



UNIVERSIDAD AUTÓNOMA DE MADRID

COMPUTATIONAL ENHANCEMENT BY NEURAL VARIABILITY

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Abstract

We used a model based on the olfactory system of insects to analyze the impact of neuron threshold variability in the mushroom body (MB) for odorant discrimination purposes. This model is a single-hidden-layer neural network (SLN) where the input layer represents the antennal lobe (AL), which contains a binary code for each odorant; the hidden layer represents the Kenyon cells (KC) and the output layer named the output neurons. The KC and output layers are responsible for learning odor discrimination. The binary code obtained for each odorant in the output layer has been used to measure the discrimination error and to know what kind of thresholds (heterogeneous or homogeneous) provide better results when they are used in KC and output neurons. We show that discrimination error is lower for heterogeneous thresholds than for homogeneous thresholds.

Contents

| | | |
|----------|---|-----------|
| 1 | Introduction | 1 |
| 2 | State of the art | 5 |
| 3 | Olfactory model and methods | 9 |
| 3.1 | Neuron model | 9 |
| 3.2 | Network model | 10 |
| 3.3 | Hebbian learning | 11 |
| 3.4 | Odorants | 13 |
| 3.5 | Discrimination error | 14 |
| 3.6 | Limit thresholds | 15 |
| 3.6.1 | Homogeneous thresholds. | 16 |
| 3.6.2 | Heterogeneous thresholds. | 17 |
| 4 | Experiments and results | 21 |
| 4.1 | Model parameters relevance | 21 |
| 4.1.1 | Input properties | 22 |
| 4.1.1.1 | Overlapping | 22 |
| 4.1.1.2 | Gain control | 24 |
| 4.1.2 | Network properties | 24 |
| 4.1.2.1 | Connection probabilities | 24 |
| 4.1.2.2 | Hebbian probabilities | 26 |
| 4.2 | Threshold comparison | 27 |
| 4.2.1 | Different sets of odorants and connection probabilities | 28 |

CONTENTS

| | | |
|----------|---|-----------|
| 4.2.2 | Discrimination error - spike rate | 28 |
| 5 | Conclusions and future work | 31 |
| 6 | Publications | 33 |
| | Bibliography | 35 |

Introduction

The olfactory system is a complex neural machinery that is able to classify a large number of odorants, from stimuli that are highly variable and infinite [13] (different concentrations, mixtures, etc). This is why we are interested in learning how this system processes this information and achieves a successful classification from the different patterns that it receives. In order to study this we focused on olfactory systems of insects; these have a simple mechanism able to realize a quick and stable odorant discrimination, a goal we want to achieve through computer modelling.

Normally, these models are simulated using fixed neural thresholds. However, recent applied research on artificial noses found that, if you use different detection thresholds for different odorants, you can improve gas discrimination [6]. This is one of the motivations why we study and use neuron threshold variability in the information process achieved by neural olfactory system.

On the other hand, in findings on the olfactory system of insects has been reported that neural thresholds vary in olfactory receptor neurons (ORN) [2] and Kenyon cells (KCS) in the insect mushroom body (MB) [37]. Neural variability in the form of threshold variability is a general property of neurons in the brain.

1. INTRODUCTION

Is this threshold variability an evolutionary advantage that allows better odorant discrimination? Or does this happen because there is a biological impossibility to produce the same threshold for each neuron?

To investigate if neural threshold variability increases odorant discrimination performance, we use a simple model of the olfactory systems of insects [21, 22] based on McCulloch-Pitts neurons [31]. The insect olfactory pathway starts at the antenna, where a massive number of receptors encode the odor stimulus in a high-dimensional code. In locusts [28], this number is approximately 100,000 neurons. This information is then sent to the AL for additional processing. In the locust, the AL approximately has 1,000 neurons that compress the ORN information. The AL exhibits complex dynamics produced by the interaction of its excitatory and inhibitory neural populations [4, 9, 29]. The excitatory cells are called projection neurons because they only transmit the result of AL computation to deeper regions. The projection neurons deliver the AL output to the 50,000 cells of the MB, KC, in a fan-out phase which increases the separability between different odor encodings. This fan-out phase combined with the sparse firing for these KC [15, 37, 48] facilitate the odorant discrimination process, which is realized by output neurons in a fan-in phase.

We focus on the AL and MB (model in Fig.1.1), where the input to single-hidden-layer neural network (SLN) is AL, which is connected to MB through a non-specific connectivity matrix. The reason for this non-specific connectivity matrix is due to the individual connection variability of insects of the same species [30, 46]. The other layers of the SLN, hidden and output, are composed by KC and output neurons respectively. These are connected by a connectivity matrix that implements Hebbian-like learning [7].

Our goal is to analyse how information is processed in the olfactory system and what is the role of threshold variability in this system. For this purpose, we compare homogeneous and heterogeneous thresholds to investigate whether neural variability improves odorant discrimination. To determine this, we measure the

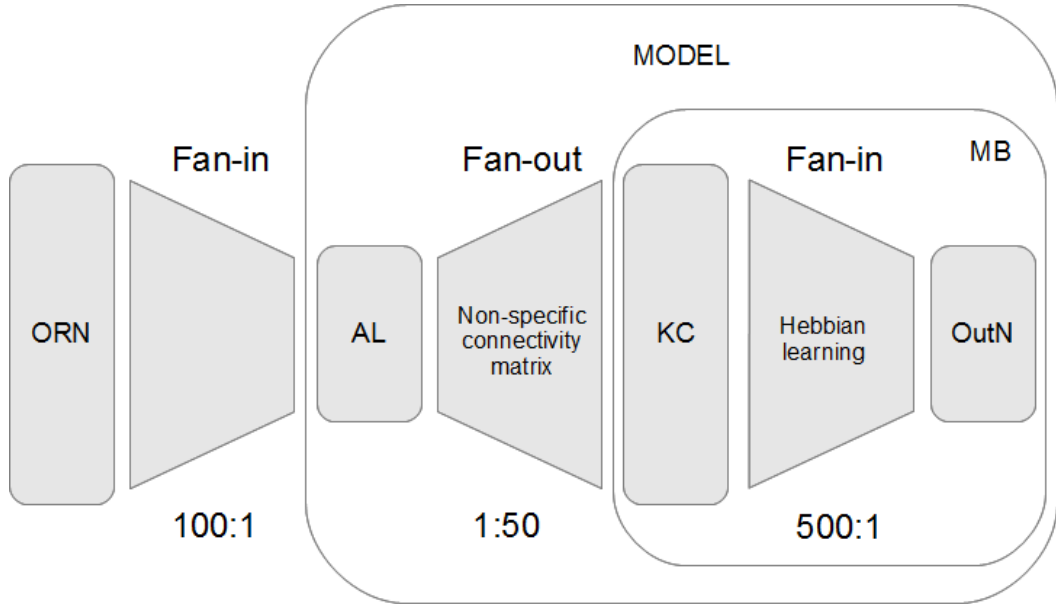


Figure 1.1: The structure of the model is divided into two parts: antennal lobe (AL) and mushroom body (MB). MB is divided into two additional layers: Kenyon cells (KC) and output neurons (OutN). The ratios shown are for locust.

discrimination error obtained in the output layer. This discrimination error represents the percentage of odors that has not been correctly classified. A correctly classified odorant always generates the same output pattern A' for a certain input pattern A . Furthermore, we calculate the percentage of KC spikes to prove that discrimination success is related to the sparseness condition observed in the KC layer.

We conclude that odorant discrimination improves with neuron threshold variability and that the discrimination performance is closely related to sparse activity of the KC population, for odorant sets that we chose.

State of the art

Modelling a simple system, that can discriminate odorants and allow us to know how information is processed in the olfactory system, is a task that led us to study olfactory systems of insects.

For an example, honeybee can visit over 100 flowers in a day. On average, a floral scent contains 20–60 different odorants [26]. The majority of floral odorants are terpenes or terpene derivatives, but there are also large numbers of alcohols, aldehydes, ketones, and esters. Different flower species emit different scents due to a difference in chemical composition, or in concentration and ratio of the components. A floral bouquet can even vary within a species, depending on the environmental conditions such as the location of an individual flower, the time of day, the pollination status, nectar content, and the age of the flower [38]. Despite the complexity and variability of natural scents, honeybees display an amazing ability to learn, discriminate, and recognize floral odours, in fast and reliable way.

