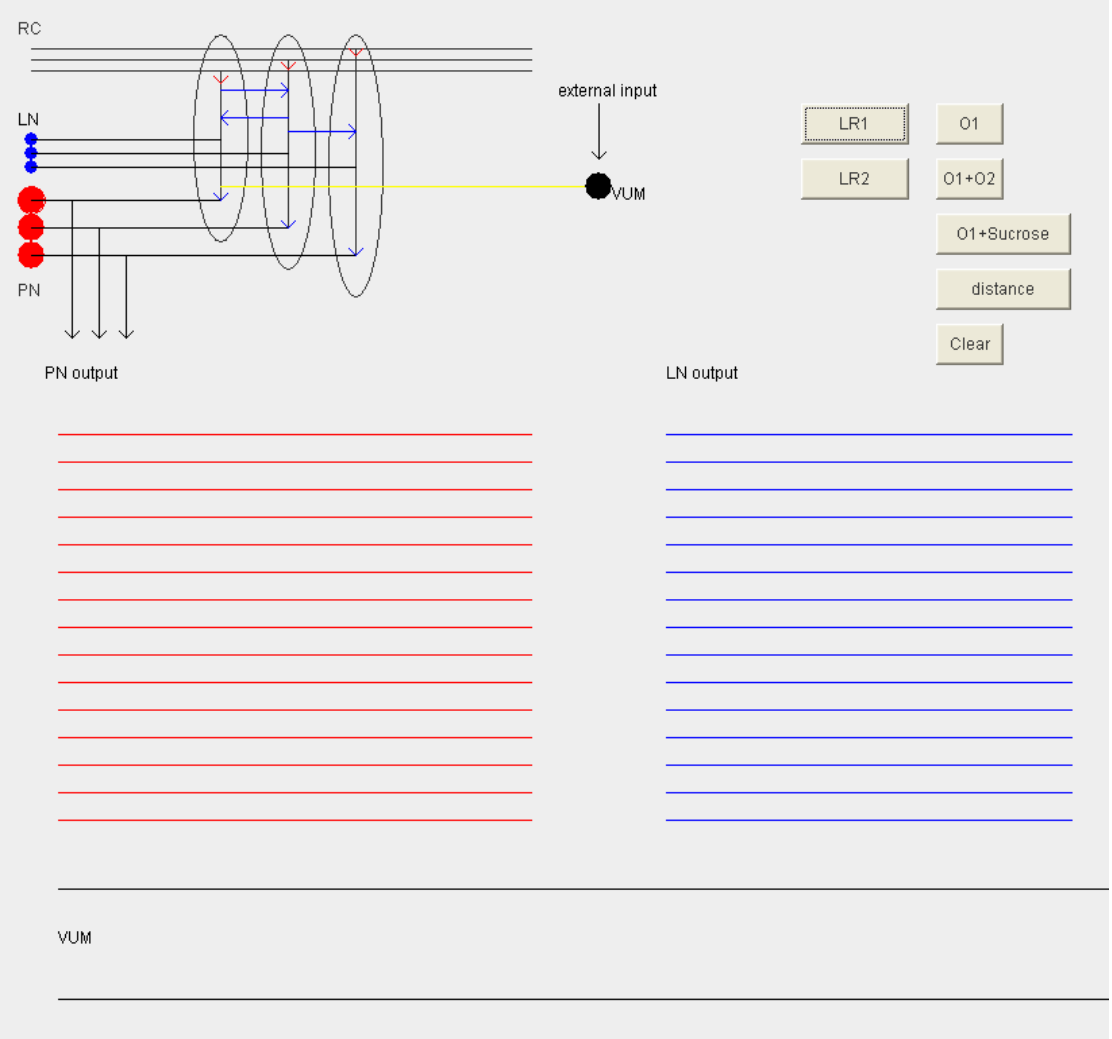

Figure 3.6: program GUI

On the upper-left corner is the general model architecture proposed by Linsgter and Smith. Some function buttons will be explained below:

LR1 and LR2 are different learning rules that different synapses are submitted to Hebbian Learning.

O1 performs the function of pure odor stimulation. The LN and PN output will be displayed in the middle part of the GUI.

O1+O2 performs the function of binary odor mixture stimulation.

O1+Sucrose adds the function of associative learning. The output will be

displayed on the bottom two lines. For example:

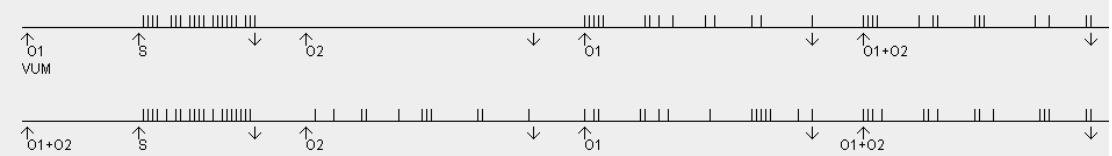

Figure 3.7: the output sample

It shows the response of VUM neuron. Arrows stand for stimulus onset and offset. The horizontal axis represents the time. The time interval is 10 ms. The stimulation of pure odorant O1, O2 and mixtures O1+O2 lasts for 500 ms. The stimulation of S(sucrose) lasts for 250 ms.

The first line shows during a control simulation, O1 is paired with sucrose, and then during the test stage, the response to the components of O2, O1 and the mixtures respectively.

The second line shows during the training time, the mixtures are paired with sucrose from 250ms to 500ms, and next is the response to the components of O2, O1 and the mixtures respectively.

The button “distance” adjusts the overlapping parameter, the diagram below shows the changeable values:

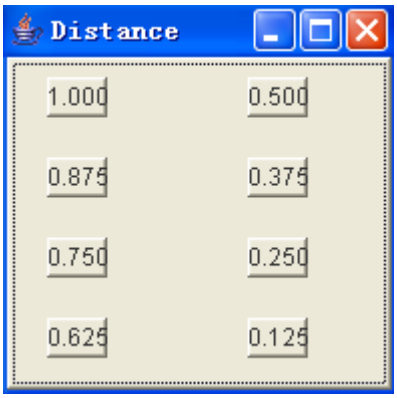

Figure 3.8: the overlapping degree

In the middle part, 15 blue lines corresponding to the output of 15 local interneurons during the 500ms training time. And 15 red lines displayed the outputs of the projection neurons.

For each LN on the right side, there is a corresponding PN output on the left side. For instance, when adopting the LR1, the distance is 0.875, the responses of LNs and the corresponding PNs are shown below:

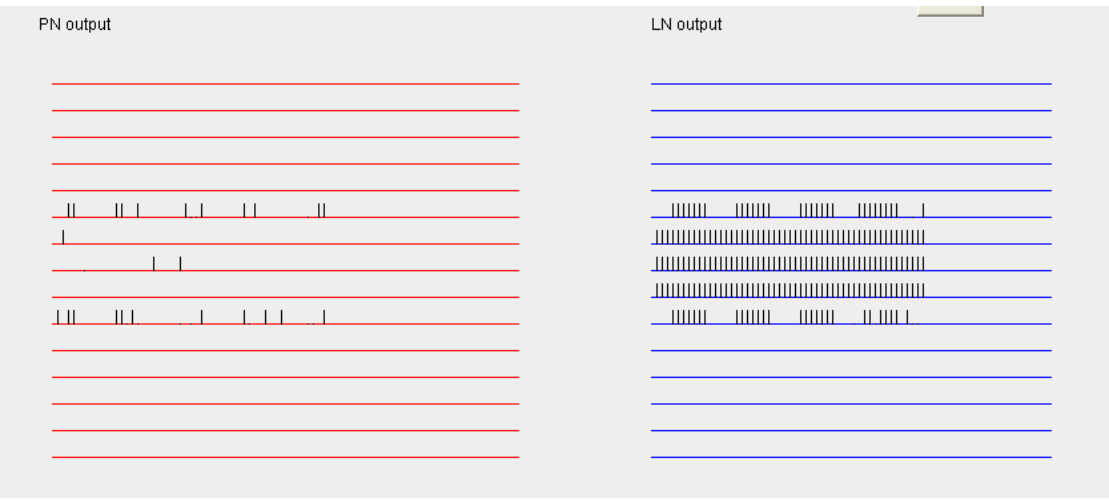

Figure 3.9: the relationship between LNs and PNs

4 Experiments and Results

4.1 LN, PN and lateral inhibition

When O1 is involved in the training stage as the conditioned stimulus, the No.8 RC has the maximal sensitivity to the odorant, because of the Gaussian distribution with the No.8 RC is regarded as the distribution center, its neighbors have different sensitivity to it. The outputs of 15 LNs within 500ms are displayed below:

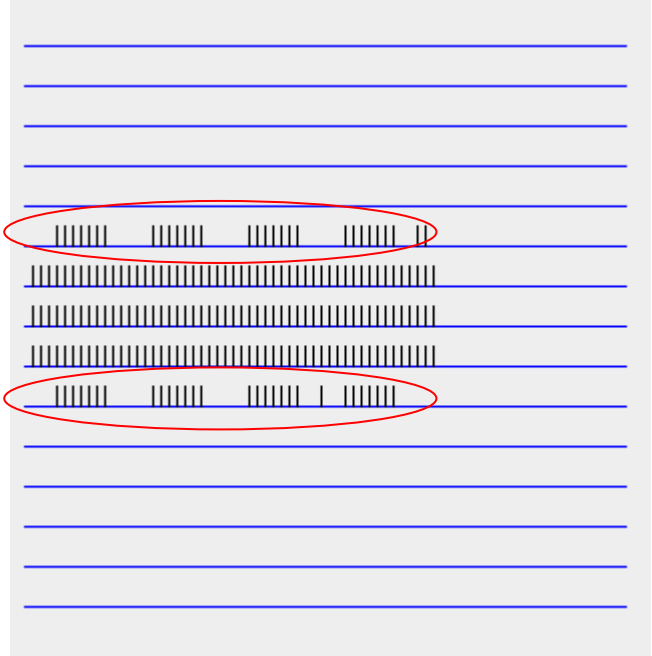

Figure 4.1 LN output sample

It is known that three local interneurons have continuous strong firing rates throughout the whole process. For the neurons on two sides whose responses are not so strong, they are affected by their neighbors' inhibit signals.

