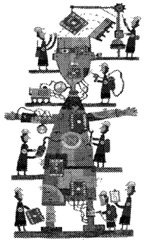

Odors lead to stable neuron relations beyond synchronization

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Studies in the olfactory system motivate the hypothesis, that odors are represented by spatially and temporally distributed populations of synchronized neurons. We use alternative criteria for neuronal population identification based on the Lempel-Zif-distance and superparamagnetic clustering. In this paradigm, the number of stable clusters is significantly higher during stimulus presentation compared to the absence of an olfactory stimulus. This effect is much less expressed, if the degree of synchronization is used as similarity measure for clustering. This indicates, that synchronization alone may not be sufficient for understanding olfactory coding.

1. Introduction

Odor encoding is a paradigmatic example of a neuronal population code. It has been proposed [1] that the identity of odors is represented by spatially and temporally distributed groups of neurons. The usual criteria determining membership of a specific neuron to such a group are, whether the neuron fires in synchrony with the other group members. In invertebrate olfactory systems, it has been shown that synchronization is essential for discrimination between different odors. In vertebrate systems, however, a similar confirmation has not yet been provided. This motivates the question, whether aspects in neuronal firing other than synchronization might enable identification of specific populations encoding for specific odors. We investigate this matter using criteria for neuronal population identification based on the Lempel-Ziv distance (LZ-distance) of spike trains [2] and the sequential superparamagnetic clustering paradigm [3].

2. Methods

Experimental procedure: Neuronal activity was sampled from electrodes in a micro-electrode array positioned in the olfactory bulb of anaesthetized rats (6×5 electrodes 350 μm separation). Four odors in four concentrations each were delivered to the rat. Neuronal activity was sampled in the 10s period before odor onset (the pre-stimulus period) and the 10s period of odor presentation (the during-stimulus period). In this way, a total of 54 neurons were simultaneously sampled. Pre- and during-stimulus recordings were made under a total of 16 different stimulus conditions. For each condition, there were three trials, resulting in a total of 96 spike trains per neuron.

Distance measures: The LZ-distance between two bitstring coded spike trains X_n and Y_n of length n is defined as

$$d(X_n, Y_n) = 1 - \min\left\{\frac{K(X_n) - K(X_n|Y_n)}{K(X_n)}, \frac{K(Y_n) - K(Y_n|X_n)}{K(Y_n)}\right\},$$

where $K(X_n) = \frac{c(X_n)\log c(X_n)}{n}$ is the Lempel-Ziv complexity and $c(X_n)$ denotes the number of phrases generated by a parsing of X_n [2]. Using the LZ-distance for clustering [3], neurons belong to the same cluster, if they show similar, but not necessarily synchronous patterns in their firing. The correlation distance (C-distance) [4] considers spike trains as close if they share a large number of synchronous spikes. As the intertrial-variability was high, we focussed our analysis on differences between the pre-stimulus and the during-stimulus condition. The analysis has been performed in three steps: First, we determined the mean number of clusters of neurons in each of the 96 trials, using both the LZ-distance and the C-distance. Second, based on the result of clustering of step 1, we calculated for each neuron the mean size of the clusters, in which the neuron participated in all trials of the pre-stimulus and during-stimulus period (excluding trials, where no split in clusters was observed).

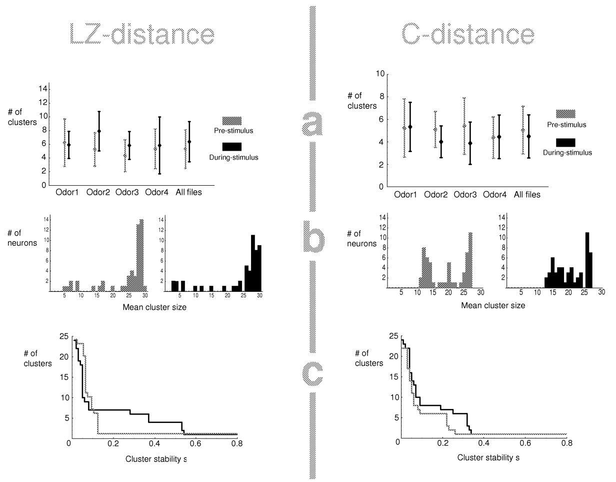

Figure 1: Olfactory neural network behavior, measured by the LZ-distance (left) and the C-distance: a) Number of clusters in the pre- and during-stimulus condition for the four odors and for all files. b) Histogram of mean cluster sizes in which each neuron of the network participated in either stimulus condition. c) Stability of 'partner-clusters'.