Insects have three known processing stages of odor information before classification: the antenna, the antennal lobe (AL), and the mushroom body (MB) (Fig. 1.1).

2. STATE OF THE ART

Each olfactory receptor cell in the antenna expresses one type of receptor, and all olfactory receptor cells expressing the same receptor type connect to the same glomerulus in the AL [14, 42, 49]. Thus, a chemosensory map of receptor activity in the antenna is formed in the AL: the genetically encoded architecture induces stimulus-dependent spatial code in the glomeruli [5, 10, 11, 23, 39]. Moreover, the spatial code is conserved across individuals of the same species [12, 50] as would be expected given the genetic origin of the code. The ratio between the number of neurons in the antenna and the AL is 100:1 in the locust [27].

In the locust, the AL approximately has 1,000 glomeruli that compress the ORN information. The AL exhibits complex dynamics produced by the interaction of its excitatory and inhibitory neural populations [4, 9, 29]. The excitatory cells are called projection neurons, PNs, because they only transmit the result of AL computation to deeper regions, there are 830 PNs compared to 300 LNs, local interneurons, the inhibitory cells. The projection neurons deliver the AL output to the 50,000 cells of the MB, 1:50, in a fan-out phase which increases the separability between different odor encodings. Moreover, recordings from the AL in the locust indicate that the activity in the projections of the excitatory neurons in the AL into the MB is nearly constant in time [44]. Therefore, a gain control [41] mechanism maintaining a nearly constant average neuronal activity in the AL must exist, which would be, according to recent research, in the LNs [35]. It seems that 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.

The mushroom bodies (MB) are areas of the insect brain that have been shown to be involved in memory formation [7, 8, 19, 32, 33, 34, 51]. The MBs are organized in two modules: the calyx/Kenyon cells (KCs) and the mushroom body lobes [45]. The calyx receives and integrates multimodal sensory information [19, 45], and the mushroom body lobes are involved in memory formation and storage [7, 32, 51]. There is a large number of KCs in the MB: 200,000 in cockroach, 170,000 in the honeybee, 50,000 in locust, and 2,500 in the fruit fly *Drosophila*. This large group of neurons sends afferents to the MB lobes, which contain on the

order of a few hundred output neurons [22].

The KC neurons of the MB show very low activity. They are in the quiescent state most of the time with a mean firing frequency lower than 1 Hz. These neurons behave as coincidence detectors [47](Fig.2.1), which implies that, when one KC receives a specific number of spikes from a set of the AL neurons within some time frame (± 10 ms), then the KC neuron fires a single spike (it rarely yields more than one) [37]. Another property of this system is the global inhibitory role played by the lateral horn neurons [35]. Every 50 milliseconds these neurons acting as a clock reset the activity of the whole system into the same initial conditions. By means of this inhibition the system resets the state that it was previously.

Considering this dynamical simplicity, we have chosen a simple McCulloch-Pitts neuron [31] as sufficient representation of the activity of the KC neurons. The McCulloch-Pitts neuron is expressed as:

$$y_j = \Theta\left(\sum_{i=1}^{N_{AL}} c_{ji}x_i - \theta_j\right) \quad (2.1)$$

where x_i and y_j are activation states for the PNs in the AL and the KC neurons respectively, c_{ji} is a weight which links two neurons, θ_j is a threshold for a KC neuron, and Θ is the activation function. The synaptic model is a binary. This implies that the values for the neural activation states or connectivity weights will be 0 or 1. The probability of placing a 1 in c_{ji} is p_c . The values of the connectivity matrix are drawn from a statistically independent random process [15].

The biomimetic approach to represent our network is the Rosenblatt perceptron [40], a three-layered neural network resembling the MBs of insects, which allows to solve pattern recognition problems. More recently, approaches trying to replicate the structure of the cortex have proved useful for solving complex pattern recognition problems [1, 3, 24, 36]. In these approaches, feature extractors are used, in analogy to the visual cortex, that are associated by means of attractor networks [20]. To place an attractor network in the cortex might be optimistic, but the common language to all these approaches is the use of Hebbian learning and of inhibition as

2. STATE OF THE ART

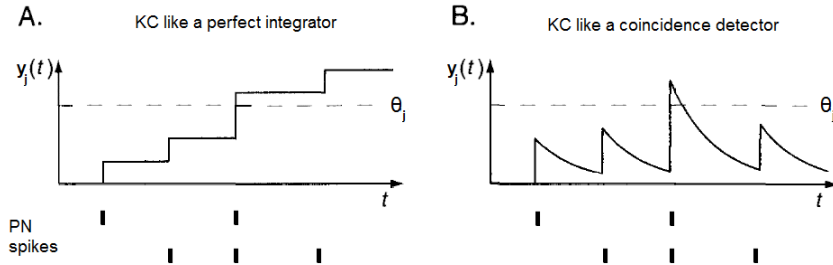


Figure 2.1: Schematic illustration of (A) a perfect integrator and (B) a leaky integrator that can be utilized as coincidence detector. In this example the membrane potential $y_j(t)$, with a threshold θ , integrates short current pulses of the two spike trains shown at the bottom [47].

a way to enhance competitive learning.

So it remains to solve the neural thresholds calculation, neural network bias, knowing that according to recent studies these could be different for all neurons [2, 37]. This objective is one that we plan to solve in the future using an ELM-based algorithm [17, 18], applying supervised learning. This algorithm will be modified to make it minimize discrimination error and neuronal activity in the hidden layer (sparseness condition).

All these tools allow us to develop a model, with a quick and stable odorant discrimination, similar to olfactory systems of insects.

Olfactory model and methods

3.1 Neuron model

In locusts, activity patterns in AL are practically time-discretized by a periodic feedforward inhibition onto MB calyces, and activity levels in KCs are very low [37]. Thus, information is represented by time-discrete, sparse activity patterns in MB in which each KC fires at most once in each 50 ms local field potential oscillation cycle. Because of these neurons are inactive most of the time, but being activated, their neuronal response is produced by the coincidence of concurrent spikes followed by a reset, we have used the McCulloch-Pitts model [31] in all neurons of the hidden and output layers, as mentioned above. This neuron model uses the threshold step function as activation function. Therefore, we have the following (see network model in Fig.3.1):

$$y_j = \Theta\left(\sum_{i=1}^{N_{AL}} c_{ji}x_i - \theta_j\right), \quad z_l = \Theta\left(\sum_{j=1}^{N_{KC}} w_{lj}y_j - \varepsilon_l\right) \quad (3.1)$$

3. OLFACTORY MODEL AND METHODS

where x_i , y_j and z_l are activation states for a input, hidden and output neuron respectively, c_{ji} and w_{lj} are weights which links two neurons, θ_j and ε_l are thresholds for the hidden and output neuron respectively, and Θ is the activation function.

3.2 Network model

The network model is a SLN (Fig.3.1) with an input layer with 100 neurons, a hidden layer with 5000 neurons (locust has a ratio of 1:50 between neurons of the input and hidden layer) and an output layer with 10 neurons [22]. These dimensions were chosen because they ensure a high probability of discrimination for the input used [21] for a relatively low computational cost.