For the corresponding projection neurons, the outputs are displayed in Figure 4.2.
For the two projection neurons in the glomeruli in where the local interneurons are circled by red lines, they have more firing frequencies. This is because that the LNs inhibited by the neighbors do not impose the inhibition on the connected PNs. By comparison, the No.8 projection neuron is completely inhibited.

When these projection neurons are associated with VUM, the synaptic changes will be always added on the weights involved in the circled PNs.

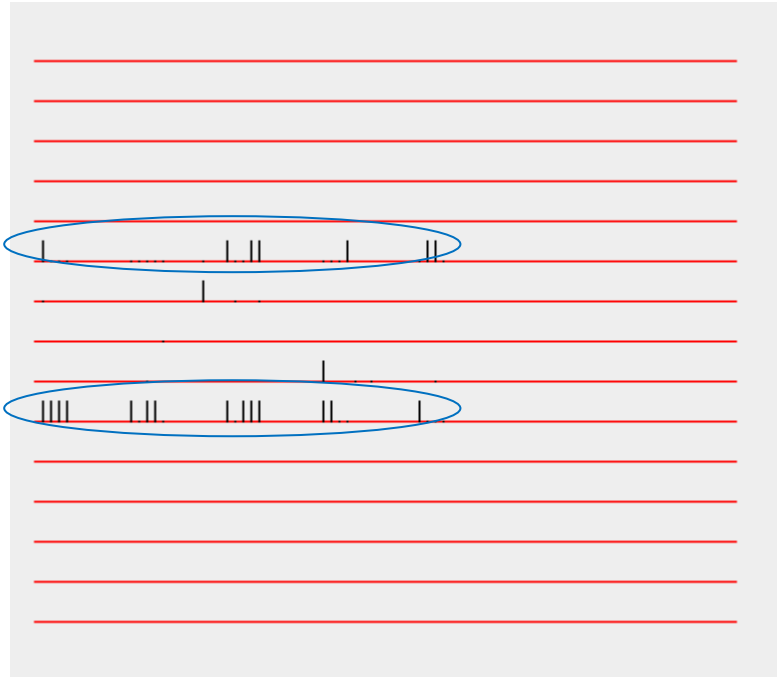

Figure 4.2: PN output sample

When it comes to the binary mixture stimulation, the process is a little more complex. When the overlapping parameter is 0.125, the output of PNs is shown in Figure:

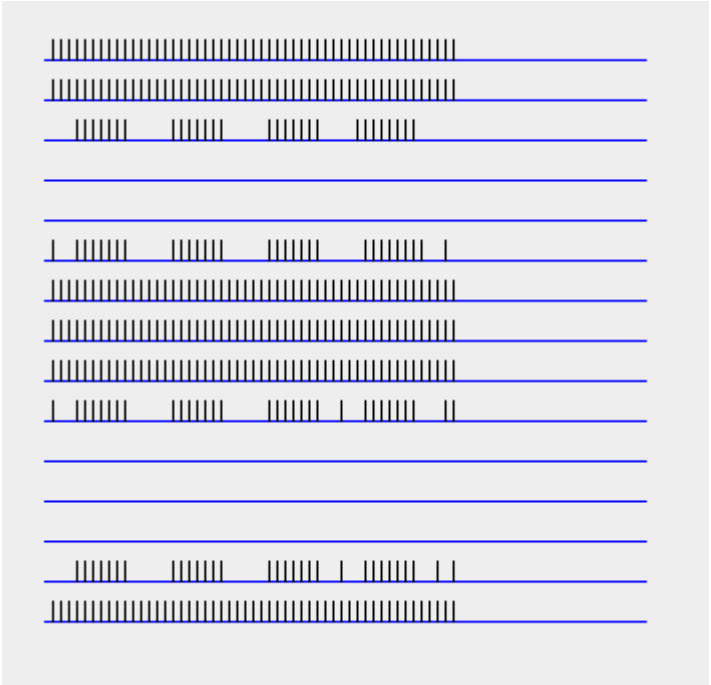

Figure 4.3 PN output sample

For the distance of two reception cells which are most sensitive to two odorants respectively is very far, there is seldom interruption for the single LN's odor processing.

However, for the overlapping parameter is 0.375, some LNs are disturbed by the neighbors, and the output computed by program is as below:

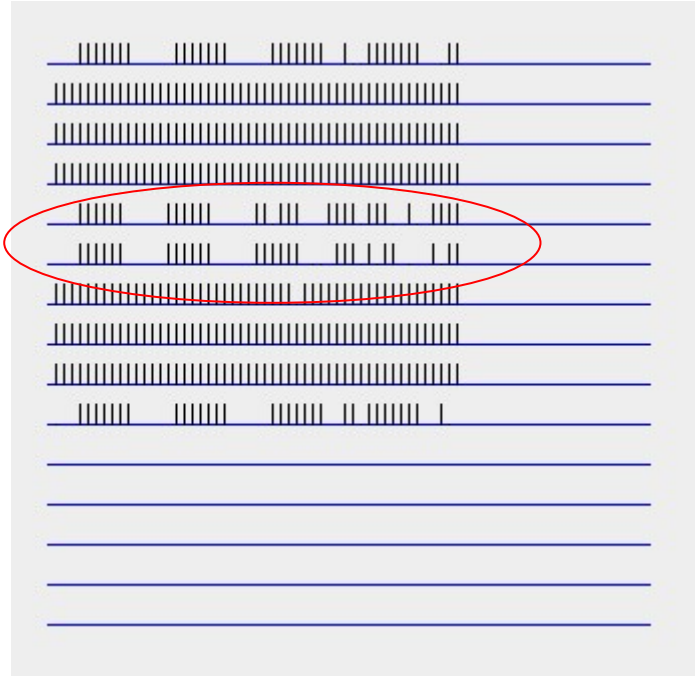

Figure 4.4: PN output sample

It can be seen that some local interneurons are disturbed by their neighbors, the output of these LNs is different from that stimulated by the pure odorant. The more firing rates are increased and shown in below PNs.

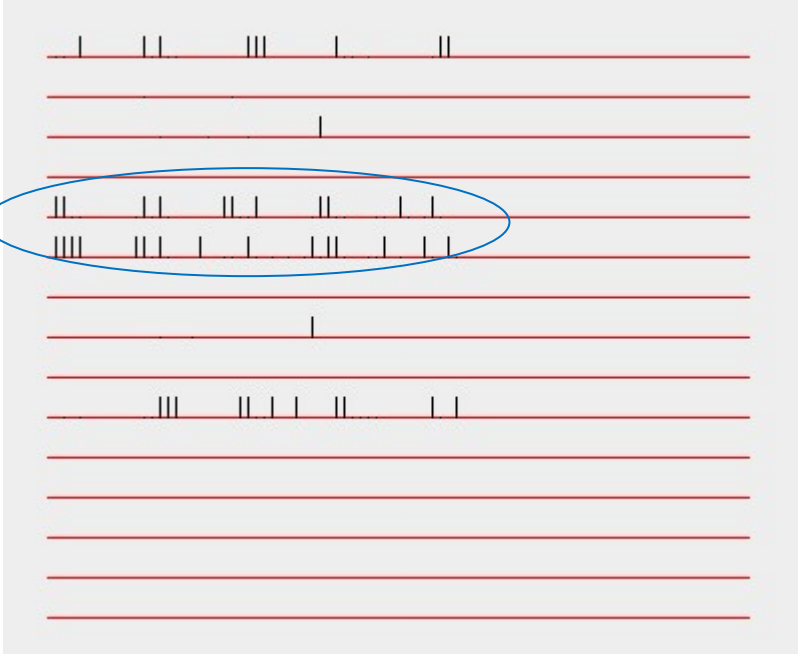

Figure 4.5: LN output sample

4.2 Learning

The basic function of the model is that it can differentiate the odorants by a kind of learning ability.
Figure presents that VUM doesn't change its spiking frequency responding to O1, O2 and the mixture without learning.

