The role of neural synchrony and rate in high-dimensional input systems. The Antennal Lobe: a case study.

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***Abstract*— Dealing with high-throughput information systems is becoming an everyday problem in many fields of science, as technological advances improve our ability to gather data. In particular, the information encoding problem in high-dimensional spaces is a crucial aspect to consider. In fact, biological systems are known to be very efficient at encoding and processing high-dimensional information. Here we propose a biologically-based solution that mimics the neural processing performed by the Antennal Lobe of insects. Based on our understanding of this system, our model exploits plausible neural mechanisms to transform the massive and high-dimensional spatial and temporal input of the olfactory receptor neurons into a neural population encoding based on synchrony and frequency, consistent with known physiology. We demonstrate the capabilities of our Antennal Lobe model in the context of a classification task of different olfactory stimuli of varying concentrations. We show that the generated neural representation conveys both the identity and the concentration of each stimuli.**

I. Introduction

Making sense of large amounts of information is a growing issue in disciplines as diverse as astronomy, biology, engineering or economics to name but a few. Many techniques for feature extraction and feature selection have been proposed but the question of what the optimal encoding system would be remains unanswered. Biological systems face also this kind of problems, since they are equipped with massively high-dimensional sensor modalities. In effect, they have developed specialized neural structures to deal with these high-throughput sources of data. Understanding how neural systems recode their perceptual input to enable further processing by subsequent systems may provide us with valuable tools to approach that same problem. Consequently, we set forth to analyze the moth olfactory system, which has been widely studied and whose functional and anatomical organization is well understood.

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Insects in general and moths in particular are studied because of their keen sense of olfaction. While they are capable of detecting minute amounts of chemicals (pheromones, plant volatiles, etc.), they are also able distinguish among similar stimuli – carrying different ratios of the same odorants [1] – and to classify different concentrations of the same chemical as belonging to the same stimulus. Contrasting with the moth's astounding capacity to deal with odors, the size of its brain is of only about 1 mm^3, which makes it an ideal target to study. In this paper we will analyze the properties of the moth Antennal Lobe (AL), the first neuropil in the olfactory pathway that is known to play a crucial role in the preprocessing and encoding of olfactory information.

A. Overview of the Antennal Lobe

The Antennal Lobe represents the first stage in the olfactory processing in insects [2]. It is divided in globular structures called glomeruli which receive sensory input from the axons of Olfactory Receptor Neurons (ORNs). ORNs express receptors in the antennae and respond to the binding of odor molecules to these receptors. ORNs expressing similar receptors usually converge onto a single glomerulus, so there is a close relationship between the number of ORN classes and the number of glomeruli in the AL. It has been suggested that the convergence of related ORNs onto the same glomeruli makes the AL capable of coping with noise and variability at the sensory level [3].

Two types of neurons receive input from ORNs in each of the glomeruli: Projection Neurons (PN) and Local Neurons (LN). PNs integrate the activity of a glomerulus and transduce it to higher brain areas such as the Mushroom Bodies (MB), known to be involved in the learning and memory of odors. The LNs are populations of neurons that laterally interconnect PNs, shaping their activity through inhibitory interactions and giving rise to a spatio-temporal code in the AL that encodes the features of odor stimuli [4], [5]. Figure 1 provides a functional diagram of this neuropil.

The interplay of two kinds of inhibitory mechanisms, associated with two subtypes of LN and mediated by the fast $GABA_A$ and the relatively slow $GABA_B$ neurotransmitters, gives rise to characteristic Local Field Potential (LFP) oscillations of around 20 Hz [6]. PNs fire in synchrony with those oscillations in response to odor stimuli and their action potentials are picked up by Kenyon Cells (KC) [7]. KCs are the intrinsic neurons of the Mushroom Body, each of which samples approximately half the PN population [4] and generates sparse representations of olfactory stimuli [8].