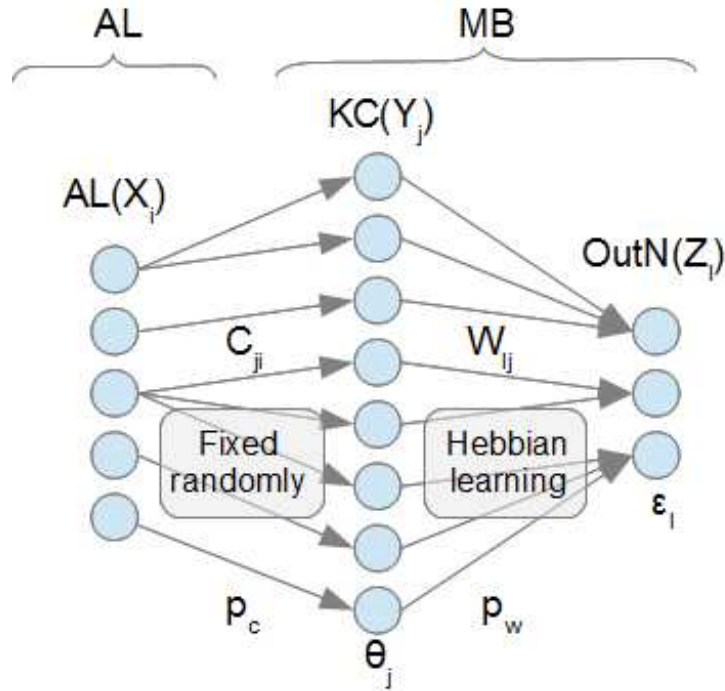


Figure 3.1: Network model composed by its 3 layers: antennal lobe, Kenyon cells and output neurons.

The connectivity matrices, C and W , are initialized at the beginning of each odorant discrimination process. We generate a matrix with random values uniformly distributed, $[0, 1]$, with the same dimensions as our connectivity matrix. We

establish connections in our connectivity matrix using the probability of connection matrix, p_c and p_w , as a threshold on the values of the random matrix: If a float value is equal or less than the probability of connection, one connection is established, otherwise no connection. In the case of the connectivity matrix C , this configuration remains fixed throughout the odorant discrimination process. However, for the connectivity matrix W , its configuration will be updated using Hebbian learning.

Finally, we have to mention that the synaptic model of this network is completely binary. Therefore, activation states for a neuron and weights can only take values of 0 or 1.

3.3 Hebbian learning

As mentioned above, the connectivity matrix W , which links KC and output neurons, has olfactory associative learning, which can be simulated by using Hebbian learning [7]. It allows the strengthening or weakening the connections of a connectivity matrix, as follows [21, 22]:

$$\begin{aligned}
 w_{lj}(t+1) &= H(z_l, y_j, w_{lj}(t)), \\
 H(1, 1, w_{lj}(t)) &= \begin{cases} 1 & \text{with probability } p_+, \\ w_{lj}(t) & \text{with probability } 1 - p_+, \end{cases} \\
 H(1, 0, w_{lj}(t)) &= \begin{cases} 0 & \text{with probability } p_-, \\ w_{lj}(t) & \text{with probability } 1 - p_-, \end{cases} \\
 H(0, 1, w_{lj}(t)) &= w_{lj}(t), \quad H(0, 0, w_{lj}(t)) = w_{lj}(t).
 \end{aligned} \tag{3.2}$$

where the future connection state $w_{lj}(t+1)$ is determined by a function $H(z_l, y_j, w_{lj}(t))$, which depends on the output layer neuron z_l , the hidden layer neuron y_j and the current connection state $w_{lj}(t)$. If the output layer neuron has not fired, the connection state is not changed. However, if the output layer neuron has fired, the connection state depends on the hidden layer in the following ways:

- If the hidden layer neuron has fired, then the connection between these neurons is created with a probability p_+ .

3. OLFACTORY MODEL AND METHODS

- If the hidden layer neuron has not fired, then the connection between these neurons is destroyed with a probability p_- .

This Hebbian learning allows to decrease discrimination error ($derror$) and variation of weights of matrix W (dw) along interactions (time steps) (Fig.3.2):

$$derror(t) = \frac{|\#P_{in}^d - \#P_{out}^d(t)|}{\#P_{in}^d}, \quad dw(t) = \sum_{l=1}^{N_{OutN}} \sum_{j=1}^{N_{KC}} |w_{lj}(t) - w_{lj}(t-1)| \quad (3.3)$$

where $\#P_{in}^d$ is the number of different patterns at input, $\#P_{out}^d(t)$ is the number of different patterns at output for a t instant, $w_{lj}(t)$ is the current connection state and $w_{lj}(t-1)$ the previous state, and N_{KC} and N_{OutN} are the number of neurons for KC and output neurons respectively.

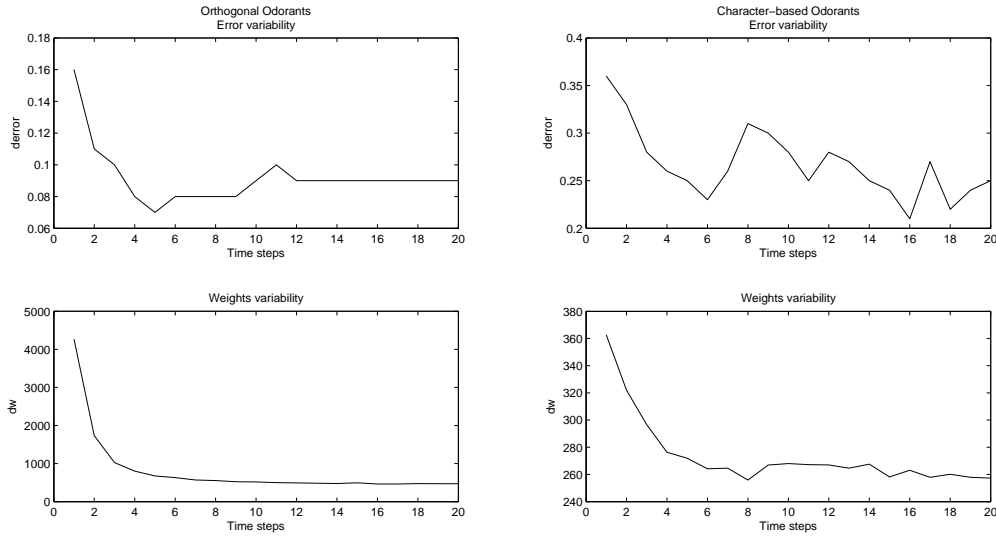


Figure 3.2: Examples of error variability (top panels) and weights variability (bottom panels) using Hebbian learning for network dimensions of $N_{AL} = 100$, $N_{KC} = 5000$, $N_{OutN} = 10$, probabilities of $p_c = 0.1$, $p_w = 0.5$, $p_+ = 0.2$ and $p_- = 0.1$, and orthogonal (left panels) and character-based (right panels) odorants.

3.4 Odorants

The odorants used in our model as input have no correspondence to real odorant data, because in this first approximation we want to test our hypothesis about the benefits of neuronal variability. Instead, we have used orthogonal and character-based encodings (Fig.3.3). The reason for using these encodings is because we need these odorants have a minimum distance between them to ensure they are different odorants. In the case of orthogonal encoding, we have wanted to observe what happens if different odorants do not share activated neurons in the input layer, AL. We have used orthogonal encodings all of which have the same number of active neurons in the input layer. Also, this number of active neurons is maximal. Therefore, if we have 100 input neurons, we will have 10 active neurons for 10 different odorant patterns, and 20 for 5 different odorant patterns. In the case of character-based encodings, we have used numerical characters represented in matrices of dimensions 10×10 , which we have later converted to vectors of dimension 100. The minimum Hamming distance between these encodings is 4 activated neurons, for the numerical characters 5 and 6.

We have worked with four set of odorants, they have been created from a initial set of odorants, which have been replicated three times and introduced them some noise. This noise represents a set of input neurons which have changed their state of activation (active/inactive). We have used a noise that affects a specific number of neurons, which is in proportion (20%) to the number of active neurons. The four set of odorants are as follows:

- 15 Orthogonal odorants: 5 orthogonal odorant patterns (20 active neurons) repeated 3 times with noise in 4 neurons.
- 15 Character-based odorants: 5 character-based odorant patterns (with a minimum of 28 active neurons) repeated 3 times with noise in 6 neurons.
- 30 Orthogonal odorants: 10 orthogonal odorant patterns (10 active neurons) repeated 3 times with noise in 2 neurons.

3. OLFACTORY MODEL AND METHODS

- 30 Character-based odorants: 10 character-based odorant patterns (with a minimum of 28 active neurons) repeated 3 times with noise in 6 neurons.