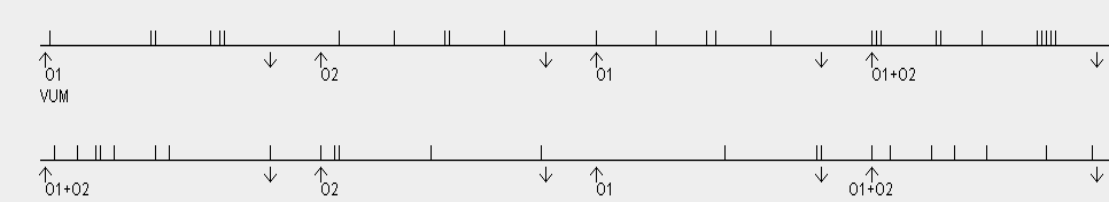

Figure 4.6: the response of VUM without learning

Ii is clear that the VUM neuron makes the similar response to O1, O2 and the mixture, it is difficult for VUM to apart one component from the other by the response no matter whether the pure odorant or the mixture is used in the training stage.
However, when the learning is involved in the training phase, the change can be seen below:

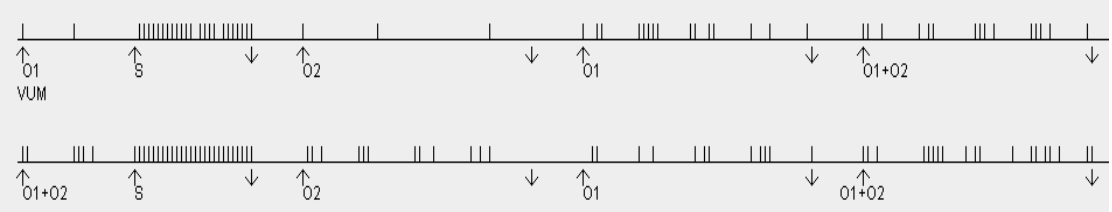

Figure 4.7: the response of VUM with learning

When the sucrose is introduced 250ms after the start of odorant stimulation in the training stage, the VUM has intensive response to the conditioned stimulus. It is clear that when O1 is paired with sucrose, VUM increases the spiking frequency to O1 and the mixture(contains O1), but does not change the firing frequency to O2. When the mixture(O1 and O2) is adopted as the conditioned stimulus, the firing rates are increased in O1, O2 and the mixture.

Learning leads to the change of certain connection weights associated with some PNs and LNs. However, it is uncertain about the initialized weight value and the relevant learning rate. In the experiment, the initialized value is set to 0.25 and the learning rate is set to 0.8.

When adopting LR1 and pure odor stimulation, the connection weights of all glomeruli after learning are shown below:

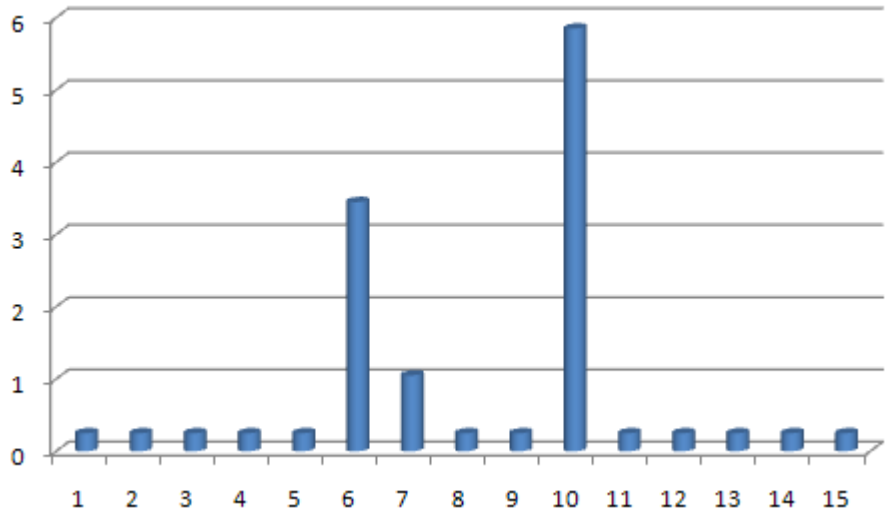

Figure 4.8: the change of synaptic weights

When adopting LR2, the graph is described as:

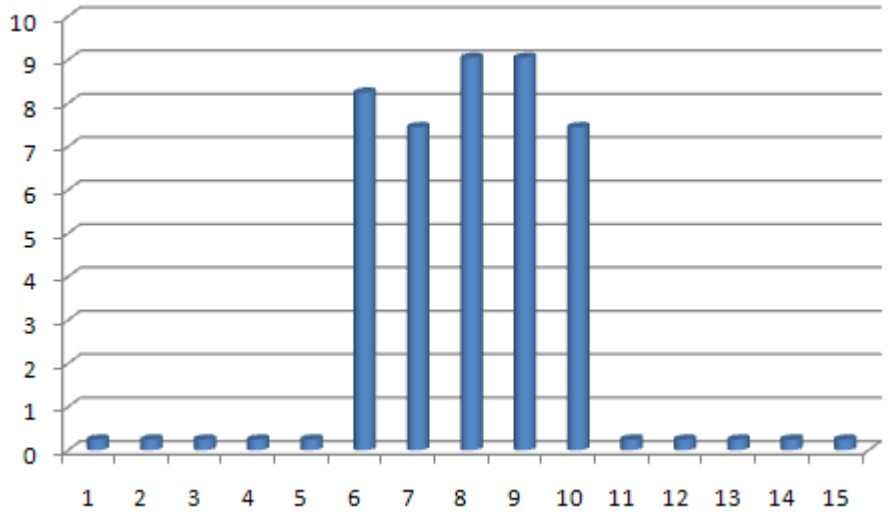

Figure 4.9: the change of synaptic weights

The bar chart below shows the average response of VUM to O1, O2 without being paired with sucrose.

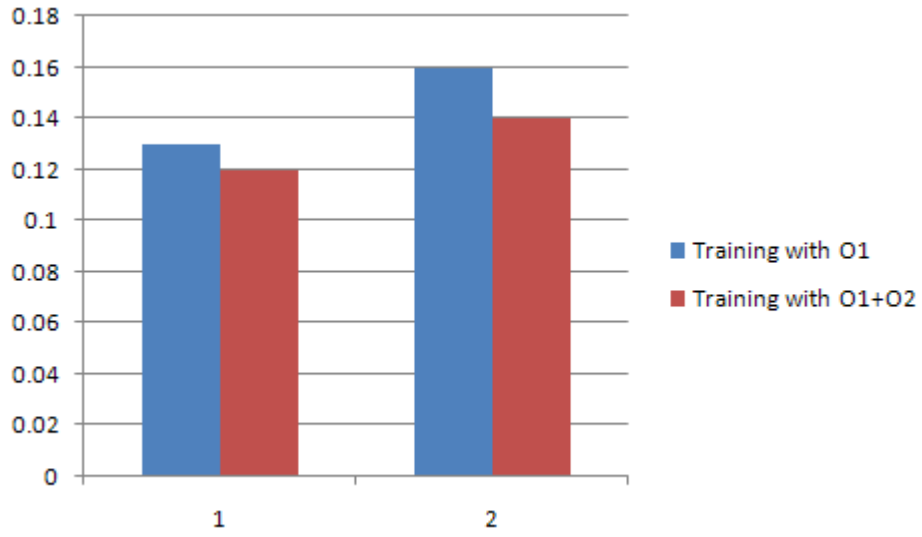

Figure 4.10: the response of VUM without learning

1 stands for the response of the VUM neuron to O1 in the test stage. And 2 presents the response to O2. It shows the similar responses to components in the binary mixture.

Then after the training with sucrose, the data of response of VUM is recorded as below:

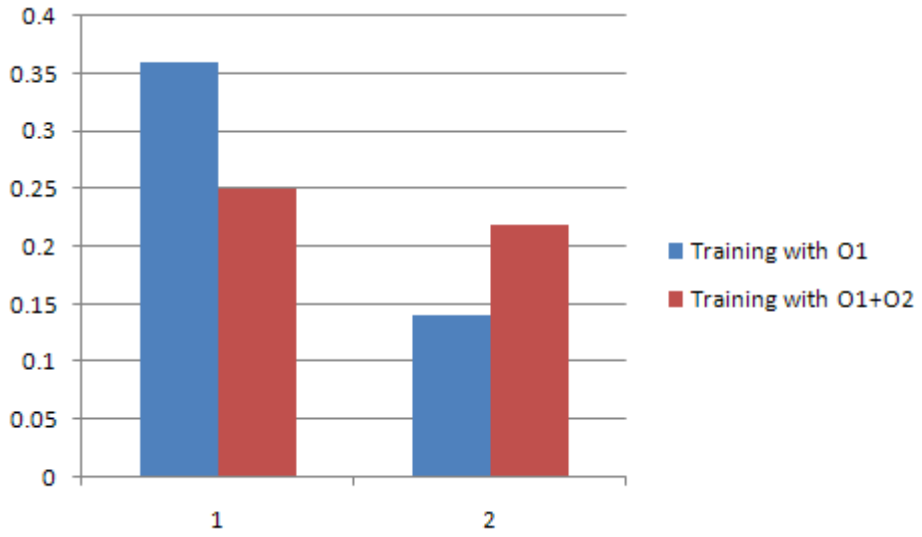

Figure 4.11: the response of VUM with learning

It is clear that the average response (0.36) to O1 after learning with O1 is much higher than that to O2 (0.14). And the response to O1 (0.25) after VUM was trained with the mixture is similar with that to O2 (0.23).

