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Research Report

Data-driven honeybee antennal lobe model suggests how stimulus-onset asynchrony can aid odour segregation

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ABSTRACT

Insects have a remarkable ability to identify and track odour sources in multi-odour backgrounds. Recent behavioural experiments show that this ability relies on detecting millisecond stimulus asynchronies between odourants that originate from different sources. Honeybees, *Apis mellifera*, are able to distinguish mixtures where both odourants arrive at the same time (synchronous mixtures) from those where odourant onsets are staggered (asynchronous mixtures) down to an onset delay of only 6 ms. In this paper we explore this surprising ability in a model of the insects' primary olfactory brain area, the antennal lobe. We hypothesize that a winner-take-all inhibitory network of local neurons in the antennal lobe has a symmetry-breaking effect, such that the response pattern in projection neurons to an asynchronous mixture is different from the response pattern to the corresponding synchronous mixture for an extended period of time beyond the initial odourant onset where the two mixture conditions actually differ. The prolonged difference between response patterns to synchronous and asynchronous mixtures could facilitate odour segregation in downstream circuits of the olfactory pathway. We present a detailed data-driven model of the bee antennal lobe that reproduces a large data set of experimentally observed physiological odour responses, successfully implements the hypothesised symmetry-breaking mechanism and so demonstrates that this mechanism is consistent with our current knowledge of the olfactory circuits in the bee brain.

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1. Introduction

Airborne odourants distribute in turbulent odour-plumes that fluctuate at multiple temporal scales, spanning from milliseconds to minutes (Murlis et al., 1992; Riffell et al., 2009). In a natural environment the odour-plumes of a variety of odour sources intermingle. In order to form a meaningful perception of the olfactory landscape, animals need to segregate concurrent odours from independent sources within this mixture. Generally, odourants that are emitted together from

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one odour source will travel together in the same odour filaments while compounds emitted from other sources will arrive in separate filaments at the sensory organs. The temporal relationships between odourant stimulus onsets thus contains information about whether the odourants belong to the same or a different odour source (Hopfield, 1991).

Insects possess a remarkable ability to segregate odourants from different sources based on the exact timing of the onset of concurrent odour stimuli. In honeybees, a 6-millisecond temporal difference in stimulus onset is sufficient to segregate an odour-object from amixture (Szyszka et al., 2012). Moth and beetles can distinguish blends of attractive pheromones with antagonistic odours in which the components arrive at the same time (synchronous mixture), from blends of the same substances where the components arrive with temporal differences (asynchronous mixture): In asynchronous mixtures the antagonistic effect of the additional odour becomes weaker as soon as the arrival of the mixture components is separated by only one or a few milliseconds (Baker et al., 1998; Andersson et al., 2011).

Two previous studies, in locusts and honeybees, have shown that central olfactory neurons are sensitive to odour-onset asynchrony: their responses to mixtures partly match those evoked by the individual components if the onsets of the stimuli differ (Broome et al., 2006; Stierle et al., 2013). In particular, differences in responses were found in the projection neurons (PNs) of the antennal lobe (AL), the first relay of olfactory information in the insect brain. The AL is subdivided into smaller spherical areas called glomeruli. In *Drosophila*, olfactory receptor neurons (ORNs) with the same receptor protein converge onto the same glomerulus, and thus provide every glomerulus with a distinct response profile (Vosshall et al., 2000). We will here assume the same connectivity pattern for the bee. Within the AL, a network of intra- and inter-glomerular inhibitory local neurons (LNs) and excitatory local neurons has been found to be involved in odour processing in the fly (Olsen et al., 2007; Shang et al., 2007; Silbering and Galizia, 2007; Silbering et al., 2008) and the bee (Sachse and Galizia, 2002). It is however currently unknown how the AL network contributes to odour segregation based on millisecond stimulus onset-asynchrony. In this paper we investigate the hypothesis that the network of inhibitory LNs in the AL could aid distinguishing asynchronous mixtures and synchronous mixtures of odours. The fundamental idea can be thought of as a symmetry-breaking effect of a winner-take-all LN network: Assuming that for two given odourants A and B there are two different response patterns in ORNs and hence two different "winning" activity patterns in the network of LNs, say LN_A and LN_B, and potentially a third pattern for the synchronous mixture AB of A and B, say LN_{AB}. Then, if an asynchronous mixture A-t-B of A, t ms delay, then B arrives at the antenna, the initial activation by odourant A will activate pattern LN_A, which will inhibit other LN activity patterns, such that when odourant B arrives, the pattern LN_A remains active and the response appears different from the response to the synchronous mixture AB where pattern LN_{AB} is active. The same reasoning applies to the asynchronous mixture B-t-A.

We test our hypothesis in a detailed model of the honeybee AL, using a large data set from the literature (Ditzen, 2005; Strauch et al., 2012) to calibrate the responses to 16 odourants that we then use to make predictions for the responses to their synchronous and asynchronous mixtures.

2. Methods

In this paper we investigate a model of the honeybee early olfactory pathway. We implemented the model using the typical rules for the olfactory system: Each ORN expresses only one type of receptor and ORNs of the same type connect to the same glomerulus. The detailed connectivity of the model is given below. In order to obtain realistic receptor responses to mixtures, we implemented a rate description of binding, unbinding, activation and inactivation of receptors which implements a syntopic mixture model that has been found to be accurate for many observations in bee olfaction (Münch et al., 2013). We then generate Poisson spike trains from the receptor activation data to take account of the known unreliability of ORNs. The output of the ORN population feeds into an AL model of PNs and LNS implemented with Hodgkin–Huxley type conductance based neuron models which were tuned to reproduce the electrophysiological data obtained in honeybees (Krofczik et al., 2008). One of the larger unknowns in the model are the activation of different receptor types in response to different odours. To obtain an estimate of the binding and activation rates, we used an indirect parameter estimation that matched the activation patterns of the AL to experimental data (Ditzen, 2005) by adjusting the activation rates on the level of the receptors (see "Bootstrapping" below). In order to relate our spiking neuronal network output to the experimental data from calcium imaging experiments, we employed spike density functions (SDFs). We then used correlation analysis of glomerular activation patterns in terms of averaged SDFs of PNs to analyse the simulation results with respect to the question of odour segregation.

The details of each of the model elements and analysis methods are explained in the following sub-sections.

2.1. Spike density functions

We used SDFs as a proxy of the Ca^{2+} signal observed in experiments. SDFs were calculated by convolving the spike trains with the asymmetric kernel:

$$k(\hat{t}) = \hat{t} \exp\left(-\frac{\hat{t}}{\tau}\right) \quad (1)$$

where $\hat{t} = t - t_{spike} + \tau$, so that the maximum of k is situated at the occurrence of the spike, t_{spike}. The timescale of the kernel was chosen as $\tau = 50$ ms.

2.2. Olfactory receptors

We describe olfactory transduction in ORNs as odourant binding and unbinding at olfactory receptors comprising a set of reactions from unbound receptors R to bound receptor-odourant complexes R_i to activated bound complexes R_i^*, where $i = A, B, \ldots$ labels the different odourants. For odourants A, B, … present at a population of receptors we have the