Specialist neurons in feature extraction are responsible for pattern recognition process in insect olfaction

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\textbf{Abstract.} In the olfactory system we can observe two types of neurons based on their responses to odorants. Specialist neurons react to a few odorants, while generalist neurons respond to a wide range of them. These kinds of neurons can be observed in different parts of the olfactory system. In the antennal lobe (AL), these neurons encode odorant information and in the extrinsic neurons (ENs) of the mushroom bodies (MB) they can learn and identify different kinds of odorants based on the selective and generalist response. The classification of specialists and generalists neurons in Kenyon cells (KCs), which serve as a bridge between AL and ENs, may seem arbitrary. However KCs have the unique mission of increasing the separability between different odorants, to achieve a better information processing performance. To carry out this function, the connections between the antennal lobe and Kenyon cells do not require a specific connectivity pattern. Since KCs can be specialists or generalists by chance and olfactory learning performance relies on their feature extraction capabilities, we analyze the role of generalist and specialist neurons in an olfactory discrimination task. Role that we studied by varying the percentage of these two kind of neurons in KC layer. We determined that specialist neurons are a decisive factor to perform optimal odorant classification.

\textbf{Keywords:} Pattern recognition, specialist neuron, generalist neuron, olfactory system, neural variability, supervised learning, heterogeneous threshold lateral inhibition.

\section{Introduction}

Insects possess an olfactory system that identifies a large number of odorants using a simple structural organization. This neural network allows pattern recognition under different environmental conditions, gas concentrations, and mixtures. Inside this network, there are two kind of neurons based on their
response to odorants: specialists and generalists. Specialist neurons have selective responses to stimuli and generalist neurons code for multiple stimuli [19, 4, 20, 26, 21]. The role of both classes of neurons in the olfactory system is still under debate [10, 4]. However, it is suggested that specialist neurons are crucial for discrimination, while generalist neurons play a key role in extracting and discovering common features [25]. This Hypothesis has been supported, in the case of the role of specialist neurons using experimental studies [7, 2] and computational models [16]. In this paper we investigate the impact that changing the ratio of specialists and generalists has in the performance in a pattern recognition task.

To answer this question, we focused on Kenyon cells of the mushroom body. While projection neurons of the antennal lobe and extrinsic neurons of the mushroom body have a reason to react to certain odorants, the first ones encode the odorants and the second ones identify them, the response to different odorants of Kenyon cells is circumstantial. The role of Kenyon cells in the olfactory systems is primarily to increase the separability of different odorants to facilitate subsequent learning and identification. It has been observed that for this task the Kenyon cells do not require specific connections with the antennal lobe [14, 24]. In fact, these connections vary between individuals of the same species. Thus, it seems that there is not a criterion by which a neuron is defined as a generalist or specialist. Therefore, aspects of KCs as:

- arbitrary creation of their connections from AL and, therefore, their specialist and generalist neurons,

- large number of neurons (50,000 in locust), and

- being the final stage of feature extraction started in the olfactory receptor neurons (ORNs).

are the reasons why we consider them the best ones to analyze the implications of varying the number of generalist and specialist neurons for pattern recognition process.

In order to classify Kenyon cells as specialist or generalist neurons, we use neural sensitivity. This can be estimated from the distribution of neurons that respond to $n$ out of $N$ different stimuli [20, 21]. However, because the boundary between specialists is arbitrary in a continuous distribution of sensitivity, a systematic analysis is required for a proper differentiation of these neurons. We will define, therefore, the minimum percentage of reaction to an odorant for which a neuron can be considered sensitive to this, as well as the sensitivity degree that makes a neuron be specialist or generalist.

To perform this study, we used a single-hidden-layer neural network that represents a computational model focused on the AL and MB, which we can see in Fig. 1. The input of this neural network is the AL activity, which is connected to MB through a non-specific connectivity matrix [14, 24, 6]. The other layers, hidden and output, are made of KCs and ENs respectively. These neurons are connected by a connectivity matrix subjected to learning that is modulated by
Hebbian learning [3, 1]. ENs give us the final result of the classification once the lateral inhibition process between them has finished [13, 3].

We will show in results that the most specialist neurons as responsible for odorant classification.