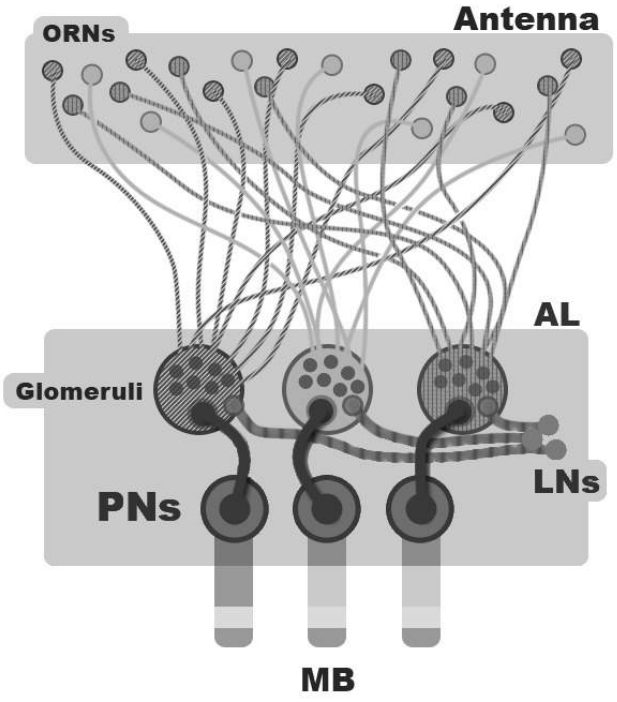

Fig. 1. Functional representation of a generic AL. ORNs belonging to the same class converge onto the same glomerulus. LNs interconnect PNs by arborizing in the glomeruli and shaping their activity. PNs axonal ends travel to higher brain centers such as the MB.

B. Dimensionality reduction in the Antennal Lobe

In a recent study, it has been proposed that $GABA_A$ and $GABA_B$ inhibitory synapses modulate synchrony among PNs, giving rise to stimulus-dependent assembly activation patterns [9]. This is complementary to the, so called, Temporal Population Code (TPC), that has been observed in vertebrate neo-cortical networks and seems to depend on dense excitatory coupling [10] and that has shown to be consistent with both invertebrate and vertebrate physiology [5], [11], [12]. The model presented in [9] explains the rise of oscillations in the AL and explores the possibility of storing and retrieving information in laterally interconnected networks. However, it makes several assumptions that undermine its ability to inspect the role of the AL in dimensionality reduction. Here, we propose several improvements to that model in order to make it able to process real-world stimuli. We show that the new model is able to recode high-dimensional sensory input in compact neural representations that retain information of its identity and concentration.

II. Methods

A. Original model

Our model is a further extension of the one presented in [9]. The original model uses quadratic Integrate-and-Fire neurons to simulate one hundred PNs which receive constant excitation and are interconnected by two populations of inhibitory noisy LNs. The topology of the inhibitory connections is trained so that when a particular subset of them is active, a specific assembly of PNs fires synchronously. The presence of noise in the synapses of that model, which have a 50% probability of failure, is essential for the appearance of these synchronous assemblies. An in-depth description of the model can be found in the Methods section of [9].

B. Changes to the original model

The oscillatory properties of the original model provide us with a useful starting point for our own. The interactions of $GABA_A$ and $GABA_B$ LNs generate LFP oscillations consistent with those of the model's biological counterpart and give us a clear reference for the readout of PN activity. However, since the model assumes constant PN excitation, it does not allow for explicit sensory input. Removing that constant excitation to make the model able to deal with real input abolishes its oscillatory behavior for inputs that activate less than 70% of the PNs. To overcome that problem we apply a soft Winner-Take-All to the PN activity to make sure that 80% of those neurons will always be active. Although the existence of such a mechanism in the AL remains unknown, strong lateral inhibition, such as the one present in this neuropil, has been found to play an important role in its biologically plausible implementation[13].

The original model poses another problem, since it uses binary patterns of activation for assessing the properties of the simulated AL. In contrast, as our model allows explicit input, we exploit the analog nature of the incoming signal, assigning randomized thresholds of activation to the $GABA_A$ interneurons. In this manner, we expect to enrich the representation of odors in our model.

Figure 2 summarizes these changes graphically.

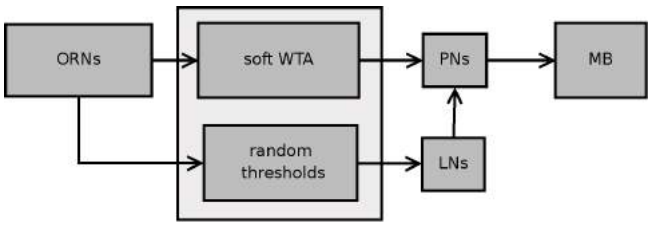

Fig. 2. Overview of the changes to the model. Sensory input coming from the ORNs is preprocessed via a soft-WTA before reaching the PNs and by means of the randomized activation thresholds of the LNs.

C. Model parameters

Our simulated AL consists of one hundred PNs which sample fifty glomeruli associated with fifty different classes of ORNs. The PNs are interconnected via two inhibitory networks of local neurons.

In order to define the topology of the two lateral networks we use the method employed in the original article to calculate the connectivity between the foreground and background of a trained pattern (the *foreground* and *background* categories only make sense in the context of the original article, since its target patterns are trained. We use the same terminology to avoid confusion). The process involves selecting a subset of PNs from the entire PN population as the

foreground group and using the two following rules to define which PNs are connected and by which type of inhibitory neuron:

- Two PNs are linked through a $GABA_A$ LN if the origin and destination PNs belong both to the foreground of the pattern.
- Two PNs are linked through a $GABA_B$ LN if the origin PN belongs to the foreground and the destination PN belongs to the background of the pattern.