4.3 Generalization

The basic method to analyze the generalization is to compute the activity of the VUM neuron. The response of VUM to the conditioned stimulus and unlearned stimulus are gained and computed. When the response to the unconditioned stimulus is above the threshold, the phenomenon of generalization is found.
When adopting learning rule 1, the ratio of the response to unconditioned stimulus over the response to learned one is computed 5 times for each kind of the binary mixture and shown below:

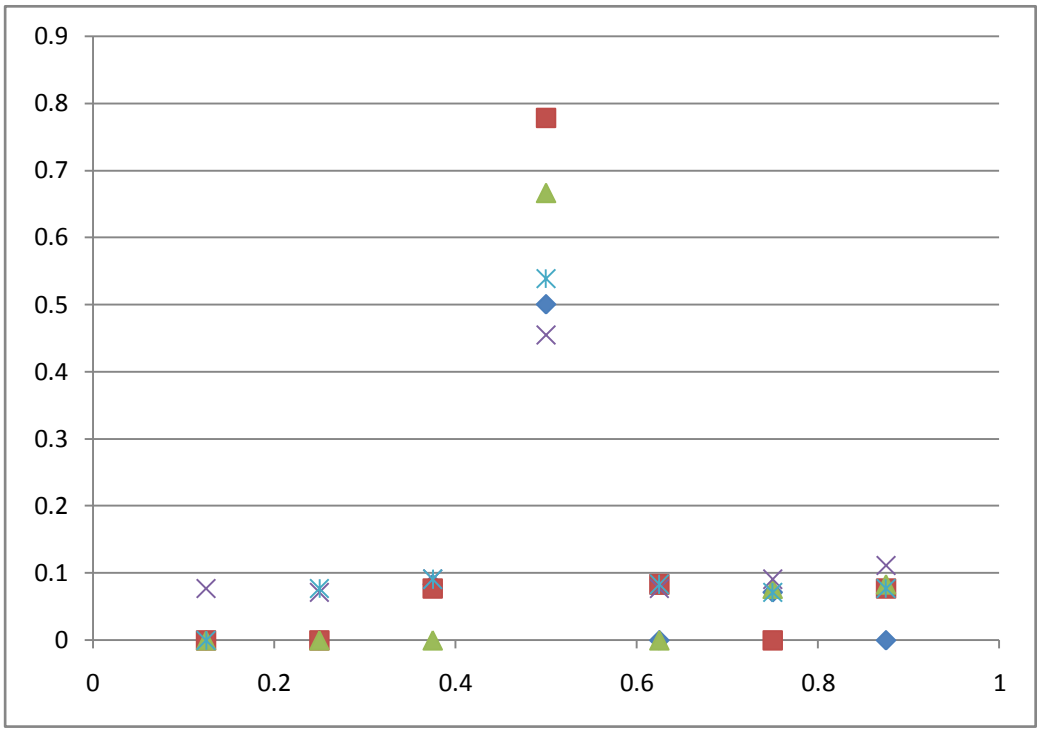

Figure 4.12: Generalization in LR1

In the figure above, the horizontal axis presents the degree of overlap and the vertical axis stands for the ratio, which is computed by the firing numbers of VUM to the unconditioned odor divided by the numbers to the learned one.

Generalization occurs when the ratio is above 0. When the overlapping degree is 0.5, the model has strong generalization, this happens just when the stimulation by unlearned odor to the glomeruli are outside the radius of conditioned odorant stimulation. The described figure is shown:

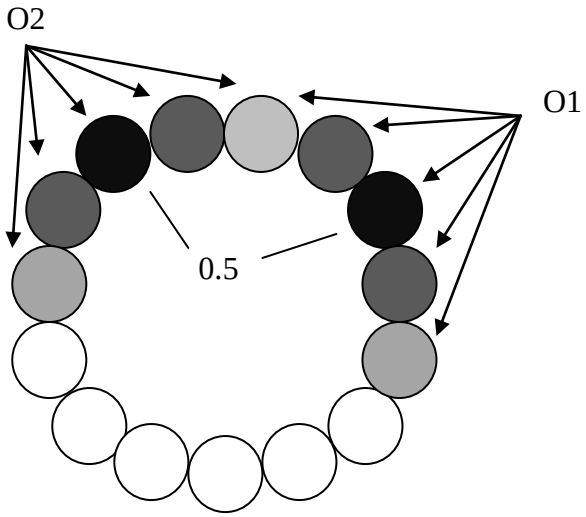

Figure 4.13 : the overlapping

By contrast, the weak generalization occurs for other circumstances. As normal, the strong generalization should occur when the degree of overlap is above 0.5, however, the lateral inhibition impose this type of signals to the neighbors which suppresses the strong generalization and make it weak or distinguish. But in general, the ratio is bigger with the increase of the degree of overlap (except 0.5).

When it comes to LR2, the data is recorded below:

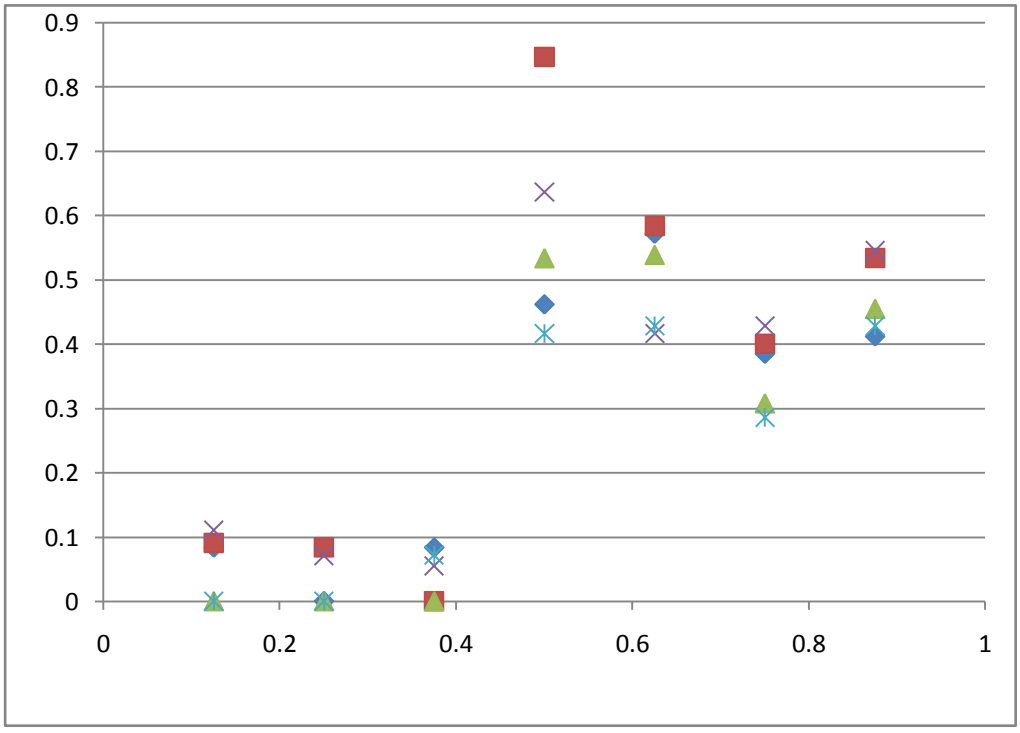

Figure 4.14: Generalization in LR2

Different from LR1, when the overlapping degree is above 0.5, the results are higher than previous ones. It seems that the effect of lateral inhibition is not as strong as LR2. LR1 only trains the connection weights involved in the activity of PNs which are sensitive to the conditioned odorant, however, certain connection weights are also

trained in LR2 where some relevant PNs are associated with the unlearned odorant. So the lateral inhibition fails to completely restrict these PNs activity.

This is different with the model of Linster et al[1]. In their model, when adopting LR2, the similar pattern is found compared with LR2.

In their data graph[1] below, Generalization is always weak except when the overlapping degree is 0.5. When the degree is 0.125, 0.25, 0.625 or 0.75, generalization is restricted within 0.1 or so, and less than 0.4 for generalization when the degree is 0.375 or 0.875. However, compared with their data, generalization is stronger when the degree is 0.625 or 0.75, which is around 0.3~0.6, and this difference is caused by the training of the connection weights involved in PNs which have been analyzed before.