Fig 1. Neural network model. Olfactory system of insects can be decomposed into 3 parts: olfactory receptor neurons (ORN), antennal lobe (AL) and mushroom body (MB). The ORNs send olfactory information in a fan-in phase to AL that transmits this in a fan-out phase to MB. The olfactory information is received by Kenyon cells (KC), which is responsible for increasing the separability of information and transmit it, in a fan-in phase, to extrinsic neurons (EN), responsible for its learning and classification. Our model is a single-hidden-layer neural network with AL as input ($X$) connected by a random matrix ($O$) to KCs, the hidden layer ($Y$), KCs are connected by a matrix with Hebbian learning ($W$) to ENs, the output layer ($Z$). The thresholds for the hidden and output layer are $\theta_j$ and $\varepsilon_i$ respectively. The Heaviside activation function $\varphi$ is 0 when its argument is negative or 0 and 1 otherwise.
2 Neural and network model

The model focuses on the AL and MB, dividing the MB into KCs and ENs (Fig. 1). Therefore, the network model is a single-hidden-layer neural network with an input layer of 1,568 neurons (due to our patterns), a hidden layer with 50,000 neurons (locust [12] has a ratio of 1:50 between neurons of the AL input layer, and KCs, hidden layer, and similar dimensions to those we selected) and an output layer with 100 neurons. These neurons of the output layer are divided into populations of 10 neurons, a population for each pattern class, and there are lateral inhibitions between these populations [1]. This facilitates that only a specific population of neurons reacts to a particular pattern class.

The KC neurons of the MB display very low activity [19]. These neurons are inactive most of the time, with a mean firing frequency lower than 1 Hz. But when they are activated, their neuronal response is produced by the coincidence of concurrent spikes followed by a reset. Bearing in mind this behavior, we chose the McCulloch-Pitts model in all neurons of the hidden and output layers.

The connectivity matrices, $C$ and $W$, are initialized at the beginning of each learning process. These matrices are created by using the connection probabilities, $p_c$ and $p_w$, as a threshold on matrices with random values uniformly distributed. The connectivity matrix $W$ is updated using Hebbian learning [8, 9], which is subjected to a target $t$ of the output layer (supervised learning), while matrix $C$ remains fixed.

The synaptic model is binary. Therefore, activation states and weights can only take values 0 or 1.

![Fig. 2. Neural sensitivity depending on the response threshold. Response threshold is the percentage of odorants from a class that a neuron needs to respond to be considered sensitive to it. When response threshold rises, the neurons that respond to few stimuli increase in number compared to those that respond to many of them.](image-url)
3 Neural sensitivity

To define KCs as specialist or generalist neurons, we use a criterion based on neural sensitivity [20, 21]. Neural sensitivity represents the number of neural responses of a neuron to different stimuli. However, it is necessary to define what is the minimum response degree to a pattern class so that a neuron can be considered sensitive to this. To analyze this response degree, we used different response thresholds and we present in Fig. 2 some cases: the neurons have to respond to 20/40/60/80% of patterns for a specific odorant to be considered sensitive to it.

As we can see in Fig. 2, when response threshold is higher, the number of neurons that respond to no or few pattern classes increases, while the number of those respond to all or many of them decreases. Since specialist neurons let odorant discrimination, we are interested to have more neurons of this kind. Also a neuron should be considered sensitive to a pattern class when it responds to this in most cases. For that, we consider that response threshold of 80% as desirable response percentage.

Fig. 3. Generation of KC layer according to the selection criteria of generalist and specialist neurons. We define specialist and generalist neurons by neural sensitivity. To perform this, we initially define that specialist neurons have a sensitivity of 5 or less and generalist ones have a sensitivity of 6 or more. Subsequently, we start to remove neurons with intermediate sensitivity until we only have neurons with sensitivity of 1 (specialists) and 10 (generalists), see left panel. Once these sensitivities are defined, we extract generalist and specialist neurons from KCs, excluding the neurons with sensitivity 0, and we create two sets with them. Then, a new KC’ layer is generated, with the same dimensions than the original one and the desired percentage of generalist and specialist neurons, see right panel.
4 Selection criteria of generalist and specialist neuron

At the beginning of each simulation, we determine which kinds of sensitivities define neurons as generalist or specialist. To perform this, we excluded neurons with sensitivity 0. Once these sensitivities are defined, we extract these neurons and create with them two sets, one generalist and other specialist, as we can see in right panel of Fig. 3. We create a new KC layer with the same dimensions than the original one by extracting neurons of these sets, which let us to control the percentages of these two kinds of neurons. The neural network starts with all generalist neurons and we gradually replace these by specialist neurons and observe how the classification error varies during this process.

Because we used 10 kinds of patterns, we established different definitions of specialist and generalist neurons in terms of neural sensitivity. First, we defined that specialist neurons have a sensitivity of 5 or less and generalist ones have a sensitivity of 6 or more. Subsequently, we start to remove neurons with intermediate sensitivity until we only have neurons with sensitivity of 1 (specialists) and 10 (generalists), see left panel of Fig. 3. This way of defining neurons as specialists and generalists allow us to assess the relevance of neurons with intermediate sensitivities.

5 Odor patterns

We used the MNIST digits [11], which have dimensions of $28 \times 28$ pixels, and binarized their information on values of 0 and 1. Since antennal lobe has a gain control mechanism [18, 22, 23] that keeps a constant neuronal activity for all odorants and their alterations (concentrations, mixtures, etc.), each MNIST pattern is subjected to gain control too. The method for performing this gain control is simple, we duplicated the information of each pattern to use their positive and negative image [9], see Fig. 4.

