Regulation of specialists and generalists by neural variability improves pattern recognition performance

Aaron Montero [a], Ramon Huerta [a,b], Francisco B. Rodriguez [a]

[a] Grupo de Neurocomputación Biológica, Dpto. de Ingeniería Informática, Escuela Politécnica Superior, Universidad Autónoma de Madrid, 28049 Madrid, Spain
[b] BioCircuits Institute, University of California, San Diego, La Jolla, CA 92093-0402, USA

ARTICLE INFO

ABSTRACT

To analyze the impact of neural threshold variability in the mushroom body (MB) for pattern recognition, we used a computational model based on the olfactory system of insects. This model is a single-hidden-layer neural network (SLN) where the input layer represents the antennal lobe (AL). The remaining layers are in the MBs that are formed by the Kenyon cell (KC) layer and the output neurons that are responsible for odor learning. The binary code obtained for each odorant in the output layer by unsupervised learning was used to measure the classification error. This classification error allows us to identify the neural variability paradigm that achieves a better odor classification. The neural variability is provided by the neural threshold of activation. We compare two hypotheses: a unique threshold for all the neurons in the MB layer, which leads to no variability (homogeneity), and different thresholds for each MB layer (heterogeneity). The results show that when there is threshold variability, odor classification performance improves. Neural variability induces populations of neurons that are specialists and generalists. Specialist neurons respond to fewer stimulus than the generalists. The proper combination of these two neuron types leads to performance improvement in the bioinspired classifier.

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1. Introduction

The olfactory system of insects is made of a complex neural machinery made of at least four processing layers [1] capable of classifying a large number of odorants from an unlimited number of stimuli that are highly variable [2] (different gas concentrations, mixtures, etc). The main reasons to chose the olfactory system of insects are the simplicity of the structural organization [3–10], the nature of the neural coding [2,11–19], the advent of the genetic manipulation techniques that isolate brain areas during the formation of memories [20–23], and the extensive odor conditioning experiments that shed light into the dynamics of learning during discrimination tasks [24–29]. Olfactory systems implement simple mechanisms to realize a quick and stable odorant discrimination [30], a goal we want to achieve through computer modeling. Our focus in this work is on neural variability. The driving question is how neural heterogeneity impacts system performance in pattern recognition.

Neural diversity is widespread in the brain, even within the same neural types there is a large heterogeneity in the intrinsic properties and the connectivity patterns, one hypothesis that explains this puzzling observation is functional differentiation within the same types [31]. Another explication is the hypothesis of homeostatic regulation of neural systems, in particular in the olfactory system [32–35]. However, as we show in this paper, neural heterogeneity can be very beneficial in terms of improving performance in pattern recognition tasks.

Typical models of the olfactory system use very little variability in the excitability in the neurons, implemented by fixed neural thresholds. However, recent applied research on artificial noses determined that using heterogeneous detection thresholds for different odorants, you can improve gas discrimination [36,37]. This is one of the motivations why we study neuron threshold variability in the information process achieved by the neural olfactory system. Additionally, it has been reported that neural thresholds vary in olfactory receptor neurons (ORN) [38] and in Kenyon cells (KCs) [39]. Neural variability in the form of a broad distribution of thresholds is a generic property of neurons in the brain.

To investigate if neural threshold variability increases odorant classification performance, we use a simple model of the olfactory system [40,41] based on McCulloch–Pitts neurons [42]. The insect olfactory pathway starts at the antenna, where a massive number of receptors encoding the odor stimulus in a high-dimensional space. This information is then sent to the AL for additional processing. The AL exhibits complex dynamics produced by the interaction of its

excitatory and inhibitory neural populations [43,44,13]. The excitatory cells are called projection neurons, PNs, because they only transmit the result of AL computation to deeper regions. Moreover, recordings from the AL in the locust indicate that the activity in the projections of the excitatory neurons of the Locust remains nearly constant despite large variations of the odor concentration [45]. Therefore, a gain control mechanism [46,47] controlling neuronal activity in the AL is likely to exist [48]. The projection neurons deliver the AL output to a very large number cells of Kenyon of the MB using a fan-out connectivity that increases the separability between different odor encodings. This fan-out phase combined with the sparse firing for these KCs [39,49,50] facilitates the odorant discrimination process realized in a fan-in phase by output neurons, which are involved in memory formation and storage [51,52,20].

We focus on the AL and MB (model in Fig. 1), where the input to single-hidden-layer neural network (SLN) is the AL activity, which is connected to MB through a non-specific connectivity matrix [50]. The reason for this non-specific connectivity matrix is due to the individual connection variability of insects of the same species [53,54]. 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 [52,55].

Our goal is to analyze, first, how information is processed in the olfactory system and, second, the role of threshold variability in this system. Hence, we compare the existence of threshold variability (heterogeneous thresholds) with their absence (homogeneous threshold) to determine whether this improves odorant classification. To this end, we measure the classification error obtained in the output layer after applying unsupervised learning. A correctly classified odorant always generates the same output pattern class A' for a given input pattern class A.