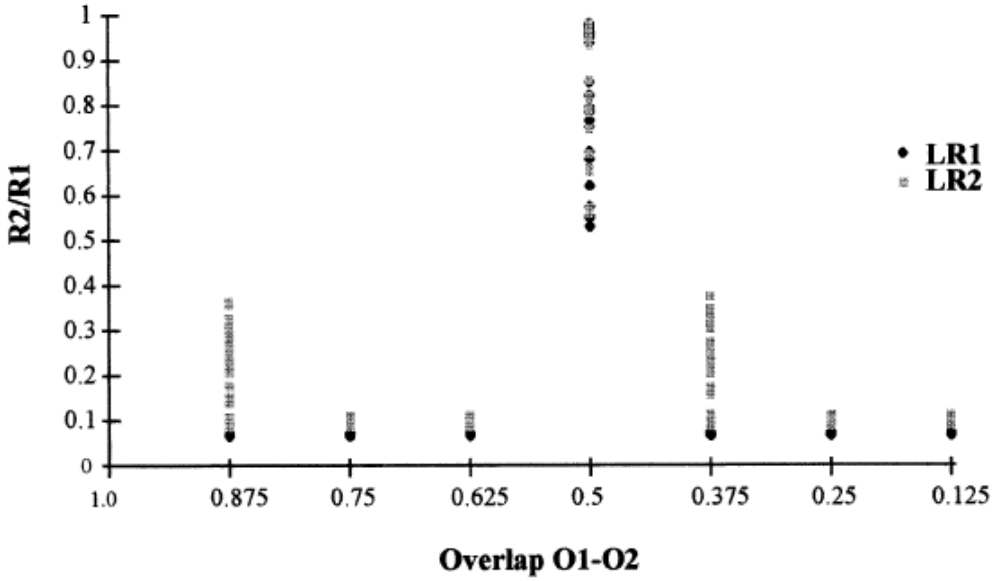

Figure 4.15: Linster et al's data distribution adopted from [1]

4.4 Overshadowing

In this part of experiment, the phenomenon of overshadowing is identified. It happens when the response of VUM to an odor A in the testing stage after that odorant A training is stronger than the response to A after the mixture (including A) training.
When using LR1, the overlapping degree is set to 0.75, the responses of VUM after pure odorant training and after the mixture training are shown separately:

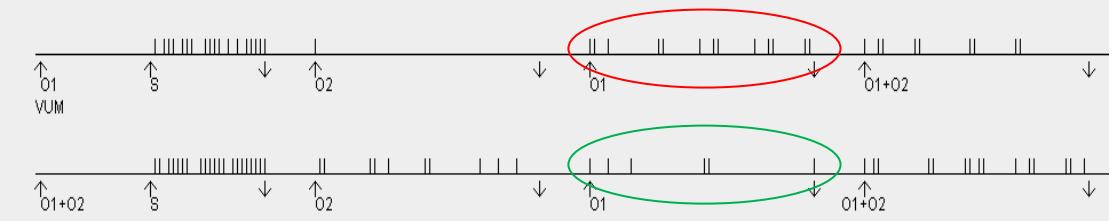

Figure 4.16: the VUM output sample

In testing stage, each stimuli lasts for 500ms. The firing times during 500ms for pure odorant training are 13. By contrast, the spiking times for mixture training are 6. This is identified biological cognitive behavior.

Next, each combination is tested and the data is recorded and displayed below:

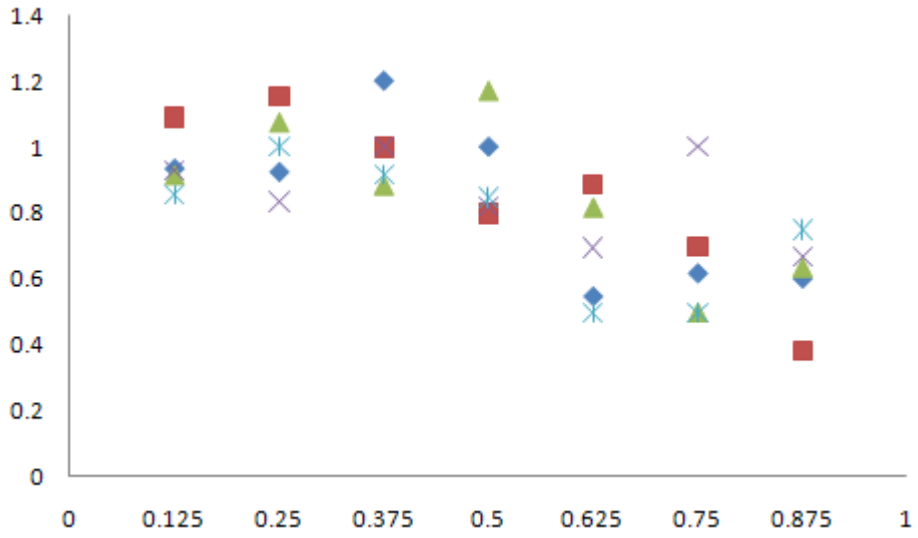

Figure 4.17: Overshadowing in LR1

The horizontal axis stands for the overlapping degree, the vertical axis represents the ratio for the firing times of response to mixture divided by those to pure odorant.

For each combination of the mixture, the ratio is computed 5 times. The overshadowing occurs when the value is below 1. It is known that for each combination, overshadowing occurs to different extent.

In general, overshadowing becomes stronger with the increase of the overlapping degree. When the two components are far away from each other, for example 0.125, the weak phenomenon is found and the ratio is around 0.9. The similar phenomenon is also found when the degree is within 0.25~0.5. Then, strong overshadowing begins from 0.625. Except one sample in 0.75 has no overshadowing, it lies in all other samples within 0.625~0.875. The strongest overshadowing is found in 0.875 and the value is around 0.4.

Because the overlapping degree decides the extent of the interaction among the LNs,

the large degree demonstrates the strong interaction among the LNs. This kind of interaction lies in LNs activity is regarded as lateral inhibition. Because the range of lateral inhibition is within 0.625~0.875, when the degree is out of the lateral inhibition region, overshadowing is weakened sharply.

LR2 is also applied and the data is recorded below, the sample distribution is similar like LR1 but a little different.

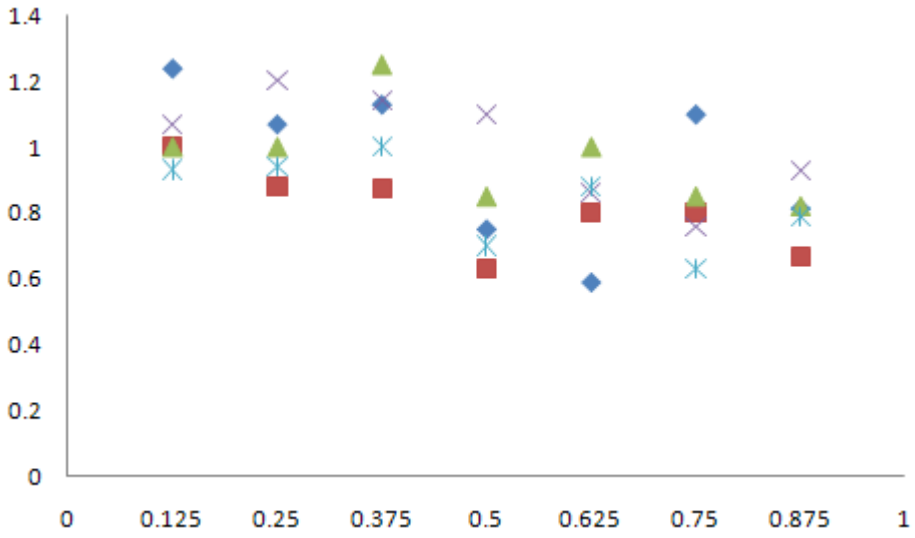

Figure 4.18: Overshadowing in LR2

Just like LR1, the data of LR2 presents the similar trend. However, the strongest overshadowing occurs when the overlapping degree is 0.625 instead of 0.875. And when the degree is over 0.5, some samples still fails to produce overshadowing.

When the lateral inhibition is imposed, the ratio is ranged from around 0.6 to around 0.9. It is generally bigger than values when using LR1. It is possible that the effect of lateral inhibition is weakened by some LNs' strong activity, which is caused by some connection weights associated with learning of unconditioned odorant.

Compared with Linster et al's overshadowing experiment, it is similar that the overshadowing occurs clearly when the degree is bigger than 0.5.

However, their data shows that when the degree is below 0.5 (including 0.5), overshadowing seldom happens and the ratios are all near 1.0, which means the response to the very odorant after pure training is almost equal to that after mixture training. In my experiment, the range of the ratio for the degree within 0.125~0.5 is larger, which is caused by the different time constant and variance of Gaussians. Their experiment data graph is shown below[1]:

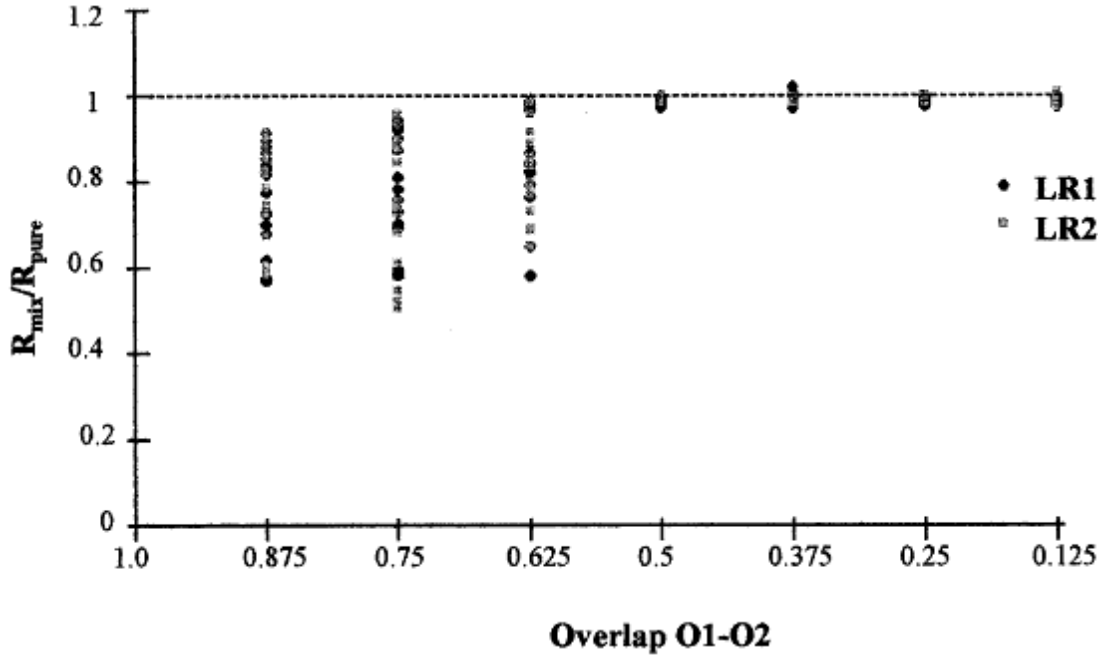

Figure 4.19: Linster et al's data distribution adopted from [1]

4.5 time constant

According to section 2.5, the integrate-and-fire model is expressed below:

$$\tau\frac{dV_m(t)}{dt}+V_m(t)=R_mI_{in}(t)=e(t)$$

Where τ is the membrane time constant, it is open parameter and part of research in the experiment.