Consistent with the behavior of the original model, only the neurons belonging to the foreground group will be able to fire synchronously with the LFP. Consequently, we choose a high percentage (80%) of the PNs as belonging to the foreground in order to retain sufficient encoding capacity. Using that number and applying the rules listed above, we simulate 6320 $GABA_A$ and 1600 $GABA_B$ LNs. Thresholds for activation of the $GABA_A$ interneurons are set randomly in the normalized range comprised between 0 and 1.

Table I presents a summary of the parameters of our model.

TABLE I
MODEL PARAMETERS

Parameter	Value
# ORN types / Glomeruli	50
# PNs	100
# $GABA_A$	6320
# $GABA_B$	1600

D. Synchrony detection criterion

A PN spike happening within the interval delimited by the 5 ms preceding or following the middle point of the falling edge of a LFP cycle is considered synchronous. The number of times a PN fires synchronously with the LFP during the course of a simulation defines its degree of overall synchrony with it.

E. Stimulus generation

Our model possesses fifty different classes of olfactory receptory neurons. We model the stimuli it will have to classify as mixes of fifty ideal components able to bind to only one class of olfactory receptor each. Consistent with other studies in the literature, we provide a static concentration of odorants during the whole stimulus period and suppose a linear response of the ORNs to their concentration.

We define four classes of stimuli, each of them described by fifty random values in the interval comprised between 0 and 0.25. Each of those values is assigned as the concentration of one of the fifty ideal odorants. In order to create different concentrations of the same inputs, we multiply by a factor of 2, 3 and 4 the original stimuli, obtaining a total of four stimuli and four concentrations whose components are normalized between 0 and 1. Figure 3 shows four sample stimuli belonging to the four categories, once read by the PN population. Every time one of these simulated ORNs is sampled during the course of a trial we distort its activation value by adding independent gaussian noise ($\mu = 0, \sigma = 0.001$) to it. We perform five trials for each odor and concentration, for a total of eighty trials.

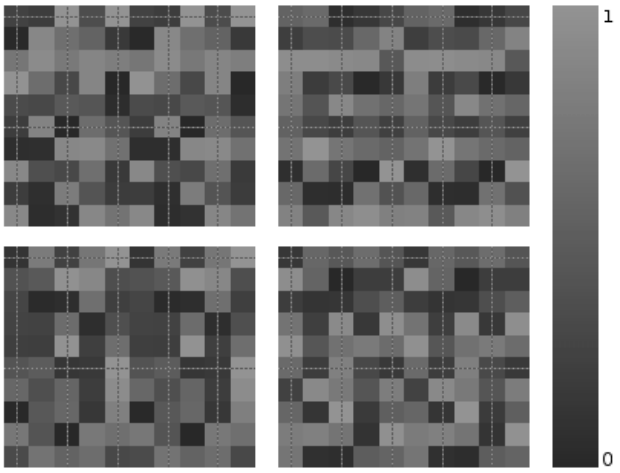

Fig. 3. Graphical Representation of the four categories of stimuli at their highest concentration after being sampled by the PN population. Lighter shades of gray indicate higher concentration.

F. Classification

In order to explore the synchrony patterns picked up by our synchrony detection criterion, we use Principal Component Analysis. We employ a trained linear classifier in order to categorize the stimuli.

G. Simulation environment

The large-scale neural network simulator **`iqr`** [15] is used to perform the experiment described and record its results.

III. RESULTS

Before assessing the coding capabilities of our model, we first establish how much time it takes our AL to achieve a stable synchronization pattern after being exposed to a certain stimulus. In order to calculate that amount of time, we first define a target synchronization pattern by exposing the model to that same stimulus. Once stability is reached, the synchronous PN assembly is defined as our target pattern. On a second simulation, we calculate the similarity between the synchrony pattern being computed and the one found during the previous run as a Signal-to-Noise Ratio value, ranging from 0, for the opposite pattern, to 100, for an identical activation. Figure 4 shows an example of a typical one-second run, in which the network can be seen reaching its final result at 800 ms. From now on, we use a conservative length of 1000 ms to run our simulations.

In our experiments, we expose the AL model to four different concentrations of four different stimuli. Because of the thresholds in the activation of $GABA_A$ LNs, we expect a bigger number of them to be recruited for more concentrated stimuli, enhancing the overall synchrony of PNs to their LFP.