![Gain control in the patterns](image)

Fig 4. Gain control in the patterns. Example of MNIST digit patterns with gain control where two populations of neurons respond inversely to each other.

We used 100 patterns, 10 patterns for each class. In the learning process these patterns are divided into 5 parts, taking one as test set and the other four as
training set. This process is repeated 5 times, in order to each part can be used as test set (5-cross-validation). Thus, the training data set has 80 patterns and test set has 20 patterns.

6 Results

To analyze what happens if we vary the proportion of generalist and specialist neurons in KC layer, we used a computational model focused on AL and MB where we introduced 100 MNIST digits, 10 for each pattern class, as input. The following averaged results for the test set were obtained by supervised learning. We ran 10 simulations with 5-cross-validation. This assumes an average of 50 results for each of the system configurations shown below.

![Image of graph showing test classification error for different combinations of generalist and specialist neurons in KC layer.](image)

**Fig 5. Test classification error for different combinations of generalist and specialist neurons in KC layer.** We can observe that the minimum error, for a $p_c = 0.1$, does not vary when intermediate neurons are eliminated. Therefore, these neurons do not seem to participate in classification success, as generalist ones increase its error. The $S$ value indicates the maximum number of different stimuli that make firing a specialist neuron. On the other hand, the $G$ value indicates the minimum number of different stimuli for a generalist ones, see left panel of Fig. 3.

We have used a $p_c$ connection probability of 0.1 [15, 17], for C matrix that connects AL to MB. We initialize the weights of W matrix which connects KCs to ENs, with an intermediate $p_w$ value, 0.5, before Hebbian learning [9]. The
combination of values for Hebbian probabilities that we selected are $p_+ = 0.1$ and $p_- = 0.05$ by their good performance [8].

6.1 Only the most specialist neurons are required for a good odor classification

The minimum classification error in Fig. 5 is 18.5% that are consistent with other studies [9]. Since the neural selection process reaches its minimum with 100% of specialist neurons, we can say that these neurons are responsible for odorant classification. This also happens when we do not introduce changes in KC layer. In this case, KC layer neurons are mostly specialists, as we can see in left panel of Fig. 3, and therefore we obtain a similar error to the previous one. Because its percentage of specialist neurons place its result on the right side of the error curve, Fig. 5. We also note that the minimum classification error does not change when we have only the most specialist neurons or we also have some neurons with intermediate sensitivities. This leads us to think that neurons with intermediate sensitivities do not contribute to achieve this minimum error. On the other hand, we can observe that classification error increases when in the KC layer there are more generalist neurons.

7 Discussion and conclusions

The objective of this work is to investigate what happens if we change the percentage of generalist and specialist neurons during the feature extraction process, to learn about how odorant information is processed at olfactory system. To investigate this point, we used a simple model that retains the most relevant structural properties of the olfactory system. This model focuses on the AL and MB, where the input to single-hidden-layer neural network is the AL activity. The other layers, hidden and output that represent the MB, are composed by KCs and ENs respectively. These latter layers are connected by a connectivity matrix that implements a supervised Hebbian learning. Also ENs possess a lateral inhibition process between the different populations of neurons that are specialized in a particular pattern class. Using MNIST digits as odorant information, we analyze the neural sensitivity of each neuron and define these ones as a specialist or generalist by this information. Once we established generalist and specialist populations, we begin to vary their proportions in the KC layer. This process that not only allows observing the behavior of the generalist and specialist neurons, but also those with intermediate sensitivities.

We show that in the feature extraction phase, pathway from ORNs to KCs, the achieved minimum error in the learning phase, ENs, is obtained by the most specialized KCs. This is clearly seen in the case of neural selection, Fig. 5, since the classification error does not change when we also have neurons with intermediate sensitivities. However, it also happens before this modification of KC layer, left panel of Fig. 3, where almost all neurons are specialist. On the
other hand, this error increases for the most generalist neurons and those with intermediate sensitivities. These results are consistent with researches about Drosophila [7, 2] that measure the KC activity by calcium images, since their experimental results reveal that KCs show high selectivity for a particular odorant.

These results raise questions on the functional role of generalist neurons and neurons with intermediate sensitivities. It is possible that in other kind of problems, with a larger degree of overlapping between patterns, these neurons could have a greater role in classification. However, for this problem, they are not needed. Other aspects such as gain control and lateral inhibition of ENs deserve further analysis, since their impact in odorant classification seem critical as we observed during this work. On the other hand, we need to study the different aspects of the neuronal network for their relationship with the existence of specialist and generalist neurons. For example, the impact on these neural populations by the network dimensionality and fan-in/out phases. Their relationship with $p_c$ and what is the value of this probability that provides an optimal configuration of specialist and generalist neurons. As if the existence of variability between neuronal thresholds affects these populations. All these points reveal details about the role of these kinds of neurons and allow us to understand how olfactory system processes odorant information.

Acknowledgments

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References