In reception cell, the Gaussian distribution is applied and the membrane potential is fluctuated in line with $N(0, \tau)$.

$$V(t)=e(t)+N(0, \tau)$$

If $e(t)<0$, then set $e(t)=0$.

And the variance of membrane potential $V'(t)$ is expressed below:

$$V'(t)=\frac{1}{\sqrt{2\pi\tau^2}}\exp(-\frac{t^2}{2\tau^2})$$

Then the total potential is like this

$$V(t)=e(t)+\frac{1}{\sqrt{2\pi\tau^2}}\exp(-\frac{t^2}{2\tau^2})$$

The graph below compares the variance of membrane potential with the different time constant.

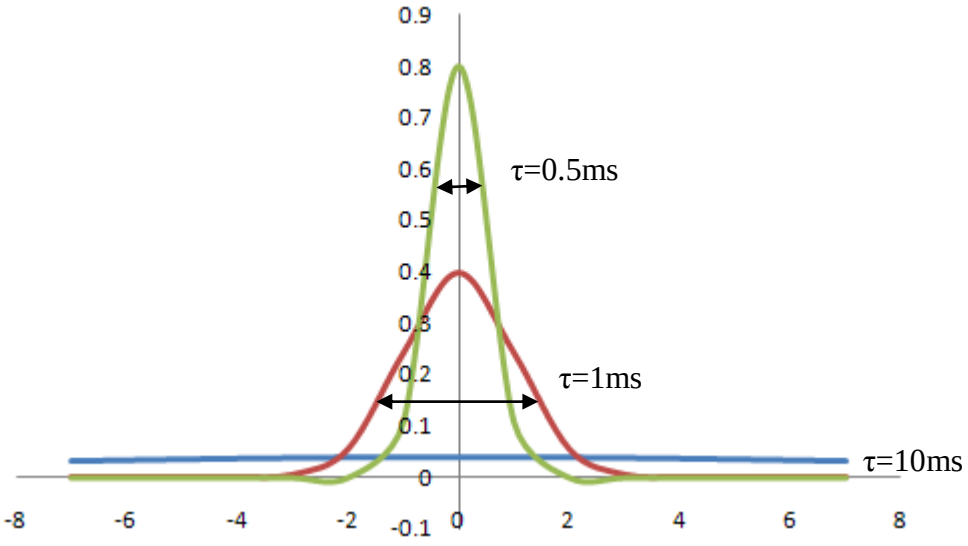

Figure 4.20: time constant with Gaussian distribution

It is interesting to invest the relationship between time constant and the lateral inhibition. Because the lateral inhibition imposes great effect on a series of cognitive behaviors, the research on time constant and the lateral inhibition could disclose some connections between cognitive behaviors and time constant.

In the experiment, the time constant value is set to 0.5ms, 1ms, 10ms respectively. The outputs of 15 LNs are different. When τ=0.5ms, adopting LR1, the response after pure odorant stimulation during 500ms epoch is like below:

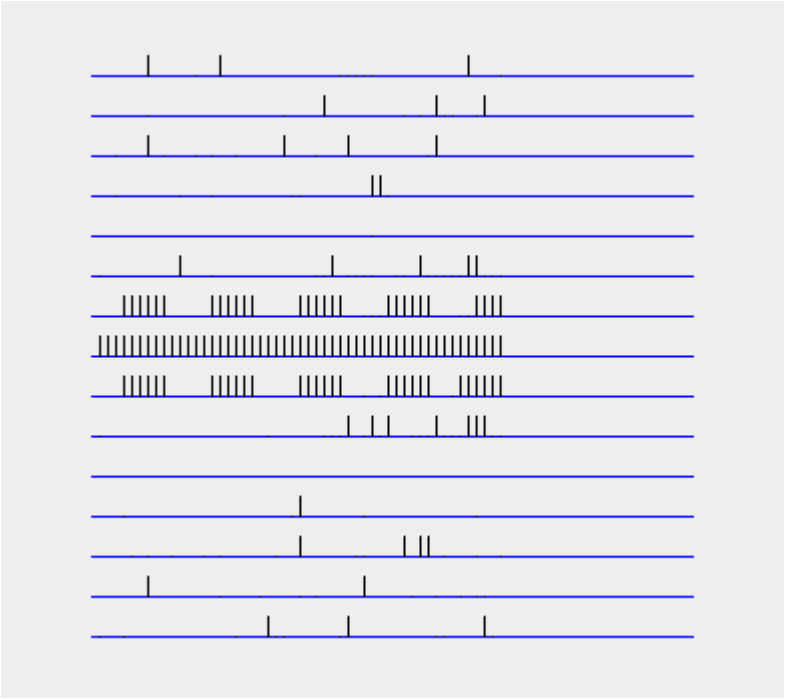

Figure 4.21: the output of LNs when τ=0.5ms

Compared with Figure, when the time constant is set to 1ms, the neighbor neurons sensitive to the trained odorant will increase their firing rates while the central neuron of odor focus decrease the spiking frequency. The relevant graph is shown below:

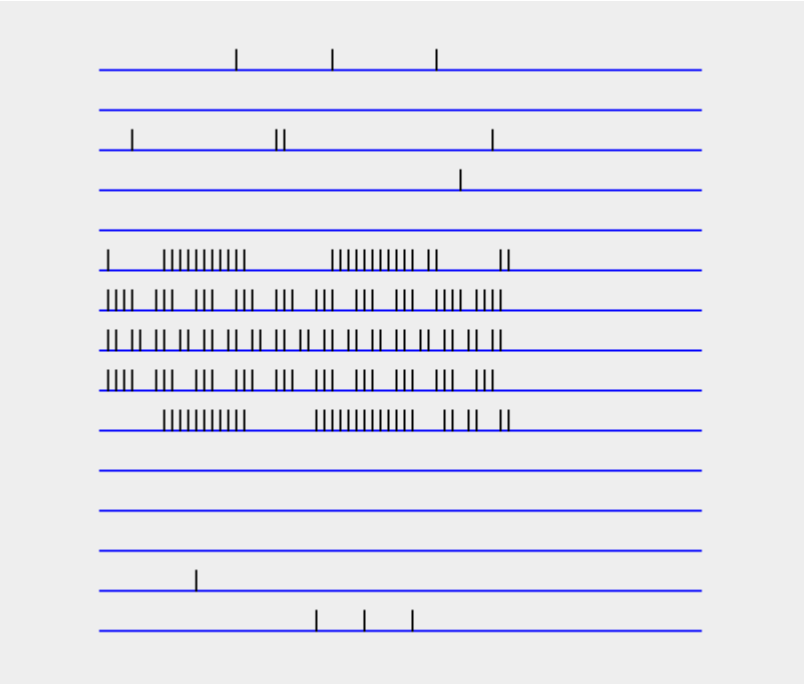

Figure 4.22: the output of LNs when τ=1ms

When it comes to 10ms, it is clear that every PN has the similar firing times during the beginning half time, however, after the break of straight spiking, it is relative late for the neurons on the sides to recover firing from the short break comparing with the central neurons.

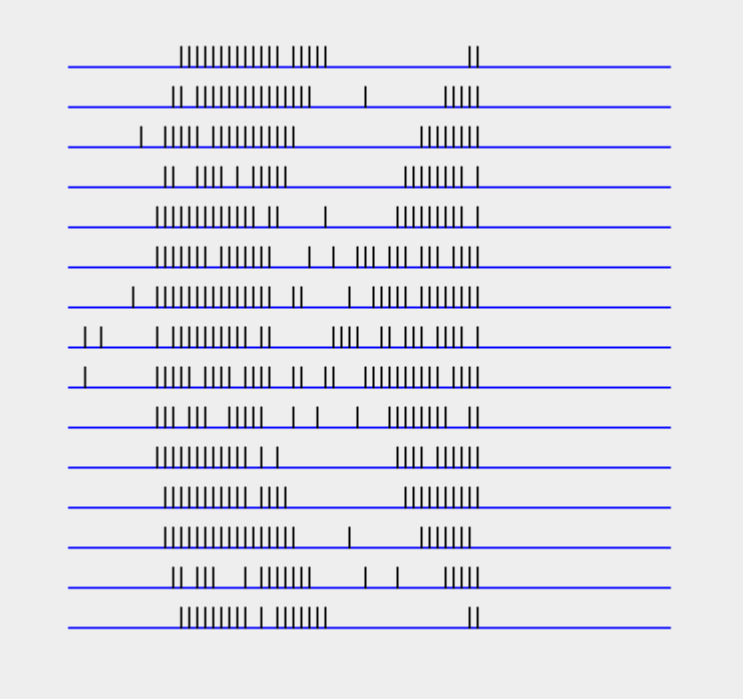

Figure 4.23: the output of LNs when τ=10ms

Next, the study about the relationship among generalization, overlapping degree and

time constant when adopting LR1 is done and the recorded data is on the graph.