Partner-clusters: Third, to quantify the interactions of each neuron with each other neuron in the during-stimulus period compared to the pre-stimulus period, we assigned to each neuron a vector, whose components indicate the number of times the specified neuron finds itself in a cluster with another neuron. For example, for the i-th neuron N_i, the vector has the form $\vec{N_i} = (x_1, \ldots, x_{54})$, where x_j indicates the number of times the neuron N_i is in the same group as the neuron N_j. The distance between two such vectors $\vec{N_i}$ and $\vec{N_j}$ is simply

$$d(\vec{N_i}, \vec{N_j}) = 1 - \frac{\vec{N_i} \cdot \vec{N_j}}{|\vec{N_i}||\vec{N_j}|}.$$

The closeness of two neurons using this measure indicates, that they are often in the same cluster. The clustering of the distance matrix obtained in this way leads to clusters that show the degree of interrelation of neurons within the network, averaged over all trials ('partner clusters'). As the clustering algorithm is equipped with an intrinsic measure for cluster stability $\mathtt{s}$, with $0 \leq \mathtt{s} \leq 1$)), we are able to determine the dependence of the number of clusters on $\mathtt{s}$.

3. Results

We performed the procedure described in section 2 using both the LZ-distance and the C-distance as a similarity measure for clustering. We see, that for both distance measures the number of clusters emerging on stimulus presentation does not *per se* indicate, whether the network is in a pre-stimulus or a during-stimulus condition (Fig. 1.a). More interesting is the analysis of the mean sizes of the clusters in which each single neuron participated. In the pre-stimulus condition using both distance measures, three groups can be distinguished (Fig. 1.b): Rather large clusters (∼25-30 members), small clusters (LZ-distance: 5-9 / C-distance: 10-15 members) and medium-sized clusters (LZ-distance: ∼10–20 / C-distance: ∼20 members). In the during-stimulus condition, the three groups are less readily distinguished. The analysis of the stability-behavior of the network (Fig. 1.c) shows, for the LZ-distance, that the number of stable clusters is lower in the pre-stimulus condition than in the during-stimulus condition; the number of less stable clusters (small $\mathtt{s}$) tends to be larger for a given $\mathtt{s}$ in the pre-stimulus condition when compared with the during-stimulus condition. For $\mathtt{s} = 0.54$, 4 clusters emerge in the during-stimulus condition and this number increases up to 7 until $\mathtt{s} = 0.08$, at which point an abrupt increase in the number of clusters occurs. In the pre-stimulus condition, there is a single cluster until an abrupt increase in number at $\mathtt{s} = 0.12$. The increase is more abrupt in the pre-stimulus condition than in the during-stimulus condition. For the C-distance, this effect is much less pronounced compared to that in the case of the LZ-distance.

4. Conclusions

Using multi-electrode measurements obtained in the olfactory bulb (mitral cells) of the rat, we showed that stable inter-neuron relationships, expressed by the Lempel-Ziv distance, emerge during presentation of an odor. These clusters reflect stimulus-evoked changes in network-dynamics. This stabilization of the network can be interpreted as follows: In pre-stimulus activity, the network is in a state where many unstable clusters are present. The network is thus in a 'preparatory state' such that many potential neuronal groups are available for encoding a given stimulus. During stimulus presentation, stable clusters emerge out of these 'potential' clusters, possibly representing the odor. This type of behavior is much less visible using the C-distance, indicating that the effect of synchronization is of less importance than anticipated for understanding population coding in the vertebrate olfactory system.

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