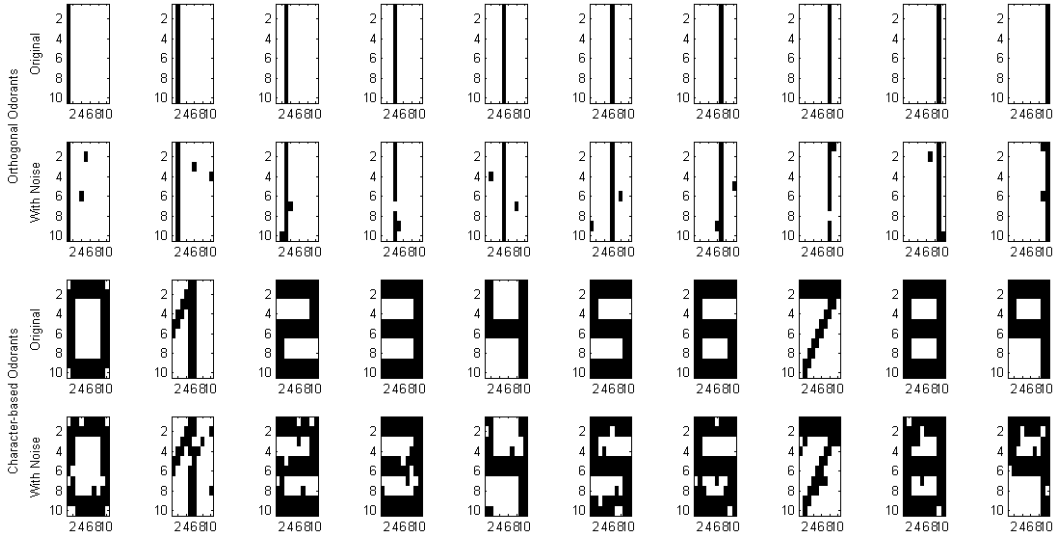


Figure 3.3: Examples of orthogonal (top panels) and character-based (bottom panels) encodings without and with noise. Colours: black (1, active neuron), white (0, inactive neuron).

We have used these odorants with noise to observe if they can be well classified despite noise, after we have known the discrimination error when these odorants are presented without noise. This error for odorant discrimination in the absence of noise will be shown in the results section.

3.5 Discrimination error

Discrimination error represents the percentage of odorants which have not been correctly classified. To calculate this percentage, we assume that a correctly classified odorant always generates the same output pattern A' for a certain input pattern A . Therefore, since we know how many clusters are in the input, we will expect the same clusters appear in the output. This is expected clustering is used to measure the error of discrimination by comparison. So after obtaining the output of our model, this is clustered and compared with the original clustering, all of those odorants that are inconsistent with this clustering is our discrimination error.

$$error = \frac{|\#P_{in}^d - \#P_{out}^d|}{\#P_{in}^d}, \quad error = derror(T) \quad (3.4)$$

where $\#P_{in}^d$ is the number of patterns at input, $\#P_{out}^d$ is the number of patterns at output and T is the total number of iterations (time steps).

3.6 Limit thresholds

A limit threshold is the minimum threshold value which prevents a neuron from spiking for an odorant. This value has been used as threshold in our neurons, in order to prove how important threshold variability is in the problem of odorant discrimination. This limit threshold is calculated for each neuron and each odorant as follows:

$$\theta_j^O = \sum_{i=1}^{N_{AL}} c_{ji} x_i^O, \quad \varepsilon_l^O = \sum_{j=1}^{N_{KC}} w_{lj} y_j^O \quad (3.5)$$

where neuron j spikes $\forall \theta_j, 0 \leq \theta_j < \theta_j^O$, and neuron l spikes $\forall \varepsilon_l, 0 \leq \varepsilon_l < \varepsilon_l^O$. Being θ_j^O the limit threshold for a KC (j) and an odorant (O), and ε_l^O the limit threshold for an output neuron (l) and an odorant (O), and both are natural numbers. These thresholds are calculated only one time in the odorant discrimination process, both before Hebbian learning. Therefore, the limit threshold matrix stores all limit threshold of a layer. In case of hidden layer, it has dimension $N_{KC} \times N_{ODOR}$, and dimension $N_{OutN} \times N_{ODOR}$ for the output layer.

$$\theta_j^O = \begin{pmatrix} \theta_1^1 & \dots & \theta_1^{N_{ODOR}} \\ \vdots & \ddots & \vdots \\ \theta_{N_{KC}}^1 & \dots & \theta_{N_{KC}}^{N_{ODOR}} \end{pmatrix} \quad \varepsilon_l^O = \begin{pmatrix} \varepsilon_1^1 & \dots & \varepsilon_1^{N_{ODOR}} \\ \vdots & \ddots & \vdots \\ \varepsilon_{N_{OutN}}^1 & \dots & \varepsilon_{N_{OutN}}^{N_{ODOR}} \end{pmatrix} \quad (3.6)$$

The purpose of these matrices (Fig.3.4, Fig.3.5) is to know all possible thresholds for each layer, for all neurons and odorants, and choose the one which improves odorant discrimination.

As we have already explained the meaning of limit threshold, we will explain how they are calculated for the cases of homogeneous and heterogeneous thresholds.

3. OLFACTORY MODEL AND METHODS

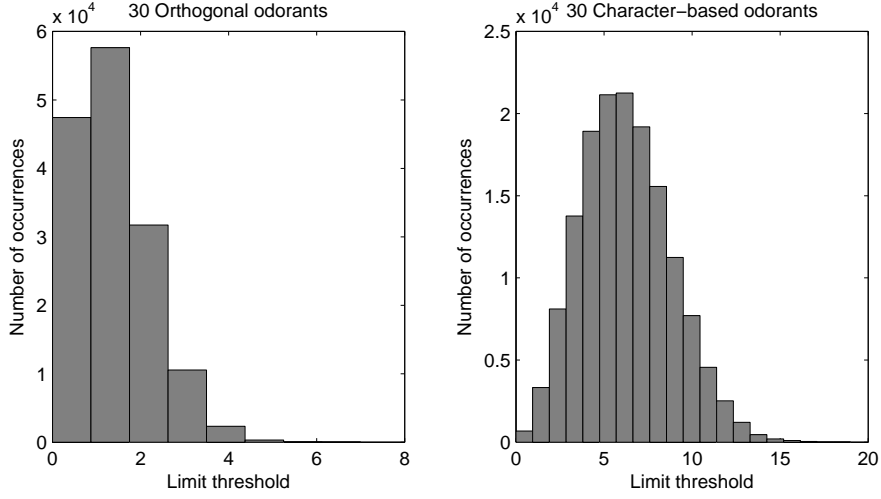


Figure 3.4: Example of limit threshold distributions in KC for different odorant sets: 30 Orthogonal odorants (left panel), 30 Character-based odorants (right panel).

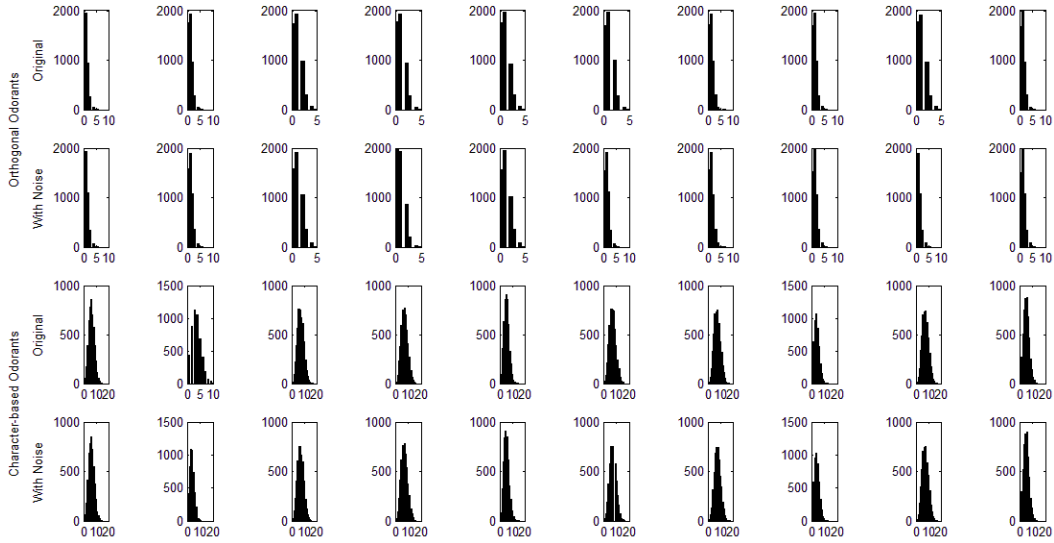


Figure 3.5: Example of limit threshold distributions in KC for all odorants: Orthogonal odorants (top panels), Character-based odorants (bottom panels).