We conclude that odorant classification can improve with neuron threshold variability or heterogeneity, leading us to label neurons as generalists or specialists [56,57]. Moreover, the classification performance is closely related to sparse activity of the KC population [39,58] which can be regulated by neural thresholds too in addition to the connectivity degrees [50].

2. Olfactory model

2.1. Neuron model

In locusts, activity patterns in the AL are practically time-discretized by a periodic feedforward inhibition onto the MB
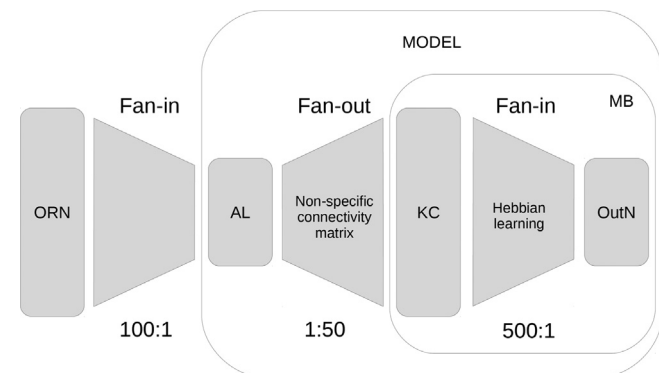
calyxes [59] with very low KC activity [39]. Thus, the information is represented by time-discrete, sparse activity patterns with the KCs locked on the 50 ms local field potential oscillation cycle. Because of these neurons are inactive most of the time, but being activated, their neuronal response is produced by the coincidence of concurrent spikes followed by a reset, we have used the McCulloch–Pitts model [42] in all neurons of the hidden and output layers, as mentioned above. This neuron model uses the threshold step function as an activation function. Therefore, we have the following (see network model in Fig. 2):

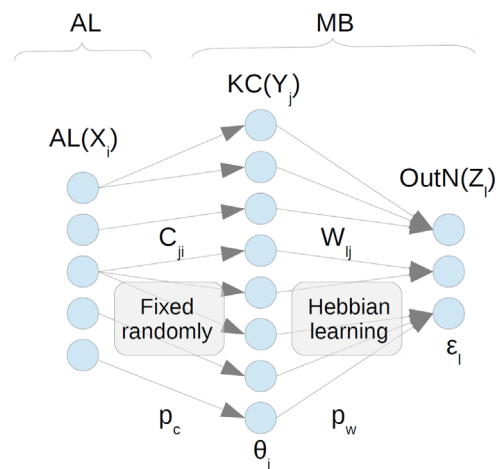$$y_j = \varphi\left(\sum_{i=1}^{N_{AL}} c_{ji}x_i - \theta_j\right), \quad j = 1, \ldots, N_{KC},$$

$$z_l = \varphi\left(\sum_{j=1}^{N_{KC}} w_{lj}y_j - \varepsilon_l\right), \quad l = 1, \ldots, N_{OutN}, \quad (1)$$

where x_i, y_j and z_l are activation states for an input, a hidden and an output neuron, respectively, c_{ji} and w_{lj} are weights linking two neurons, θ_j and ε_l are thresholds for the hidden and output neuron, respectively, and φ is the Heaviside activation function. The Heaviside activation function φ is 0 when its argument is negative or 0 and 1 otherwise.

2.2. Network model

The network model is a SLN (Fig. 2) with an input layer of 50 neurons, a hidden layer with 2500 neurons (locust has a ratio of 1:50 between neurons of the input and hidden layer) and an output layer with 5 neurons [41] (Table 1). These dimensions were chosen because they ensure a high probability of classification for the input used [40] for a relatively low computational cost.

The connectivity matrices, C and W, are initialized at the beginning of each learning process. We generate a matrix with random values uniformly distributed in the range [0, 1]. The binary connection values in the connectivity matrix use p_c and p_w, as a threshold on the values of the random matrix such that if an entry value is equal or less than p_c or p_w, the connection is established otherwise is set to 0. The connectivity matrix C remains fixed throughout the learning process, while the connectivity matrix W is updated using Hebbian learning. The synaptic model of this network is completely binary. Therefore, activation states for a

Fig. 1. The structure of the model is divided into the antennal lobe (AL) and mushroom body (MB). The MB is divided into the Kenyon cell (KC) layer and output neurons (OutN). The ratios shown are taken from the locust brain size in this particular case.

Fig. 2. Network model composed of three layers: antennal Lobe, Kenyon cells and output neurons. The input layer X is connected to the hidden layer Y by a random matrix C. This hidden layer is connected to the output layer Z by other random matrix W, whose weights are updated by Hebbian learning. These random matrices are created with connection probabilities p_c and p_w. The thresholds, biases, of hidden neurons and output neurons are θ and ε respectively.