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Research Report

Population coding is essential for rapid information processing in the moth antennal lobe

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ABSTRACT

We investigated how odorant information is transmitted by neurons in the moth antennal lobe (AL). The neurons were repeatedly stimulated by three different odorants and their activity was intracellularly recorded. First, the response properties of single neurons were analyzed. The neurons exhibited highly reliable responses to the odorants and 43% of AL neurons responded to two or three odorants. The population distribution of firing rates in response to odorant stimulation was relatively broad in moth AL neurons, which is consistent across insects. Second, we attempted to decode the odorant identity from the activity of the recorded neurons using the maximum likelihood method. The decoding performance rapidly improves with increasing the number of neurons. Notably, an increase in the size of neural population results in faster transfer of information and increased the duration to retain odorant information. In conclusion, the AL neurons encode odorant information reliably and the population coding can transmit odorant information to olfactory centers. Population coding allows AL to encode and transmit olfactory information faster than the discrimination latency demonstrated in behavioral experiments.

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1. Introduction

How the brain processes sensory information is one of the fundamental issues in neuroscience. Olfaction plays an important role in the detection of food, natural predators, and mating partners for many animals. In insects, odorants are first detected by olfactory receptor neurons (ORNs) on the antennae. These ORNs transform the odorants into electrical signals that are then transmitted to the antennal lobe (AL), which is the equivalent of the olfactory bulb (OB) in the mammalian brain (Hildebrand and Shepherd, 1997). Here, we investigate the information representation of odor identity in AL of the silkmoth *Bombyx mori*. Specifically, following questions are examined: (1) How reliable and selective is odorant information encoded in AL neurons. (2) How fast AL neurons can transmit odorant information. (3) How much odorant information AL neurons can transmit. These questions are essential for understanding the mechanisms of olfactory information processing.

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AL is the first olfactory processing center in the insect brain and is composed of glomeruli, which are the basic units of odor processing. There are two kinds of neurons in AL: projection neurons (PNs) and local interneurons. The local interneurons do not have connections outside AL, while PNs send information to higher brain areas such as the mushroom body and the lateral horn. The anatomical structure of AL is much simpler than that of OB; the number of glomeruli in AL is small (silkmoth ~60: (Masante-Roca et al., 2005; Kazawa et al., 2009), honeybee ~166: (Arnold et al., 1985)), compared to that in OB (mouse ~1800: Royet et al., 1988, human ~5500: Maresh et al., 2008). This simplicity in its structure makes AL as an effective model for investigating olfactory processing.

Olfactory information processing must be fast and reliable. Behavioral studies have demonstrated that animals can discriminate odorants in a very short time period. For example, rodents, when trained to discriminate between odorants, can make a decision within 200–300 ms (Uchida and Mainen, 2003; Abraham et al., 2004). There is a physiological evidence that mushroom body neurons in honeybee respond to odorants within 200 ms (Strube-Bloss et al., 2011).

In addition to the anatomical features (Rospars, 1988; Hansson, 1999), the computational features of AL (Laurent and Davidowitz, 1994; Perez-Orive et al., 2002; Stopfer et al., 2003; Mazor and Laurent, 2005; Bhandawat et al., 2007; Krofczik et al., 2009; Buckley and Nowotny, 2012) (see also a review: Wilson and Mainen, 2006) are necessary to understand olfactory information processing. A useful approach to investigate the computational aspects of AL is decoding analysis (Stopfer et al., 2003; Mazor and Laurent, 2005; Miura et al., 2012), which aims to reconstruct odorant information from recorded spike trains. The amount of information transmitted by neurons can be quantified by evaluating the discrimination accuracy. To address these questions, we analyzed the spike responses of single neurons and decoded the odorant identity from the activity of a PN population.

2. Results

2.1. *Response properties*

We examined the response properties (reliability and selectivity) of PNs ($n=35$) to the odorants. The properties were analyzed based on the response index Z and the spike count N_k. Since PNs often generate spikes without stimulation (Fig. 1A), we defined whether a neuron significantly responded to a stimulus or not and the response indexes were evaluated from each recording (see Experimental procedures).

First, we analyzed the reliability of the response index Z, namely, we examined how randomly a neuron responded to an odorant. The PNs were classified into three categories: responsive, unreliable and unresponsive neurons. If a neuron responded to the odorant in all three trials, it was classified as a responsive neuron. If it responded to the odorant in one or two trials only, it was classified as an unreliable neuron. If it did not respond at all, it was classified as an unresponsive neuron. The distribution of the response types is shown in Table 1. Most PNs (86%) were reliable in their responses, which meant that they belonged to the first or third category (Hex: 33 PNs,

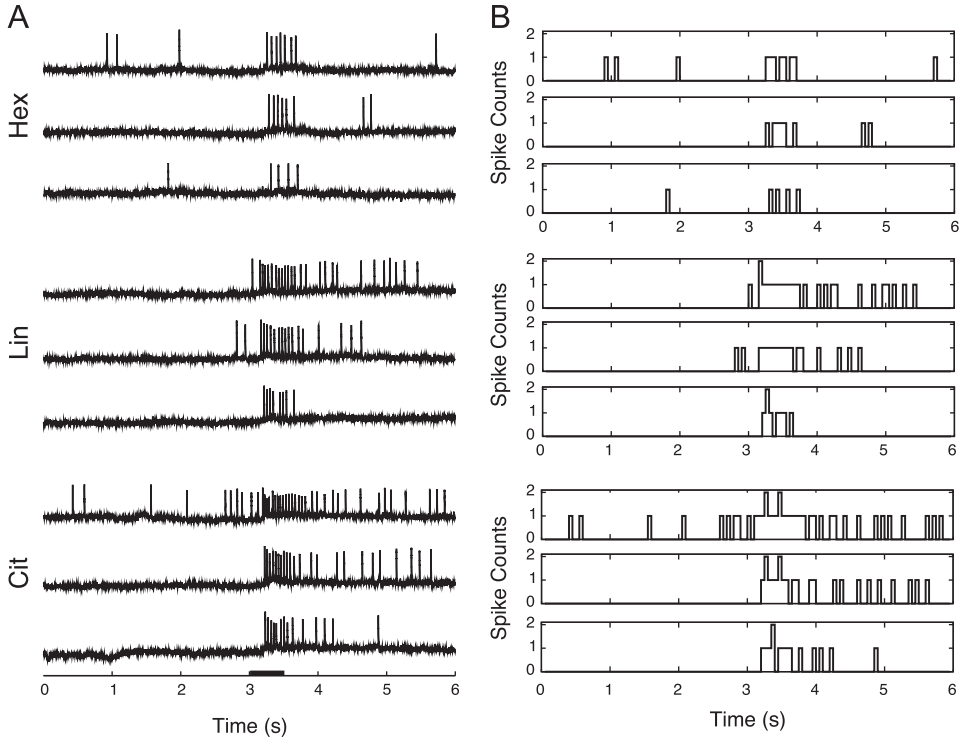

Fig. 1 – Examples of responses of a PN to three applied odorants, *cis*-3-hexen-1-ol (Hex), linalool (Lin) and citral (Cit). (A) Each line shows the recorded voltage from a PN in one experiment. The stimulus duration (3–3.5 s) is indicated as a black bar. Trials in the last 5.5 s are not shown, as firing returned to the spontaneous activity. (B) Spike counts N_k for trials shown in (A).