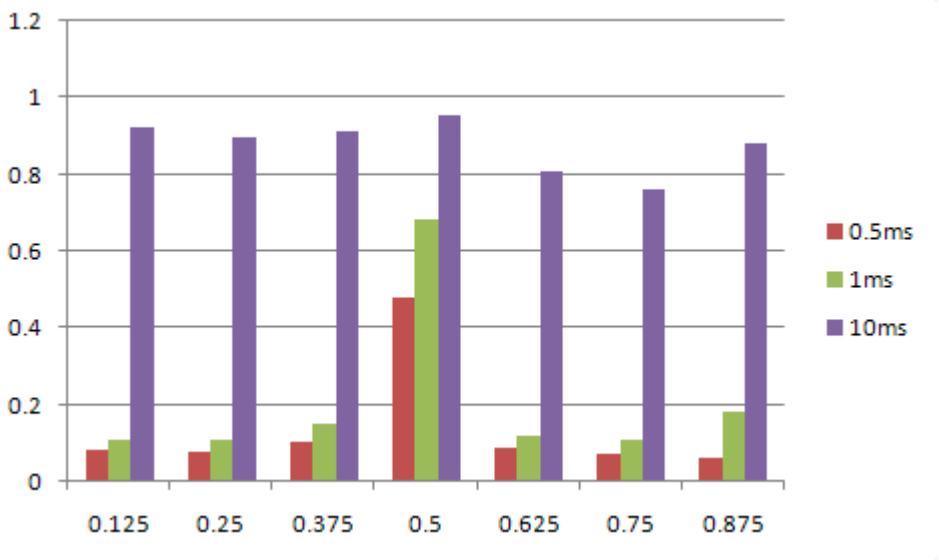

Figure 4.24: time constant, overlapping and generalization

From the diagram, 0.125-0.875 is the overlapping degree of the binary components. The vertical axis stands for the ratio R1/R2, where R1 represents the response to the conditioned odor and R2 is the response to the unlearned odorant. For each circumstance, five values are computed and the average value is taken.

It can be seen that in general, generalization is always high when the time constant is 10ms, and there is little relationship between the degree and the ratio. The ratio of around 0.9 explains that VUM could weakly differentiate the conditioned odor from the unconditioned one.

The similar trends lie in 0.5ms and 1ms. Data is in the range of 0-0.2 except the cases with the degree 0.5. Generalization is a little higher for 0.5ms than that for 1ms. For the overlapping degree which is 0.5, the sample for 1ms is near to 0.7 and almost 0.2 higher than that for 0.5ms.

In the experiment, it is clear that the small time constant contributes to low generalization, the VUM neuron could make more precise judge upon the binary components. And with the increase of time constant, this function is becoming weaker and weaker.

Consequently, there must be a critical point for time constant that the variance of generalization is in relationship with the overlapping degree within this point. When time constant is larger than this critical point, the lateral inhibition also imposes the effect on neurons relevant to unconditioned odor. It means time constant is in line with the effect of the lateral inhibition.
However, it has not been found out yet that what this critical point is, so it is a

question left for the future work to look for this critical point.

4.6 Summary

In this chapter, several experiments are introduced and the results of data are analyzed. These experiments are divided into implement part and research part.

In implement part, generalization and overshadowing phenomenon are introduced and the relationship between phenomenon and the lateral inhibition is identified. The relevant diagrams are analyzed and compared with previous results. Although the similar data distribution and trend are verified, there are some small differences in the range of data. The differences come from two reasons. One is that the values of open parameters such as the synaptic weight, time constant are not fixed and they are adjusted according to the structure of the experimental model. Another is that adopting the Gaussian white noise increases some uncertainty.

In research part, one of the open parameter time constant is researched. From the experiment, the effect of time constant on one of cognitive behaviors generalization is disclosed, the high time constant contributes to the strong response to the untrained odorant. And a critical point is supposed that when time constant is over the point, the lateral inhibition will influent the whole system so that there is seldom relationship between the overlapping degree and the generalization ratio. However, how to identify the critical point is a problem and will be further researched in the future.

5 Future Work

5.1 Improvement of Odor Processing

In the model, the odorant is simulated by the Gaussian distribution, and the spiking probability is line with the uniform random. This is simple and easy to process the binary mixture but does not meet the objective laws. It is more reliable and reasonable to adopt the Christiane and Thomas' method, their algorithm to measure a reception cell firing or not is as below[45]:

$$P(x_i(t)=1)=\sum_{n=1}^{N}\frac{1}{\sigma_i\sqrt{2\pi}}\exp(-\frac{(t-nT)^2}{2\sigma_i^2})$$

The probability of neuron I at time t spikes is expressed as Gaussian function. Where σ_i measures the distance from neuron i to the central neuron of the odor focus, the expression is shown below[45]:

$$\sigma_i = \sigma_{max} + \exp\left(-\frac{d_i^2}{5.0}\right)(\sigma_0 - \sigma_{max})$$

Where σ_0 is the neuron just at the odorant focus.
In the future work, the algorithm will be applied in the model and the performance will be compared with the initial one.

5.2 Open Parameter

It is still uncertain how to decide signal transmission delay and time interval. For convenience, signal transmission delay is identical to time interval in my program which is 10ms. In this way, it is easy to operate the delay data with the change of time. In the future, both factors will be adjusted to adapt to the model.

Time constant, another open parameter, is researched in the experiment. However, the critical point has not been decided yet. The research on the critical point helps finding the influent scope of lateral inhibition.

5.3 Classification Method

In this essay, some cognitive behaviors are identified. The VUM differentiating the learned odorant from the unconditioned one which is similar to classical conditioning is simulated in program. However, this kind of classification is based on the training of one particular odorant.
In the future work, the classification based on the built model with no training will be researched.
In the whole model, the output of projection neuron is paramount to the AL layer, so

the research on the PN spiking is meaningful.
The classification method is based on R.Huerta's idea, which is divided into two steps: the first is the nonlinear transformation from the antennal lobe(AL) to the mushroom body(MB), and the second is the classification in the MB.
In the beginning, the spatiotemporal output of 15 PNs will be recorded, take 2 of 15 PNs as examples[46]:

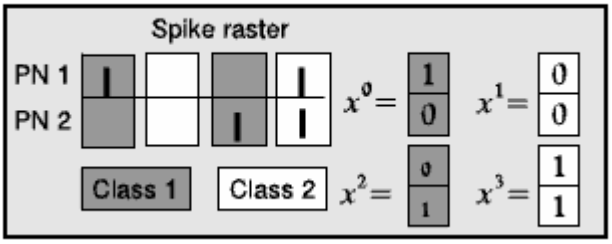

Figure 5.1: the state vector x^i

The nonlinear transformation is as below[46]:

$$Y_j=\begin{cases}1, & \text{if} \quad \sum_{i=1}^{N_{AL}} c_{ji}x_i-\theta_{KC}\geq 0\\ 0, & \text{otherwise}\end{cases}$$

where x_i is the state vector mentioned in Figure, N_{AL} is the number of PNs, θ_{KC} is the firing threshold and c is the connectivity matrix. The output y_j is the vector in MB. In this step, $y^i=[y_1,y_2,\ldots,y_{AL}]$ for the corresponding x^i is computed. The number of neurons decides the dimensional space. Take 2 neurons as an example, the positions of y^i in a two dimensional space are displayed like this[46]:

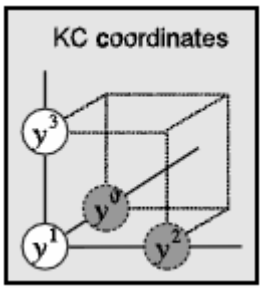

Figure 5.2: nonlinear transformation from AL to MB

Then the linear classification in the MB is continued[46]:

$$z_i=\begin{cases}1, & \text{if} \quad \sum_{j=1}^{N_{KC}} W_{ij}y_j-\theta_{LB}\geq 0\\ 0, & \text{otherwise}\end{cases}$$

where y_j is the state vector in Figure, W_{ij} is the connectivity matrix and θ_{LB} is the threshold in the MB. After the hebbian learning in adjusting the W_{ij}, the output of Z_i is the result of classification. During this process, $W_i=[W_{i1},W_{i2},\ldots,W_{ij}]$ is computed and plays as a hyperplane in the space. The figures which are above this hyperplane are claasified from ones under the plane.

The diagram shows how this hyperplane divides the data in a two-dimensional space[46]:

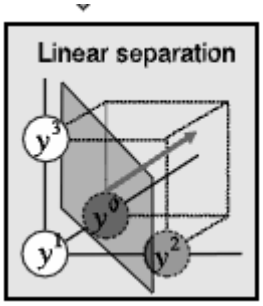

Figure 5.3: linear classification in MB

In this way, the odorants are discriminated in the mixture. In future work, it is interesting to implement this process utilizing the built model.

6 Conclusion

This essay has introduced a re-implement honey bee olfactory model and done some research based on this model.

