Encoding in a network of sparsely connected spiking neurons : application to locust olfaction

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Abstract

Electrophysiological measurements in the locust antennal lobe have suggested that the odor could be encoded spatially and temporally during the network oscillation in the firing patterns of the excitatory cells. Interested by the mechanisms responsible for such a spatial code we have found that, for a sufficient level of inhibition, strong network oscillations appear in corresponding networks of excitatory and inhibitory spiking neurons during which a part of the excitatory cells fire at stimulus-dependent and precise times. This particular behavior is then investigated to unravel the underlying encoding properties.

Key words: Oscillations, Precise firing, Coding, Olfaction, Antennal lobe
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1 Introduction

When the locust antennaes are stimulated by an odorant, the antennal lobe (AL) displays a $20 - 30$ Hz oscillation associated with an odor-specific behavior of the excitatory projection neurons (PNs) [10,6] : at each cycle of the oscillation, a subset of the emiting PNs reliably fire around a preferred phase relative to the oscillation. These findings have suggested that odors could be encoded by these successive PN subsets, leading to a spatio-temporal code. This hypothesis is reinforced by the fact that in the mushroom body, a memory related area of the insect olfactory system, the Kenyon cells (KCs), which receive projections from the PNs, are able to detect the coincidence level of their inputs [8,9].

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Our main interest in this study is to understand how such a spatial code can emerge during an oscillation of such a kind of excitatory and inhibitory network. In other words, what controls the firing of a particular excitatory cell and what makes its activity stimulus specific ? A biologically detailed modeling study of the AL [1] has shown that the level of inhibition received from local neurons (LNs) is correlated to the precision of PN firing. Our goal here is, from a theoretical point of view, to define the kind of oscillation where this kind of E-cell behavior occurs, to describe it and to unravel the relevant parameters.

In the following section we present the model studied here. Then, we study the firing properties of E-cells during oscillations, and describe the regime where E-cells fire precisely. In conclusion, we discuss the implications of our results, particularly for locust olfaction.

2 The model

Our model is a simplified version of the one proposed in [1] which uses conductance-based neurons and synapses. We have tried to retain only the parameters that are essential for the observation of the same kind of dynamics. We consider a randomly connected network of N_E excitatory (E) and N_I inhibitory (I) quadratic integrate-and-fire (QIF) neurons [4]. The dynamics of the neuron n in the population α ($\alpha = E, I$) is described by

$$\tau_\alpha \frac{dv_{\alpha n}}{dt} = v_{\alpha n}^2 + i_{\alpha n}^{app}(t) + i_{\alpha n}^{syn}(t) - i_\alpha^{th}, \tag{1}$$

where $v_{\alpha n}$ is the membrane potential, τ_α the membrane time constant, $i_{\alpha n}^{app}$ the applied external current, $i_{\alpha n}^{syn}$ the synaptic current and i_α^{th} the threshold current. One important feature of the model is that E-cells are more excitable than I-cells, *i.e.* $i_I^{th} > i_E^{th}$ (> 0). When the potential diverges towards $+\infty$, the neuron emits a spike and the potential is reset to $-\infty$ [1]. A spike elicits exponential postsynaptic currents with a decay time τ_α^s. When the postsynaptic neuron belongs to the population β, the amplitude of this current is given by $g_{\beta\alpha}$. The connection probability is p.

The class of stimuli we consider consists in choosing a subset of N_E^s E-cells and N_I^s I-cells and apply to them the current $i^{app}(t) = i + \sigma_i \eta(t)$ where $\eta(t)$ is a white noise with $< \eta(t)\eta(t') > = \delta(t - t')$ and σ_i is the noise amplitude. In the AL, this current represents the input coming from the glomerulus, where many olfactory receptor neurons converge. The other cells have no applied

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[1] In the simulations, the equivalent non-diverging theta neuron has been used.

current. Another important feature of the model is that $i_E^{th} < i < i_I^{th}$, so that E-cells receiving the stimulus will have the natural tendency to fire and I-cells will fire when sufficiently excited by the E-cells. As we will take $g_{EE} = 0$, E-cells which do not receive the stimulus cannot fire. In the following, we will consider that i_I^{th} is sufficiently high to prevent the I-cells which do not receive the stimulus to fire [2]. Under these conditions, only the cells receiving the stimulus will fire, the others having no role in the dynamics : thus, these cells will be discarded from the network, the stimulus being now represented in the number of remaining neurons and in the remaining connectivity.