3.6.1 Homogeneous thresholds.

To calculate the homogeneous thresholds, we obtain the limit threshold matrix for the hidden layer and we take the minimum and maximum of this matrix. We take all values between the minimum and maximum, including these, to use as thresholds

for the hidden layer. The aim of this process is to obtain the minimum discrimination error for each threshold and the spike rate for this minimum.

To achieve this minimum discrimination error, for each hidden layer threshold we obtain its limit threshold matrix for the output layer and we take the minimum and maximum of this matrix. We calculate the discrimination error for all possible combinations and take the minimum observed. This value is the minimum discrimination error for a hidden layer threshold:

Algorithm 1 Homogeneous threshold

```

 $\theta_{min} = \min(\theta_j^O)$  //minimum matrix  $\theta_j^O$ 
 $\theta_{max} = \max(\theta_j^O)$  //maximum matrix  $\theta_j^O$ 
 $N = \theta_{max} - \theta_{min} + 1$  //number of thresholds
 $error[N] = 1$  //vector that stores the minimum error for each  $\theta$ 
for  $n = 0 \rightarrow N - 1$  do
     $\theta = \theta_{min} + n$ 
     $M = \varepsilon_{max} - \varepsilon_{min} + 1$ 
    for  $m = 0 \rightarrow M - 1$  do
         $\varepsilon = \varepsilon_{min} + m$ 
        if  $error < error(\theta)$  then
             $error(\theta) = error$ 
        end if
    end for
end for

```

3.6.2 Heterogeneous thresholds.

In the case of heterogeneous thresholds, we obtain the limit threshold matrix for the hidden layer but we do not take all possible combinations. We obtain the distribution of limit thresholds for each hidden layer neuron and we select the value which prevents each neuron from firing for a certain percentage of odorants. These values will be the limit thresholds for these neurons (Fig.3.6).

3. OLFACTORY MODEL AND METHODS

We have taken all possible integer percentages, 0-100, and calculated the threshold for each neuron in the hidden layer. We have obtained the minimum discrimination error for each percentage and the spike rate for this minimum.

To achieve this minimum discrimination error, for each percentage used in the hidden layer we take all possible integer percentages and calculate the threshold for each neuron in the output layer. We calculate the discrimination error for all possible combinations and take the minimum observed. This value is the minimum discrimination error for a percentage used in the hidden layer:

Algorithm 2 Heterogeneous threshold

```
error[101] = 1
for  $n = 0 \rightarrow 100$  do
   $\theta = \text{thresholds}(n)$  //thresholds(x) returns a thresholds vector for all neurons,
  that prevents these fires for a percentage of odorants
  for  $m = 0 \rightarrow 100$  do
     $\varepsilon = \text{thresholds}(m)$ 
    if  $\text{error} < \text{error}(\theta)$  then
       $\text{error}(\theta) = \text{error}$ 
    end if
  end for
end for
```

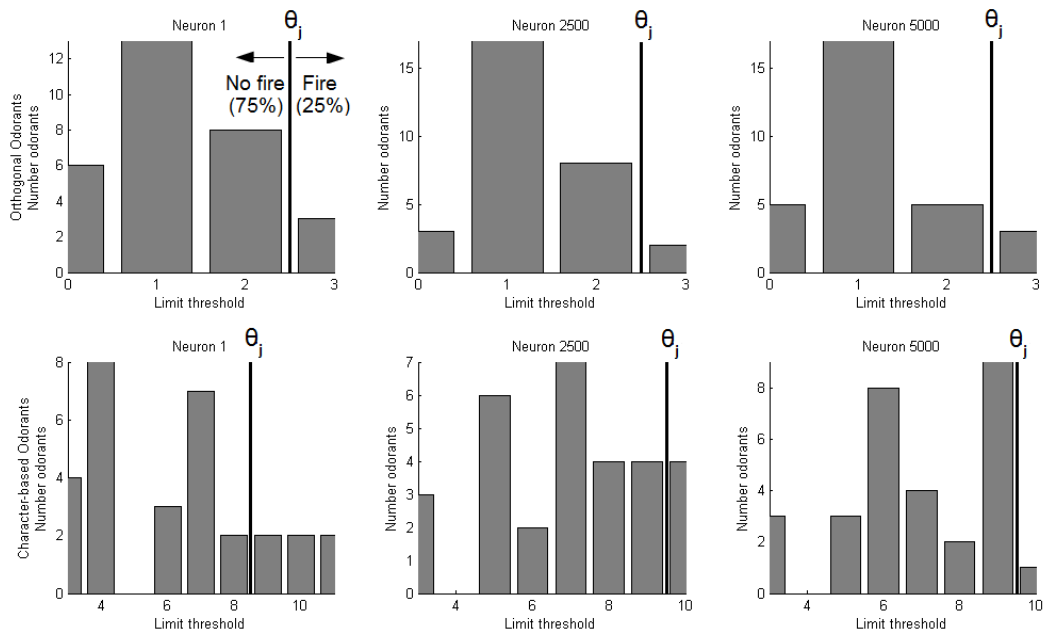


Figure 3.6: Example of distribution of limit thresholds for a hidden layer neuron, a set of 30 odorants with noise and a $\theta = thresholds(75)$ (Alg.2). The value selected as limit threshold, θ_j^O , for these neurons, represented by a black line, allows the neurons only fires for 25% odorants. Therefore, if the selected percentage is high, the limit threshold will be high too and the neuron will fire for a few odorants, the neuron will be more selective. If the percentage is low, the selectivity of the neuron is also low.

Experiments and results

As mentioned above, our goal is to compare which kind of thresholds (homogeneous or heterogeneous) improves odorant discrimination. However, before focusing on the results of this comparison, we analyse the relevance of the different parameters of the model to use this knowledge in obtaining our final results.

4.1 Model parameters relevance

Besides the most important parameters for us, which are the thresholds, there are many others that can condition the odorant discrimination ability of our model. That is why, although previously have been seen slightly, we focus on analyzing them in this section as follows:

- Input properties
 - Overlapping
 - Gain control
- Network properties
 - Connection probabilities

4. EXPERIMENTS AND RESULTS

– Hebbian probabilities

For this analysis, we use mainly orthogonal odorant patterns, or derivatives thereof, homogeneous thresholds, obtained through its exhaustive search, and 20 iterations of Hebbian learning. The following results are the average of 10 simulations.

4.1.1 Input properties

The first parameter of our model is the input, and whatever the origin of this, artificial or real, there are some properties that can influence the success of its discrimination.