In chapter 2, the relevant background knowledge is introduced. First, honey bee olfactory system and some cognitive behavior triggered by this system are described. Then, the academic nouns such as generalization, overshadowing and the relevant mechanism involved in the experiment are presented. Next, the model and some classic algorithms associated are shown.

Chapter 3 mainly describes how the model is constructed and designed. Because the paper which the model is on the basis of did not describe the model clearly and has some ambiguous places, it is a challenging task to design the model in every detail and set many open parameters. The program's GUI is shown that is an essential part to analyze the output data.

In next chapter, a serious of experiments had been done and the results are analyzed. In the beginning, the connections among RC, LN and PN are identified. After that, the experiments are made around the effect of the lateral inhibition, a paramount phenomenon occurs in activity of LNs. The cognitive behaviors generalization and overshadowing emerged in the experiments and several data diagrams were made to analyze the relationship between behaviors and the lateral inhibition. Compared with previous paper's data pictures, the similar data trend and distribution are found although the range of taken value is a little different.

By the experiments, the lateral inhibition produced in the binary mixture stimulation when the overlapping degree is 0.5 contributes the high generalization which is clearly different from the other circumstances. And the overshadowing apparently occurs when the overlapping degree is above 0.5, which connects tightly with the lateral inhibition. For the research part, the time constant is further studied to disclose the effect of it to the olfactory system. In the experiment, it is found that within an uncertain critical point, the increase of time constant leads to the stronger generalization. Therefore, time constant must strengthen the activity of lateral inhibition. When the time constant is bigger than the critical point, the generalization is always high for each overlapping style.

Chapter 5 is the work left for the future. In this chapter, how to decide the value of several open parameters and evaluate the influences is a tough work. For the odorant processing, an advanced algorithm is introduced and the implement of this algorithm will be done and therefore the performance can be compared with the present model. Finally, the relevant classification method is introduced and this interests me mostly. Nonlinear transformation from the AL to the MB aims to distribute the data in 15

dimensional space. By the hebbian learning, the hyperplane is decided wich divides the space into two parts. The data above the plane is separated from others.

7. References

1 Linster, C and Smith, B.H..(1997). A computational model of the response of honey bee antennal lobe circuitry to odor mixtures: overshadowing, blocking and unblocking can arise from lateral inhibition. Behavioural Brain Research 87,1-14.

2 Drwin, C.(1871). The descent of Man, and Selection in Relation to Sex(London: John Murray).

3 Chittka, L and Niven, J.(2009). Are Bigger Brains Better? Current Biology 19, 995-1008.

4 Menzel, R., and Giurfa, M. (2001). Cognitive architecture of a mini-brain: the honeybee. Trends Cogn. Sci. 5, 62–71.

5 Goldenberg, E., Garcowski, J., and Beer, R.D., (2004). May we have your attention: Analysis of a selective attention task. In From Animals to Animats 8: Proceedings of the Eighth International Conference on the Simulation of Adaptive Behavior, S. Schaal, A. Ijspeert, A. Billard, S. Vijayakumar, J. Hallam and J.-A. Meyer, eds. (MIT Press), pp. 49–56.

6 M.Izhikevich, E.(2007). Dynamical systems in neuroscience: the geometry of excitability and bursting. Cambridge: The MIT Press.

7 Cleland, T. A. and Linster, C.(2005). Computation in the Olfactory System, Chem.Senses 30: 801-813.

8 http://nelson.beckman.illinois.edu/courses/neuroethol/models/bee_labor/ bee_labor.html

9 Flanagan D & Mercer AR (1989) An atlas and 3-D reconstruction of the antennal lobes in the worker honey bee, Apis mellifera L. (Hymenoptera: Apidae). International Journal of Insect Morphology and Embryology 18: 145-159.

10 Huerta R, Nowotny T, Garcia-Sanchez M, Abarbanel HDI, Rabinovich MI (2004) Learning classification in the olfactory system of insects. Neural Comput 16:1601–1640.

11 Gao, Q., Yuan, B., & Chess, A. (2000). Convergent projections of *Drosophila* olfactory neurons to specific glomeruli in the antennal lobe. Nat. Neurosci., 3(8), 780–785.

12 Rodrigues,V. (1988). Spatial coding of olfactory information in the antennal lobe of Drosophila melanogaster. Brain Res., 453, 299–307.

13 Fonta, C., Sun, X. Masson, C.. (1993). Morphology and spatial distribution of bee antennal lobe interneurons responsive to odours, Chemical Senses, 18 ,101–119.

14 Sun, X., Fonta, C. and Masson, C.. (1993). Odour quality processing by bee antennal lobe neurons, Chemical Senses 18 ,355–377.

15 Hammer, M. (1993) Nature 366, 59–63.

16 Rescoria, R.A. A. Rev. Neurosci. 11, 329-352(1988).

17 Rescoria, R.A. & Wagner, A.R. in Classical conditioning two: Current Research and Theory ,64-99

18 Wagner, A.R. in Information Processing in Animals: Memory Mechanisms, 5-47.

19 Hawkins, R.D. & Kandel, E.R. Psychol. Rev, 91, 375-391(1984).

20 Hammer, M.(1993). An identified neuron mediates the unconditioned stimulus in associative olfactory learning in honeybees. Nature, 366(4).

21 Frisch, K. von.(1967). The Biology of the Honey Bee. Harvard Univ. Press, Boston. 566pp.

22 Dionne, V. E., and A. E. Dubin. 1994. Transduction diversity in olfaction.J. Exp. Biol. 194: 1-21.

23 Smith, B.H.(1996). The Role of Attention in Learning About Odorants. Biol. Bull. 191:76-83.

24 Smith, B. H., and R. Menzel.(1989). An analysis of variability in the feeding motor program of the honey bee: the role of learning in releasing a modal action pattern. Ethology 82: 68-81.
25 Pearce, J. M.(1994). Similarity and discrimination: a selective review and a connectionist model. Psychol.Rev.101:587-607.
26 Bitterman, M. E., R. Menzel, A. Fietz, and S. Schafer.(1983). Classical conditioning of proboscis extension in honeybees, Apis mellifera. J.*Comp.Psvchol.97: 107-119.*
27 Pelz, C, Gerber, B and Menzel, R. (1997) Odorant intensity as a determinant for olfactory conditioning in honeybees: roles in discrimination, overshadowing and memory consolidation, The Journal of Experimental Biology 200, 837-847.
28 Smith B.H. and Cobey, S. (1994). The olfactory memory of honey bee, Apis mellifera. II. Blocking between odorants in binary mixtures, J. Exp. Biol., 195,91–108.
29 Sahley, C., J. W. Rudy, and A. Gelperin. 1981. An analysis of associative learning in a terrestrial mollusc. I. Higher-order conditioning, blocking and a transient US-pre-exposureeffect. I.Comp. Physiol. 144: 1-8.
30 Smith, B. H., and Cobey,S. 1994. The olfactory memory of honey bee, Apis mellifera: II. Blocking betweenodorants in binary mixtures.J.Exp.Biol.195:91-108.
31 Gerber, B. and Ullrich, J. (1999). No evidence for olfactory blocking in honeybee classical conditioning. J. Exp. Biol. 202:1839 -1854.
32 Hosler, J. and Smith, B. (2000). Blocking and the detection of odor components in blends. J. Exp. Biol. 203:2797 -2806.
33 Gascuel, J. and Masson, C. (1991). Quantitative electron microscopic study of the antennal lobe in the honey bee, Tissue Cell, 23, 341–355.
34 Sun, X., Fonta, C. and Masson, C.(1993). Odour quality processing by bee antennal lobe neurons, Chemical Senses 18 ,355–377.
35 Fonta, C., Sun, X. Masson, C. (1993). Morphology and spatial distribution of bee antennal lobe interneurons responsive to odours, Chemical Senses, 18, 101–119.
36 Hagan, M. T., Demuth, H. B., Beale, M.. Neural Network Design. Page 13-2.
37 Classical conditioning. http://en.wikipedia.org/wiki/Classical_conditioning.
38 Hebbian theory. http://en.wikipedia.org/wiki/Hebbian_theory.
39 Samuelides, M., Thorpe, S. &Veneau, E.(1997). Implementing hebbian learning in a rank-based neural network. Computer Science, 1327: 145-150.
40 Thorpe, S.J., Fize, D & Marlot, C.(1996). Speed of processing in the human visual system. Nature (381): 520-522.
41 Abbott, L.F. (1999). "Lapique's introduction of the integrate-and-fire model neuron (1907)". *Brain Research Bulletin* **50** (5/6): 303-304.
42 Koch, Christof; Idan Segev (1998). *Methods in Neuronal Modeling* (2 ed.). Cambridge, MA: Massachusetts Institute of Technology. ISBN 0-262-11231-0.
43 Hammer, M. and Menzel, R.. (1995). Learning and memory in the honey bee, J. Neurosci., 9 , 3154–3162.
44 The McCulloch-Pitts Model of Neuron. http://www.ece.utep.edu/research/webfuzzy/docs/kk-thesis/kk-thesis-html/node12.html.
45 Linster, C. and Cleland, T.A..(2001). How Spike Synchronization Among Olfactory Neurons an Contribute to Sensory Discrimination. Journal of Computational Neuroscience, 10: 187-193.

46 Huerta R, Nowotny T, Garcia-Sanchez M, Abarbanel HDI, Rabinovich MI (2004) Learning classification in the olfactory system of insects. Neural Comput 16:1601–1640.