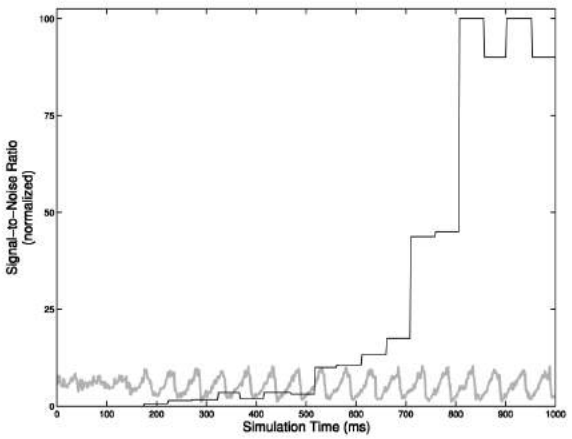

Fig. 4. Signal-to-noise ratio for a simulation of the AL model. After 800 ms of simulation, the PN activity has already converged to its final state. The SNR increases exponentially over time. Values of SNR of under 100% after the 800 ms point indicate a single PN falling out of synchrony. LFP is plotted in light gray and displays the rise of clear oscillations after 200 ms, moment in which the SNR starts to rise.

A PCA analysis of the eighty trials (five trials per class and concentration) reveals no discriminatory power of the first principal component among the four studied types of stimuli. Suspecting that component might reflect the stimuli concentration, we perform a calculation of the overall degree of synchrony of the PNs to their LFP and observed its linear relationship with the odorant concentrations as shown in Figure 5, thus confirming our hypothesis.

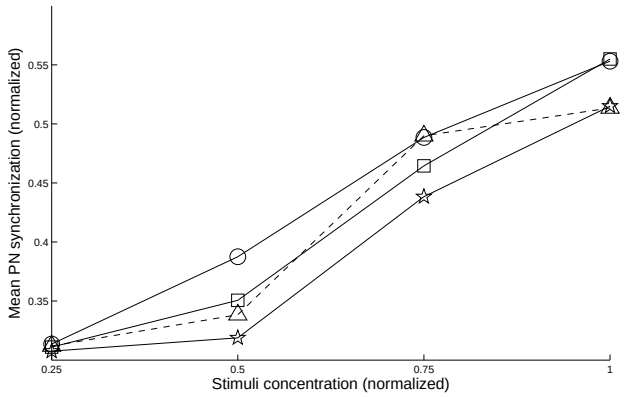

Fig. 5. Mean PN degree of synchronization to their LFP as a function of concentration of input stimuli. A linear relationship between both can be observed.

The next question we want to answer is whether the encoding mechanism our model uses also maintains intact the information about the identity of the different stimuli. In order to clear that point, we take the second and third principal components from our previous analyses and plot one against the other as can be seen in Figure 6. The different classes of stimuli clearly cluster together and a simple linear classifier confirms this intuition, being able to classify without error 32 stimuli after being trained with 48 samples.

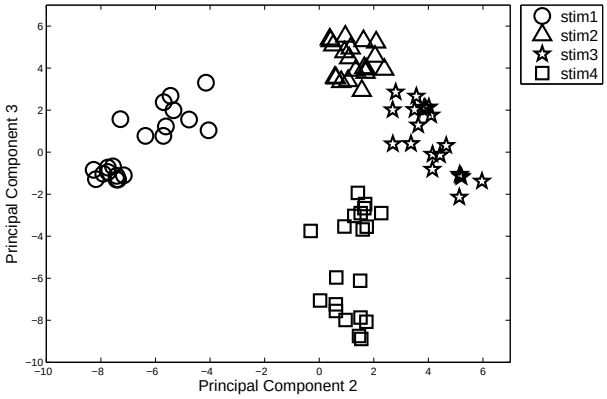

Fig. 6. Clustering of the different input categories using the second and third components of the PCA of the degree of synchrony of PNs to their LFP.

We do not resort to extra components for classification, since the amount of variance they explain falls significantly after the third one. Table II lists the percentage of explained variance for the first five components.

TABLE II
PERCENTAGE OF VARIANCE EXPLAINED BY PRINCIPAL COMPONENT

Principal Component	Explained Variance
1st	21.48
2nd	16.74
3rd	14.74
4th	7.23
5th	2.87

IV. DISCUSSION

With this study, we wanted to explore the issue of neural encoding of high-dimensional inputs, focusing our effort in the AL of insects. Our AL model is capable of encoding both the identity and concentration of synthetic olfactory stimuli, while our knowledge of its underlying mechanisms make it a plausible implementation of its biological analogue.

Further effort must be devoted to analyze in detail the limits of this promising approach. Particularly, the questions of how its classification performance depends on the number of modeled PNs and to which extend can the model cope with noise should be explored.

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