4.1.1.1 Overlapping

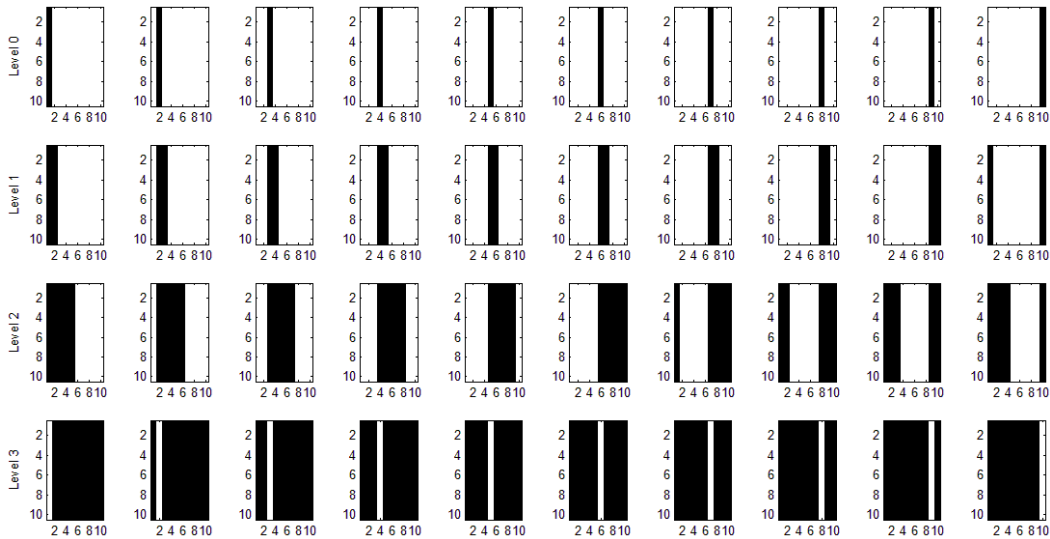


Figure 4.1: Example of different levels of overlapping: Level 0: No overlap. Level 1: Each odorant overlaps with two odorants. Level 2: Each odorant overlaps with half of odorants. Level 3: Each odorant does not overlap with an odorant. Colours: black (1, active neuron), white (0, inactive neuron).

Odorant encodings with overlapping between them, can be a serious problem for a success discrimination. So we wanted to measure overlapping influence using

4.1 Model parameters relevance

different levels of it in the input model. These levels of overlapping have been configured as follows (Fig.4.1):

- Level 0: No overlap.
- Level 1: Each odorant overlaps with two odorants.
- Level 2: Each odorant overlaps with half of odorants.
- Level 3: Each odorant does not overlap with an odorant.

Observing that overlapping does not have a great influence on the success of the discrimination of odorants, at least for the odorants used (Fig.4.2). This strange fact may have the following explanation: the odorants used must have a maximum of 80% overlap, so the remaining 20% has enough information (50% activated, 10% of the total) for odorants to be discriminated. Therefore, for these simple models, although overlapping of information is a frequent problem, the model will be tolerant to this problem if it receives enough information and the input has a gain control.

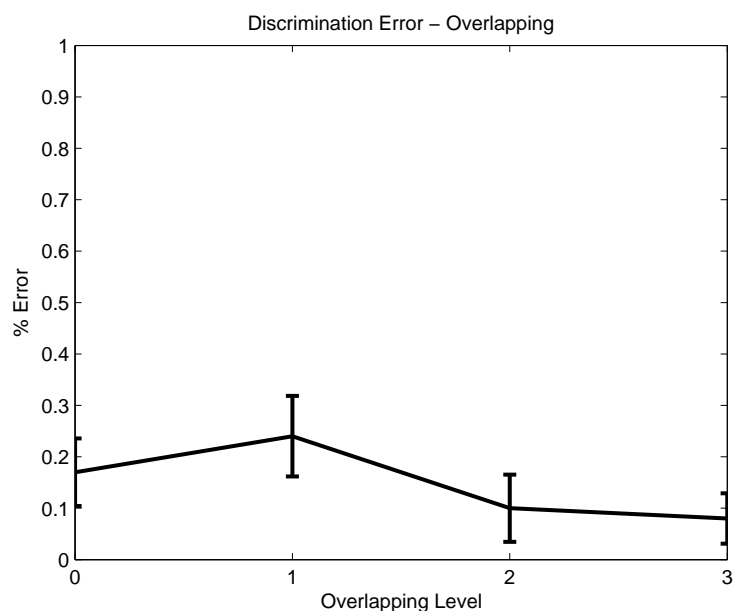


Figure 4.2: Percentage of error based on level of overlap introduced at input.

4. EXPERIMENTS AND RESULTS

4.1.1.2 Gain control

It is possible that different odorants do not have the same number of active neurons in the input model. This variation of neuronal activity may influence the success of discrimination of odorants. In fact, recent research about it, suggests that a gain control is crucial for any system that aims to separate the quality of stimuli from their intensity [43]. Gain control is present in nervous systems [41]. For example, it has been observed that it exists in the olfactory system neurons responsible for inhibition in the AL [35], LNs. So we will measure gain control influence using different levels of activation variability in the input model (standard deviation of the number of active neurons for each pattern). These activation variability levels have been configured as follows (Fig.4.3):

- Level 0: No activation variability (gain control). $\sigma = 0$.
- Level 1: Low activation variability. $\sigma = 0.876$.
- Level 2: Medium activation variability. $\sigma = 1.491$.
- Level 3: High activation variability. $\sigma = 3.028$.

Observing that gain control has a strong influence on the success of the discrimination of odorants (Fig.4.4) and therefore it is a parameter to take into great consideration in our model.

4.1.2 Network properties

Threshold is the neural network bias, but there are other network parameters which we have to take in consideration.

4.1.2.1 Connection probabilities

We mentioned above that the connectivity matrix C remains fixed throughout the odorant discrimination process, but the connectivity matrix W is updated using Hebbian learning. This fact suggests that the probability p_c is more relevant than the probability p_w , but to know if this is true and its significance level, we need to observe the percentage of discrimination error for all possible combinations of

4.1 Model parameters relevance

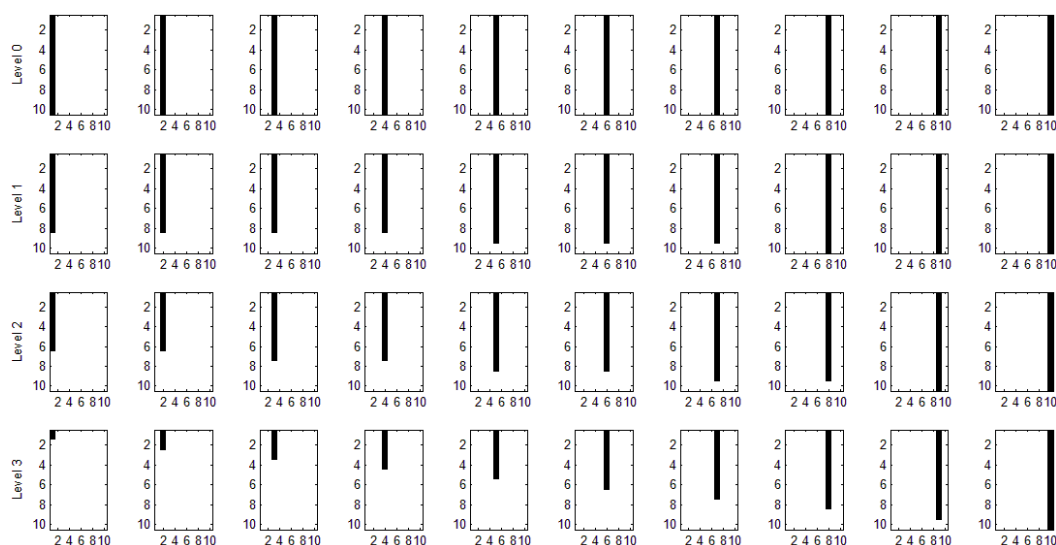


Figure 4.3: Example of different activation variability levels: Level 0: No activation variability. Level 1: Low activation variability. Level 2: Medium activation variability. Level 3: High activation variability. Colours: black (1, active neuron), white (0, inactive neuron).

