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Brain Research

Research Report

Responses of single neurons and neuronal ensembles in frog first- and second-order olfactory neurons

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ARTICLE INFO

Article history:
Accepted 8 May 2013
Available online 18 May 2013

Keywords:
Olfactory receptor neuron
Mitral cell
Dose–response curve
Intensity coding
Population coding

ABSTRACT

A major challenge in sensory neuroscience is to elucidate the coding and processing of stimulus representations in successive populations of neurons. Here we recorded the spiking activity of receptor neurons (RNs) and mitral/tufted cells (MCs) in the frog olfactory epithelium and olfactory bulb respectively, in response to four odorants applied at precisely controlled concentrations. We compared how RN responses are translated in MCs. We examined the time course of the instantaneous firing frequency before and after stimulation in neuron ensembles and the dependency on odorant concentration of the number of action potentials fired in a preselected 5-s time window (dose–response curves) in both single neurons and neuron ensembles. In RNs and MCs, the dose–response curves typically increase then decrease and are well described by alpha functions. We established the main quantitative properties of these curves, including the distributions of concentrations at threshold and maximum responses. We showed that the main transformations occurring in the transition from RNs to MCs is the lowering of the firing threshold and a large decrease in the total number of spikes fired. We also found that the number of action potentials fired by recorded neurons and hence their energy consumption is independent of odorant concentration, and that this is a consequence of their time- and concentration-dependent activities.

This article is part of a Special Issue entitled Neural Coding 2012.

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1. Introduction

In the olfactory system, odor stimuli are detected by different odorant receptors (ORs) borne by thousands first-order neurons (olfactory receptor neurons RNs) that send signals to fewer second-order neurons—mitral cells (MCs) in the vertebrate olfactory bulb and projection neurons (PNs) in the insect antennal lobe; in the bulb/lobe the olfactory information is processed by a complex neural network involving local and centrifugal neurons (Buck, 1996; Rospars, 1988; Shepherd et al., 2004). To elucidate how the olfactory signal message conveyed by RNs is transformed in the

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0006-8993/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.brainres.2013.05.018

output carried by MCs/PNs is essential for a proper understanding of olfactory processing and the properties of odor perception (Duchamp-Viret et al., 2003; Chaput et al., 2012). Moreover, this transformation is likely representative of the strategy used in cortical preprocessing (Niessing and Friedrich, 2010).

All early sensory systems possess four basic properties. First, single sensory neurons fire action potential at a rate that increases with stimulus intensity (Adrian, 1950). Second, they best process their natural stimuli that occur most frequently (efficient coding; Laughlin, 1981; Simoncelli and Olshausen, 2001). In particular, the latter property predicts the first one and indicates that the sigmoid response curve to a stimulus reflects the cumulative distribution of its intensities in nature. Third, energy consumption is a strong constraint because neural processing is metabolically expensive (Levy and Baxter, 1996; Lennie, 2003; Niven and Laughlin, 2008), which might favor codes using as few spikes as possible (Barlow, 1969; Olshausen and Field, 2004). Fourth, any specific feature of the world is encoded in the concerted activity of many neurons so that neural coding can be fully understood only at the neuron population level (Pouget et al., 2003; Kass et al., 2005).

The olfactory system clearly possesses the first and last properties. The successive neural layers of the system display population coding (Friedrich and Stopfer, 2001; Ito et al., 2009; Laurent, 2002; Lledo and Lagier, 2006; Shepherd et al., 2004; Wilson and Mainen, 2006) and each ORN obeys Adrian's law in a specific manner. It is known that the responses to monomolecular odors across RNs are highly variable in threshold, dynamic range and maximum rate (de Bruyne et al., 2001; Ito et al., 2009; Münch et al., 2013; Rospars et al., 2003, 2008), even in ORNs expressing the same OR (Grosmaître et al., 2006). Is it also true for MCs? To address this question, we compared the properties of single RNs and MCs in response to stimulations differing in quality (across four odorants) and intensity (across odorant concentrations varying over six orders of magnitudes). We examined two complementary features: the firing rate of individual neurons in order to describe the time course of the responses and the number of spikes fired during a specified time (2 s) to analyze their dependency on stimulus concentration. We found that both RNs and MCs obey the same quantitative rules in their average responses and their variability. The MCs fire less odorant-evoked spikes but more spontaneous spikes than RNs. Although their dynamic ranges are similar in width, the thresholds of MCs are shifted toward lower concentration with respects to those of RNs. Like in RNs, all response properties (maximum number of spikes fired, threshold, dynamic range) of MCs are extremely variable so that both display the "page-filling" property previously described for RNs (Rospars et al., 2003).

However, the status of the other two properties is less clear. Studies of efficient olfactory coding in insects, whose olfactory system has the same functional architecture as in vertebrates (Hildebrand and Shepherd, 1997), concluded that ORNs are relatively inefficient at quality coding (Abbott and Luo, 2007; Bhandawat et al., 2007) and efficient at intensity coding (Kostal et al., 2008). Energy consumption has been modeled in mammalian glomeruli (Nawroth et al., 2007) but not at the population level, so the problem of global energy consumption remains open. In particular, it is not known to what extent the four properties are compatible with one another. The first two properties seem in good agreement. In conjunction with the fourth one, they lead to predict that a neuron population should fire more spikes for strong than for weak stimuli. However, this may conflict with the third (spike saving) property. To address this issue we investigated the global properties of ensembles of RNs and MCs. We found that the number of action potentials encoding the same olfactory information in such ensembles is considerably smaller in MCs than in RNs in accordance with Barlow's (1969) prediction. We found also that, in both ensembles stimulated at various concentrations, the maximum rate and the total number of spikes fired in a long enough time period (2 s or more) are nearly constant, independent of odorant concentration. We show that this a priori surprising concentration-independence, previously observed also in insects (Stopfer et al., 2003), does not contradict Adrian's law for single neurons. However, we suggest that it is a property of the ensemble of recorded neurons and not of the whole system. Actually, the number of active neurons and consequently the total activity are expected to increase with concentration which solves an apparent paradox.

2. Results

The unit activity of two connected populations of neurons, receptor neurons (RNs) of the ventral olfactory epithelium and mitral cells (MCs) of the olfactory bulb, were studied before and after stimulation with four odorants (anisole, camphor, isoamyl acetate and limonene) on the whole range of concentrations to which these neurons were sensitive (Fig. 1). The number of records retained in each category were 550 (RNs) and 785 (MCs) with similar number of records per odorant in the range 276–311 (Table 2). In the first section, the time-evolution of the overall firing rate is examined before, during and after stimulation. In the second section, the effects of odorant concentration are analyzed across neurons at the single-cell level; whereas, in the third section it is analyzed on pooled neurons across concentrations.

2.1. *Time dependency of the firing rates in neuron ensembles*

We investigated first the time-dependency of neural activity. To this end, the instantaneous firing rates were estimated by convolving the spikes with a Gaussian kernel before and after stimulation with all odorants and concentrations pooled together (Fig. 2A).

Before stimulation, the activity was constant in both RNs and MCs. The spontaneous firing rate during the 30 s preceding the stimulus, determined as the total number of action potentials (APs) divided by the duration of spontaneous activity, was significantly lower in RNs (0.45 AP/s) than in MC neurons (0.55 AP/s). As shown by *t*-test, RNs and MCs were significantly different ($p<0.001$). Cumulative spike counts (Fig. 2B) confirmed the stationarity of spontaneous activity and its lower rate in RNs, which is more apparent

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