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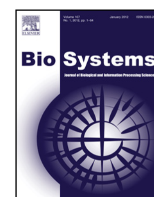

Olfactory signal coding in an odor background

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ABSTRACT

Insects communicating with pheromones are confronted with an olfactory environment featuring a diversity of volatile organic compounds from plant origin. These volatiles constitute a rich and fluctuant background from which the information carried by the pheromone signal must be extracted. Thus, the pheromone receptor neurons must encode into spike trains the quality, intensity and temporal characteristics of the signal that are determinant to the recognition and localization of a conspecific female. We recorded and analyzed the responses of the pheromone olfactory receptor neurons of male moths to sex pheromone in different odor background conditions. We show that in spite of the narrow chemical tuning of the pheromone receptor neurons, the sensory input can be altered by odorant background.

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1. Introduction

Olfaction is an essential sensory modality for insects to find a mate, a food source or an oviposition site. It is generally considered that most insects respond in a deterministic way to specific chemical blends released by their host or conspecifics. The parameters of the odor signals that will allow discrimination of the signal and orientation toward its source are the chemical components of the blend and their relative proportions in the blend (quality), their concentration in the air (intensity), and their distribution in time (dynamics). Olfactory signals are detected by olfactory receptor neurons (ORNs) housed in sensilla mainly situated on the insect antennae. Quality, intensity and dynamics of odor signals contain decisive information for insects flying toward odor sources (Cardé and Willis, 2008; Vickers, 2000, 2006). The olfactory coding process starts in the ORNs whose chemical tuning insures specific detection of odorants and coding of intensity and temporality of odor signals into spike firing patterns. However, in natural environments insects are confronted with a rich olfactory world from which their olfactory system must extract the relevant information. Terrestrial plants release in the atmosphere a great variety of volatile organic compounds and a total of 1700 compounds have been identified from floral scents (Knudsen et al., 2006). The mixing ratio of volatile plant compounds in air is typically in the range of several ppb (Kesselmeier et al., 2000; Wiedenmyer et al., 2011). Presence of such large amounts of many volatile organic compounds in the atmosphere may alter the detection of a specific signal often released in much lower concentrations. Insects communicating with pheromones for instance possess specialized olfactory receptor neurons narrowly tuned to the pheromone components (Phe-ORNs). Each pheromone component activates a specific type of Phe-ORN and the recognition of the pheromone blend is achieved by specific coding. However, the chemical specificity of Phe-ORNs can be challenged by a diversity of volatile compounds released by plants (VPCs, Deisig et al., 2014). Different modes of interactions between pheromone components and VPCs have been reported. Ochieng et al. (2002) described synergy between linalool or (Z)-3-hexenol and Z11-hexadecenal in the noctuid moth *Heliothis zea* and hypothesized that the co-perception of pheromone and plant volatile could facilitate the finding of a female. In turn, adding a VPC to the pheromone results more generally in a suppressive effect (Den Otter et al., 1978; Van der Pers et al., 1980) suggesting that a background of volatile organic compounds constitutes an odorant noise that might decrease sensitivity.

The effects of background on extraction of a signal and its consequences on behavior have been largely investigated in the sensory modalities involving physical stimuli like vision (Chen et al., 2014; Sasaki et al., 2006, 2008) and audition (Brumm and Slabbekoorn, 2005; Chan et al., 2010; Schmidt and Römer, 2011; Siegert et al., 2013). In turn, the consequences of an odor background, that can

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be assimilated to a “chemical noise”, on perception of the olfactory signals have been far less studied. The effects of VPCs on responses of individual neurons to pheromone have been analyzed (Party et al., 2009; Rouyar et al., 2011), but the consequences on reliability of sensory input at the neuron population level have been poorly documented. In Drosophila larvae, a combinatorial code of odor components involves not only precise lock and key coding of specific odors but also patterns of a stochastic and fuzzy activity in neuron ensembles (Hoare et al., 2008). In the present paper, we aimed to evaluate how much environmental odorants affect the intensity, quality, temporality and reproducibility of the response to a specific signal odorant in ensembles of Phe-ORNs. Many volatile plant compounds that constitute the odorscape of insects contain important contextual information and serve as cues for host plant detection; however, we will consider these environmental odorants as an external background, relatively to the pheromone signal.

We thus recorded, by extracellular single sensillum methods, the firing activity of the Phe-ORNs in the presence of a background of a VPC in two noctuid moths, *Spodoptera littoralis* and *Agrotis ipsilon*. We expected that, firstly, the interactions between background and signal would affect the way intensity, quality and temporality dimensions of the pheromone signal are coded within a population of Phe-ORNs. Secondly, we expected that the interactions between background and signal would increase the variability: all ORNs are not exposed the same way, there is some uncertainty in the timing of the signal/background arrival on ORNs, all ORNs might not be as sensitive to the background... To confirm our working hypotheses, the intensity and dynamics of the firing responses of Phe-ORNs to pulses of pheromone in a VPC background were analyzed.