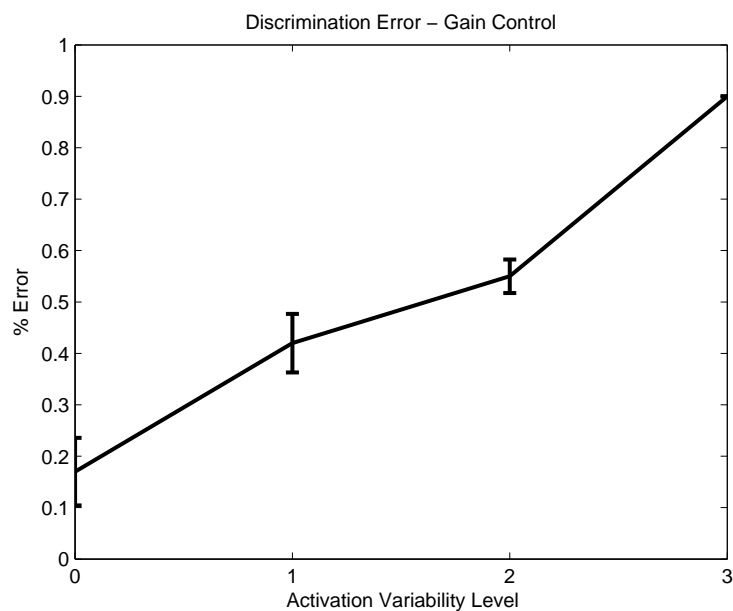


Figure 4.4: Percentage of error based on activation variability level introduced at input. Error which tends to its maximum when activation variability increases.

4. EXPERIMENTS AND RESULTS

their probabilities (Fig.4.5).

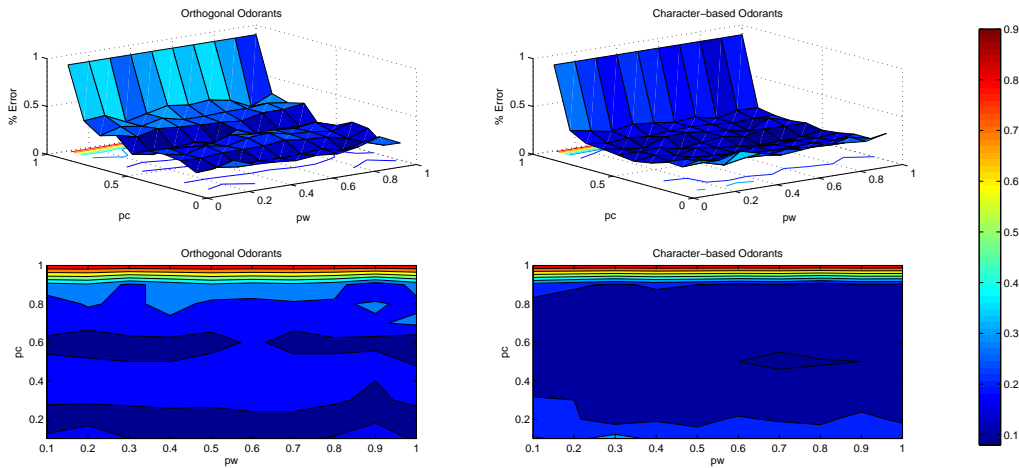


Figure 4.5: Relationship between error rate and connection probabilities for orthogonal (left panels) and character-based (right panels) odorants.

As shown, the p_c variability influences on results, while p_w variability does not have notable relevance for these. On the other hand, it seems that, at least for orthogonal odorants, discrimination error is lower when p_c probability is lower too.

4.1.2.2 Hebbian probabilities

The reason that p_w connection probability is not relevant is due to Hebbian learning, which has its own probabilities, p_+ and p_- . To know how these probabilities influence on model, we will obtain the percentage of discrimination error for all possible combinations of them (Fig.4.6).

As we can see, the discrimination error decreases when Hebbian probabilities are low, where p_+ probability seems be more relevant than p_- , at least when this probability is low.

Another observation can be made is that, for orthogonal odorants, minimum discrimination error occurs when there are not Hebbian learning. Our explana-

4.2 Threshold comparison

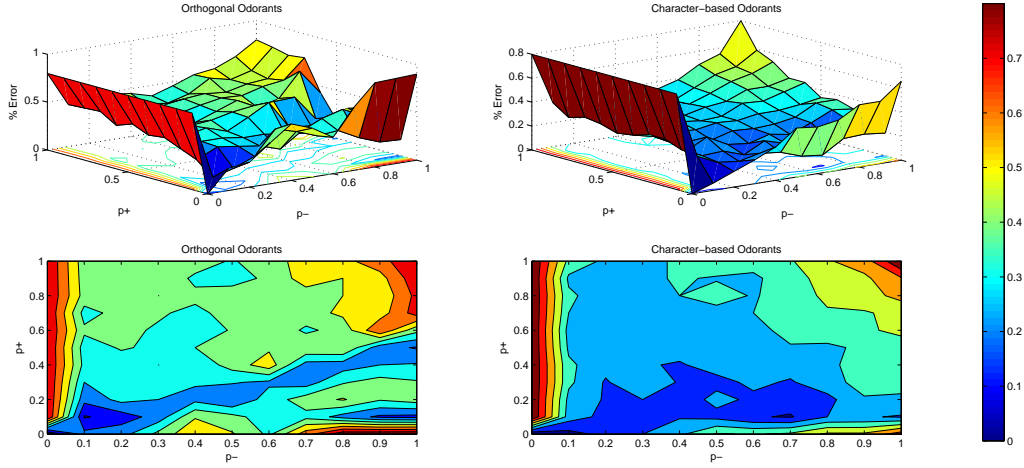


Figure 4.6: Relationship between error rate and Hebbian probabilities for orthogonal (left panels) and character-based (right panels) odorants.

tion for this behaviour is that using homogeneous threshold, which are obtained by exhaustive search, compensates the lack of learning when we have orthogonal odorants, which are very simple and completely separable. Moreover, other studies showed that Hebbian learning increases odorant discrimination when the number of training examples also increases [22]. Being observed that from 1000 training examples, Hebbian learning ability to discriminate odorants increases drastically, while, in our case, we have 15 or 30 odorants. However, this behavior may be interesting to study, as the lack of learning for the C matrix was studied [16].

4.2 Threshold comparison

Noting the relevance of in the parameters of the model, we proceed to make the comparison between different types of thresholds. We divide the results of this comparison in two parts. First, we show the results for different sets of odorants: 15 orthogonal odorants, 30 orthogonal odorants, 15 character-based odorants and 30 orthogonal odorants; and different connection probabilities for the hidden layer, p_c . Finally, we present the results for a particular case, which shows the relationship between discrimination error and spikes rate.

4. EXPERIMENTS AND RESULTS

4.2.1 Different sets of odorants and connection probabilities

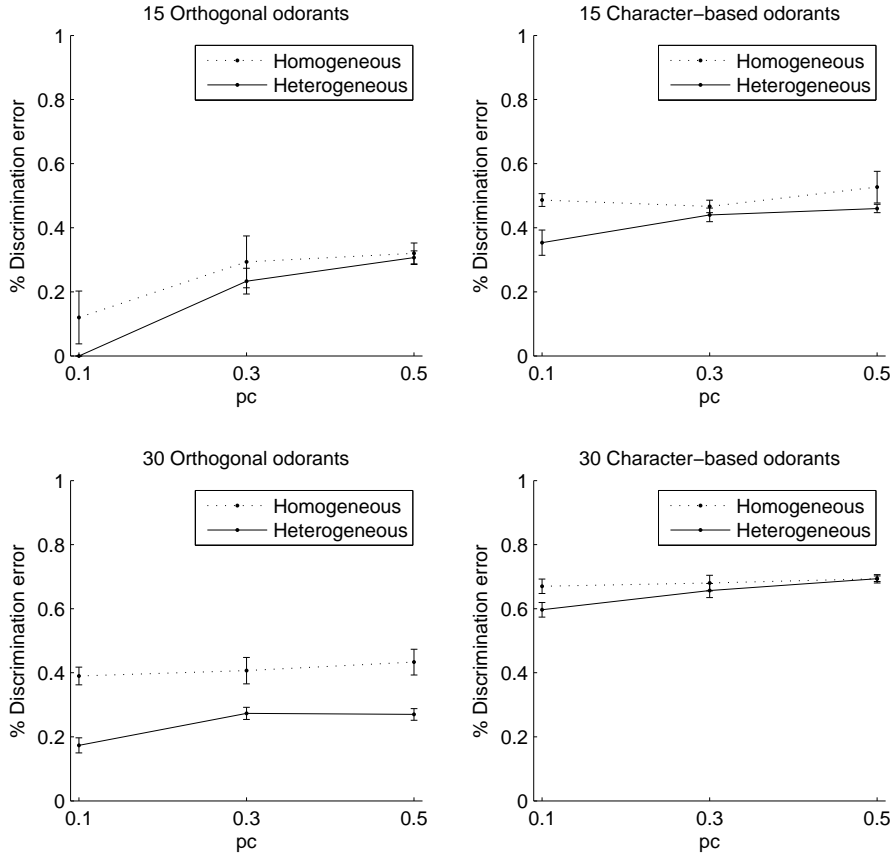


Figure 4.7: Comparison of the different types of thresholds (homogeneous and heterogeneous) for different sets of odorants and connection probabilities with noise and the Hebbian learning probabilities which minimize the discrimination error. Sample means with 95% confidence intervals of standard errors (SE).