In the following we will show simulations corresponding to the real scale locust AL for which $N_E \approx 830$ and $N_I \approx 300$ (see [1,7] for the choice of the parameters) : $\tau_E = 4.5$ ms, $\tau_I = 2.6$ ms, $i_E^{th} = 0.5$, $i_I^{th} = 0.8$, $\tau_E^s = 5$ ms, $\tau_I^s = 10$ ms, $p = 0.05$ (sparse connectivity), $g_{IE} = 0.05$, $g_{II} = -0.5$. Stimuli are characterized by $i = 0.75$, $N_E^s = 0.75\, N^s$ and $N_I^s = 0.25\, N^s$, N^s being the number of stimulated neurons varying according to the number of stimulated glomeruli. For each simulation, the initial state of the neurons is chosen randomly.

3   Network and neuronal dynamics

Beyond their frequency, network oscillations are also characterized by what we will call their strength, that is the amplitude and width of the peaks in the network firing activity. A weak oscillation will correspond to a sinusoidal-like firing activity profile. On the contrary, a strong oscillation will display sharp and separated peaks. In the following, we vary the strength of the I $\rightarrow$ E connections, g_{EI} to investigate the oscillatory behavior of the network. Under a sufficiently negative value, the network state is no longer asynchronous and both populations start to oscillate. Similar transitions have been described in sparse networks of simpler neurons and synapses with input noise [3] and in densely connected networks of similar neurons and synapses with input heterogeneity [5]. As g_{EI} decreases, the oscillation continuously changes from weak to strong. For a weak oscillation, the E-cells firing phase is modulated but can still occur at any phase. The stronger the oscillation becomes, the more E-cells tend to fire in sharper phase peaks. More precisely, Figure 1 illustrates the behavior of E-cells during an oscillatory cycle with respect to the number of inhibitory inputs they received at the preceding cycle and with decreasing values of g_{EI}. For $g_{EI} = -0.15$, a substantial number of E-cells corresponding to the less inhibited ones can still fire at any time. The more inhibited cells fire loosely around a preferred phase. As g_{EI} decreases, less and less weakly inhibited cells fire at any time. The other cells fire in groups whose sharpness and mean firing time increases with the number of received inhibitory inputs

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[2]   This has been verified for the simulations shown below.

and decreasing g_{EI}. In the meantime, an increasing mean number of I-cells, N_I^e, fire at the end of the E-cells firing period, quasi-synchronously.

A closer look at the network dynamics reveals that the lower g_{EI} is, the more robust is the emission of the I-cells with respect to noise and initial state of the network. This implies that, in these conditions, a particular E-cell will receive a preferred number of inhibitory inputs at each cycle. As this number depends on the stimulus, the preceding discussion indicates that E-cells tend to have stimulus-dependent precise firing times. This kind of firing behavior can be seen as a possibility to encode the stimulus and, in the special case of downstream coincidence detector neurons, this type of encoding can be, a priori, efficiently decoded.
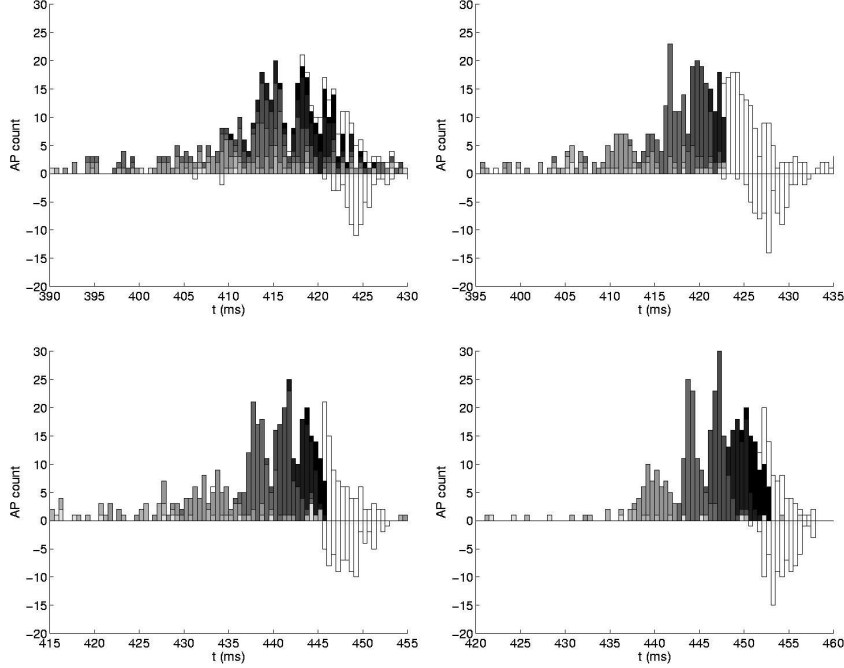

Fig. 1. Firing times histogram of the E-cells (*positive*) and I-cells (*negative*) during an oscillatory cycle for $N^s = 600$ and for $g_{EI} = -0.15$ (*upper left*), -0.2 (*upper right*), -0.25 (*lower left*) and -0.5 (*lower right*). The number of inhibitory inputs received at the preceding cycle is indicated by darker and darker grey levels.