2. Material and methods

2.1. Insects

Larvae of *A. ipsilon* and *S. littoralis* were reared in the laboratory on artificial diets at 23 °C and 60% relative humidity until pupation. Sexes were separated at the pupal stage, and females and males were kept in separate rooms under a reversed 16 h:8 h light:dark photoperiod under similar temperature and humidity conditions. Newly emerged male adults were collected every day and provided ad libitum with a 20% sucrose solution. The day of emergence was considered day zero of adult life. Two to five day old sexually mature virgin males were used for electrophysiological experiments, and all electrophysiological experiments were performed during the scotophase.

2.2. Chemicals

2.2.1. Sex pheromones

We used a sex pheromone blend of *A. ipsilon* based on the three previously identified components (Gemeno and Haynes, 1998; Picimbon et al., 1997): (Z)-7-dodecen-1-yl acetate (Z7-12:OAc), (Z)-9-tetradecen-1-yl acetate (Z9-14:OAc) and (Z)-11-hexadecen-1-yl acetate (Z11-16:OAc), mixed at a ratio of 4:1:4 (Causse et al., 1988). The three compounds were purchased from Sigma Aldrich (Saint-Quentin Fallavier, France) and diluted in hexane (>98% purity, CAS 110-54-3, Carlo-Erba, Val-de-Reuil, France). For ORN recordings from the pheromone sensilla in *S. littoralis*, we used the major pheromone component (Ljungberg et al., 1993), (Z)-9 (E)-11 tetradecadienyl acetate (Z9,E11-14:Ac; synthesized in the laboratory, courtesy of Martine Lettere).

2.2.2. Volatile plant compounds

Heptanal (98% purity, CAS 66-25-1) and a selection of VPCs belonging to different chemical families (aldehydes, acetates, terpenes) were used for some experiments: (Z)-3-hexenyl acetate (98% purity, CAS 3681-71-8), hexanal (>99% purity, CAS 66-25-1), octanal (98% purity, CAS 124-30-0), linalool (97% purity, CAS 78-70-6), geraniol (96% purity, CAS 106-24-1), geranyl acetate (mixture of isomers, >97% purity, CAS 16409-44-2), linalyl acetate (97% purity, CAS 115-95-7) and isoprene (> 98% purity, CAS 78-79-5). Mineral oil (CAS 8042-47-5) was used to prepare volume-to-volume dilutions at 0.1% and 1%. All compounds were purchased from Sigma Aldrich (Sigma Aldrich, Saint-Quentin Fallavier, France).

2.3. Olfactory stimulation

Odorants were delivered as described previously (Rouyar et al., 2011). Briefly, charcoal-filtered air was re-humidified and divided into eight equal flows (220 ml/min) directed each to a three-way miniature valve (the Lee Company, Westbrook-CT, USA). From there the flow could be directed to one 4 ml glass vial containing the stimulus source by activating the appropriate valve. The connections to the vials were made using PTFE tubing (1.32 mm ID) and hypodermic needles (18 G size). For practical reasons, due to their differences in volatility and polarity it was not possible to use the same type of stimulus sources for pheromone and VPCs. For VPCs, the vial contained 1 ml of solution in mineral oil at the appropriate concentration vol/vol. For the sex pheromone, the vial contained a section of PFTE tubing (1.6 mm ID; $L = 20$ mm) directly connected to a hypodermic needle and containing 10 or 100 ng of the sex pheromone blend. Stimulus- and clean air-carrying tubes were maintained together in a 10 cm long metal tubing constituting the stimulation pencil. A plastic cone of a P1000 pipette fixed at the output of the stimulation pencil served as a mixing chamber, approx. 5 mm in front of one of the moths' antennae, and focused on antennal sensilla. Programming of the electric valves was performed using a Valve Bank (AutoMate Scientific, Berkeley, USA) synchronized with the PC acquisition software.

In the different experiments, neurons were stimulated by individual pheromone pulses (from 0.1 to 0.5 s) or by a series of pheromone pulses in a VPC background (either 2.5 or 3 s long application starting 1 s before the pheromone pulse) compared to a clean air background, or a brief VPC pulse was provided in a pheromone background.

2.4. Electrophysiology

Males were briefly anesthetized with CO_2 and restrained in a Styrofoam holder. One antenna was fixed with adhesive tape. Single sensillum recordings were performed with electrolytically sharpened tungsten wires or glass microelectrodes. The reference electrode was inserted either in the abdomen, or in an antennal flagellomere a few mm from the flagellomere carrying the sensilla that we recorded from. The recording electrode was inserted into the base of a long trichoid hair situated on antennal branches of *A. ipsilon*, or on the edge of the antennal stem in *S. littoralis*. Recording and reference electrodes were connected to a Neurolog preamplifier (Digitimer, Hertfordshire, UK). The signal was filtered (0.2–10 kHz) and amplified 1000 times. The electrophysiological activity was sampled at 10 kHz and 12 bit resolution with a Data Translation DT3001 analogue to digital card. Signals were monitored on the computer screen using Awave software (Marion-Poll, 1995). For analysis, spike sorting and extraction of spike occurrence times from the recordings were also done using Awave software. The majority of our recordings showed the firing activity of only one ORN. When the activities of two neurons were recorded simultaneously in some of the long trichoid hairs housing Phe-ORNs (Fig. 1A), spikes were sorted by their amplitudes to analyze only the firing that showed changes in response to the sex pheromone.

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