We have made 10 simulations for each set of odorants. We have done these simulations for different connection probabilities for the hidden layer (p_c), different Hebbian learning probabilities (p_+, p_-) and noise presence (absent or present). We have used low connection probabilities for p_c (0.1, 0.3, 0.5) based on studies that confirm this [15, 25], a probability for p_w (0.5) because it is applied to a matrix with learning, and selected Hebbian learning probabilities which have been previ-

ously studied [22]. Using this Hebbian learning over 20 time steps.

These averaged results (Fig.4.7) show that heterogeneous thresholds achieve lower discrimination errors. As they show how discrimination error increases with connection probability and number of odorants. Furthermore, by comparing these results with those obtained for odorants without noise (orthogonal odorants: 0.3% Homogeneous, 0.1% Heterogeneous; character-based odorants: 0.5% Homogeneous, 0.4% Heterogeneous), we can observe that the model is tolerant to noise and therefore it is robust.

High values for the discrimination error in the case of character-based odorants can be explained by the similarity of some odorants, high noise which has been introduced in the input layer but above all because there is not a gain control. Standard deviation in the number of active neurons for orthogonal odorants is 0 (gain control), but for the character-based odorants is around 16.632 (standard deviation is 16.763 for set of 15 odorants, and 16.501 for set of 30), a high value if we take in consideration the results seen in Gain Control.

4.2.2 Discrimination error - spike rate

We have taken the averaged results, which we have seen above, and observed the relationship between discrimination error and spike rate for a particular case (spike rate can be observed in the dotted line in Fig.4.8).

These results show that minimum discrimination error is related to a low spike rate. This proves our hypothesis that high population sparseness in KC layer improves odorant discrimination.

The reason for this behavior is that if thresholds are too high, there will be very few neuron spikes in the hidden layer, and therefore odorant information which arrives to the output layer will be low, making discrimination impossible. However, if thresholds are too low, there will be a lot of neuron spikes in the hidden

4. EXPERIMENTS AND RESULTS

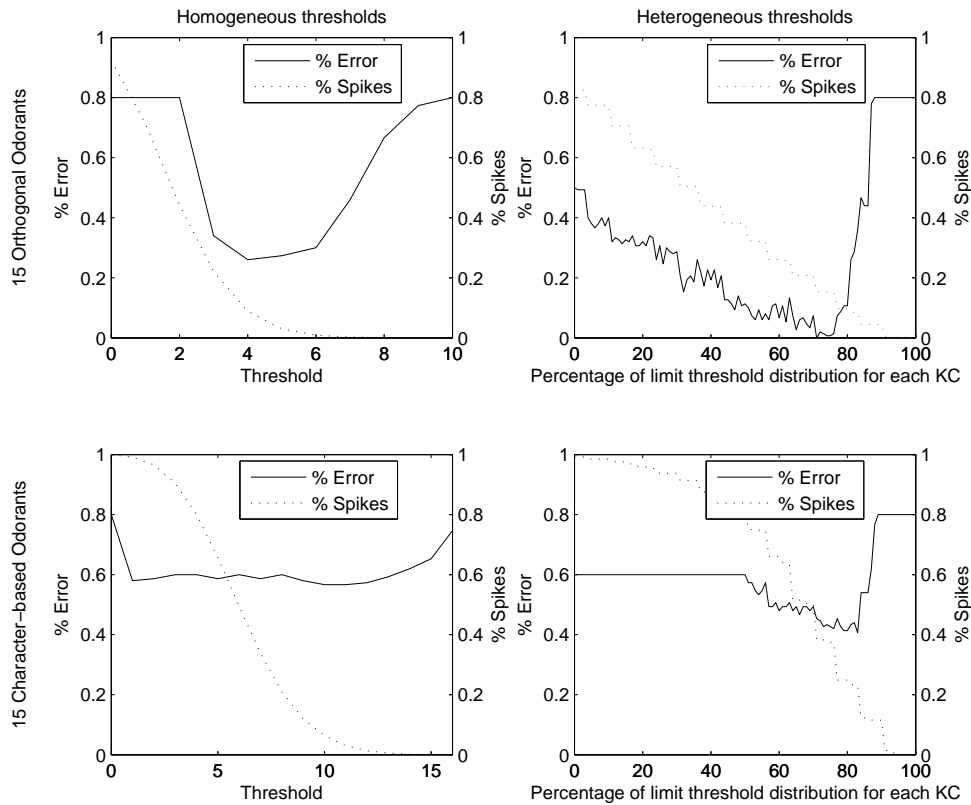


Figure 4.8: Results for 15 orthogonal and 15 character-based odorants with noise and connectivity probability $p_c = 0.1$.

layer, and the output layer will have high population sparseness to make odorant discrimination possible.

Conclusions and future work

The primary objective of this master thesis was to study how the information is processed in the olfactory system. For that we used a simple neural model based on McCulloch-Pitts. We focused on the odorant discrimination, as well as on the way the threshold variability influences this process. We compared the homogeneous and heterogeneous thresholds to find out whether the threshold variability improves the odorant discrimination.

We showed, with simple artificial odorants, that **neural variability using heterogeneous thresholds improves odorant discrimination**. Furthermore, we proved that **discrimination success is related to the sparseness condition** observed in the KC layer, and it increases for **low connection probabilities** between AL and MB.

Moreover, the analysis of the parameters that can influence the model has revealed that, in case of input properties, overlapping does not have much of an impact on discrimination success, when we have overlapping-free information. This is only proved for simple odorant patterns. While gain control is crucial for odorant discrimination. Also, in case of network properties, we proved that for the C matrix, the connection probability, p_c , is relevant, but for the W matrix, the initial connection probability, p_w , this is not the case. W matrix is conditioned by Hebbian

5. CONCLUSIONS AND FUTURE WORK

learning and, therefore, by their probabilities. These probabilities decrease discrimination error when they are low, for our model and odorants used.

Apart from this analysis, we studied other parameters such as the influence of neuronal activity at input, and network dimensionality on the model. However, the computation time needed to make a proper study of these parameters was excessive because of the exhaustive search algorithm for thresholds. Furthermore, we encountered another problem with neural activity, which was also caused by the exhaustive search algorithm. The problem was that if we increase the neural activity of the network, our algorithm will take higher thresholds, and the amount of information received by the MB will be the same, implying that the results obtained for different neural activities are similar.

Consequently, the remaining analysis is one of the works that will take place in the future, but it will not be the only one. Once we get there, the first steps will be to develop an efficient search algorithm for thresholds [17, 18], that replaces current exhaustive search of thresholds and avoids the computation time problem mentioned above. This algorithm will allow us to minimize discrimination error and neuronal activity in the hidden layer (sparseness condition) by supervised learning. Secondly, we will use in our model real odorant data obtained by artificial noses in order to test this new algorithm.

CHAPTER

6

Publications

This work resulted in the following paper presented at the conference last IWINAC 2013:

Neuron Threshold Variability in an Olfactory Model Improves Odorant Discrimination Aaron Montero, Ramon Huerta, and Francisco B. Rodriguez IWINAC 2013, Part I, LNCS 7930, pp.16-25. 2013 (Article which received the award for **”Best paper in Biocomputation”**).

Also it will lead to a new paper that will be sent to a specialized journal in the field:

Computational Enhancement by Neural Variability Aaron Montero, Ramon Huerta, and Francisco B. Rodriguez

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