In the following, we will focus our attention on this precise firing behavior. First, we have to understand why the stronger an E-cell is inhibited the more its subsequent firing time is controlled by this inhibition, quite irrespectively of its initial state and input noise. We consider an E-cell receiving a constant input current i and an exponential inhibitory current of amplitude $-g$ ($g > i$) at time $t = 0$; its initial state is $v(0)$. Using the phase plane, it can be shown that as long as the total current is negative and for many initial states, especially for $v(0) < 0$, trajectories tend to converge towards a given trajectory (see [2] for illustration). Also, the distance between two neighboring

trajectories $v(t)$ and $v(t) + \delta v(t)$ decreases when $v(t) < 0$, as it obeys, when small, to the linearized equation $\tau_E \, d\delta v/dt = 2 \, v \, \delta v$. As this situation lasts longer for stronger inhibition, trajectories get so close that the neuron fires at a time which is quasi-independent of its initial state. As shown in [2], this time can be written as $T^*(g) \approx \tau_I^s \log g + T_0(i, \tau_I^s)$, where T_0 is an unknown function here. This behavior remains almost unchanged in the presence of input noise, even when relatively strong ($\sigma_i = 0.2$) : noise tends to accumulate when $v(t) > 0$, but the neuron stays not much time in this situation as it fires rapidly. We consider now an E-cell receiving the inhibitory inputs from n I-cells. The inhibitory current decreases exponentially, but has an amplitude which depends on the firing times of these cells. It can be shown that if the I-cells fire with a standard deviation σ_I, the standard deviation $\sigma_E(n)$ of the firing times of all E-cells receiving n inputs is well approximated by $\sigma_I/\sqrt{n}$. The mean firing time is given by $T^*(n \mid g_{IE} \mid)$, which varies with n as $\tau_I^s \log n$. The number of E-cells receiving n inhibitory inputs can be theoretically given by $N_E^s \, P_{N_I^e, p}^{bin}(n)$ where $P_{N_I^e, p}^{bin}$ is the binomial distribution for N_I^e emitting I-cells and connection probability p, whose mean is $N_I^e \, p$ and standard deviation is $\sqrt{N_I^e \, p(1 - p)}$. It has been verified that the simulation results compare well with all these pedictions. Regardless of n, the E-cells can be shown to fire with a standard deviation σ_E approximately given by $\tau_I^s \sqrt{(1 - p)/N_I^e \, p}$ (see also [2]). Quantitatively, the mean number of inhibitory inputs, $N_I^e \, p$, has its importance : in the case corresponding to the AL (small number of neurons and sparse connectivity), this number is small and E-cells could precisely fire in distinguishable time windows. When this number is big (as in [2]), all the firing E-cells are almost synchronized.

Finally, the regime of precise firing is mainly controlled by the ratio between the mean synaptic current and the input current, that is $\mid g_{EI} \mid N_I^e p/(i - i_E^{th})$ and $g_{IE} N_E^e p/(i_I^{th} - i)$: the higher these ratios are, the more neurons fire precisely. From this, it can be inferred that the stimulus size N^s has to be sufficiently big to evoke precise firing.

4   Discussion

In this paper, we have shown that a strong oscillation can give rise to a stimulus-dependent and precise firing of a part of the E-cells. This kind of behavior is particularly interesting for the encoding of stimuli when the downstream neurons tend to behave as coincidence detectors, and it sheds new light on the putative role of network oscillations.

The regime illustrated in [1] corresponds more or less to the $g_{EI} = -0.25$ case shown in Fig. 1, where some PNs have preferred firing phases. QIF neurons

reproduce well this kind of behavior seen for conductance-based neurons. On the opposite, similar results with simpler leaky integrate-and-fire neurons were quite difficult to obtain : the reason for this is attributed to the fact that these neurons fire too quickly when their input current becomes overthreshold.

Experimental results in the locust AL [10,6] seem to correspond to the $g_{EI} = -0.15$ case, where neurons fire loosely around a preferred phase with a standard deviation of about 5 ms. However, this less precise encoding may still be useful for the decoding by the KCs [9]. To answer this question, a more precise characterization of the relationship between such encoding and decoding processes has to be done.

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