Behavioural Brain Research 312 (2016) 341–354

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Significance of sniffing pattern during the acquisition of an olfactory discrimination task

Laura Lefèvre*, Emmanuelle Courtiol[1], Samuel Garcia, Marc Thévenet, Belkacem Messaoudi, Nathalie Buonviso

Centre de Recherche en Neurosciences de Lyon (CRNL) Equipe Olfaction: du codage à la mémoire, CNRS UMR5292 – INSERM U1028 – Université Lyon 1, 50 avenue Tony Garnier, 69366 Lyon Cedex 07, France

HIGHLIGHTS

- During learning, rats acquired a precise and stereotyped sniffing strategy.
- Sniffing strategy and performances are correlated.
- Sniffing adjustments track top-down rather than bottom-up processes.

ARTICLE INFO

Article history:
Received 1 April 2016
Received in revised form 16 June 2016
Accepted 20 June 2016
Available online 22 June 2016

Keywords:
Sniffing
Olfaction
Rat
Discrimination
Learning
Olfactomotor act

ABSTRACT

Active sampling of olfactory environment consists of sniffing in rodents. The importance of sniffing dynamics is well established at the neuronal and behavioral levels. Patterns of sniffing have been shown to be modulated by the physicochemical properties of odorants, particularly concentration and sorption. Sniffing is also heavily impacted by higher processing related to the behavioral context, emotion and attentional demand. However, how the pattern of sniffing evolves over the course of learning of an experimental olfactory conditioning is still poorly understood. We tested this question by monitoring sniffing activity, using a whole-body plethysmograph, on rats performing a two-alternative choice odor discrimination task. We followed sniff variations at different learning stages (naïve, well-trained, expert). We found that during the acquisition of an odor discrimination task, rats acquired a global sniffing pattern, independent of the odor pair used. This pattern consists of a longer sampling duration, a higher sniffing frequency, and a larger amplitude. In parallel, subtle differences of sniffing between the two odors of a pair were also observed. This sniffing behavior was not only associated with a better and faster acquisition of the discrimination task but was also transferred to other odor sets and refined after a long-term pause so as to reduce the sampling duration and maintain a specific sniffing frequency. Our results provide additional arguments that sniffing is a complex sensorimotor act that is strongly affected by olfactory learning.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Gathering of sensory information largely depends on sampling dynamics [1]. In olfaction, stimuli are sampled intermittently, either during the resting respiration or through the voluntary inhalation of air in the context of odor-guided behavior. This stereotyped exploratory behavior is referred as sniffing and is closely linked to olfaction [2]. In behaving animals, it is well established that sniffing is highly dynamic, notably in frequency and flow rate [3,4]. In rats, the sniffing frequency is typically in the theta frequency range (4–12 Hz) during exploration or olfactory discrimination [3,5–9].

At the neuronal level, the importance of sniffing dynamics has been revealed at different stages of the olfactory processing: the olfactory epithelium [10] and [11], the olfactory bulb (OB) [12], and the piriform cortex [13] and [14]. Changes in sniffing patterns have a strong impact on the temporal structure of sensory input [15] and

* Corresponding author.
E-mail address: laura.lefevre@inserm.fr (L. Lefèvre).
[1] Current address: Emotional Brain Institute, Nathan Kline Institute for Psychiatric Research And Departments of Child and Adolescent Psychiatry New York University Langone Medical Center, 140 Old Orangeburg Road, Orangeburg, NY 10962.

http://dx.doi.org/10.1016/j.bbr.2016.06.039
0166-4328/© 2016 Elsevier B.V. All rights reserved.

subsequent brain processing [16–19]. More precisely, OB local field potential follows the sniff cycle with high reliability at every sniff frequency in anesthetized [20–22] and awake animals [9,22,23].

At the behavioral level, the importance of sniffing in animal's performance has been extensively studied. While Uchida and Mainen [6] reported that discrimination speed was independent of the discrimination difficulty, Abraham et al. [24] showed that discrimination time strongly depends on the similarity of the two odors presented. Rinberg et al. [25] nevertheless bridged the gap between both studies by evidencing a speed-accuracy tradeoff in olfaction. However, a controversy remains relative to the relationship between sniffing frequency and the animal's performance. While Kepecs and colleagues [7] showed a drop in behavioral performance when the rats were not using rapid (6–9 Hz) sniffing, Wesson and colleagues [24] showed that rapid sniffing was not necessary for odor discrimination. The question of whether sniffing faster is related to a better performance thus remains.

A second issue which remains unsolved is the question of the effect of behavioral context and experience on sniff modulation. Indeed, sniffing has been shown to be modulated by behavioral context [4,7,25], emotion [26] in rodents and attentional demand in humans [27]. Moreover, sniffing patterns can also be adjusted depending on the quality of the odorant, particularly its sorptiveness and concentration [3,28,29]. But those modulations rather than being an analytical process, seem to be adjusted synthetically depending on the odorant context of the discrimination task [30]. Importantly, all these preceding studies have been performed on animals trained with different behavioral paradigms and tested at different levels of expertise. Although Wesson and colleagues [24] followed the evolution of sniffing behavior through shaping and between different tasks, the question of the evolution of sniffing pattern through the different sessions of a discrimination task acquisition remains. To answer this question, we trained rats in a two-alternative choice odor discrimination task adapted from [6] and followed sniff variations over learning when: 1) animals were naïve regarding both the procedure and the pair of odors to discriminate, 2) animals were well-trained to the procedure but naïve regarding the pair of odors to discriminate, 3) animals were well-trained to both the procedure and the pair of odors to discriminate.

We showed that during the acquisition of an odor discrimination task, rats developed a sniffing pattern consisting of sampling longer, with a higher sniffing frequency and a larger amplitude regardless of the odor pair. Once the discrimination task was acquired, sampling duration was reduced and frequency maintained around 7–8 Hz. In parallel, we observed subtle changes consisting of sampling the two odors of a pair differently. These "global" and "differential" sniffing patterns were both associated with a faster task acquisition and correlated with better discrimination. They were also transferred to the discrimination of new odor pairs. The global sniffing pattern was even optimized, *i.e.* by decreasing their sampling duration and maintaining their sniffing frequency, when animals were tested after a long-term pause without any training. We discuss the possibility that sniffing adjustments we observed were mostly related to the acquisition of the discrimination procedure rather than to the quality of the odorants to be discriminated.

2. Material and methods

2.1. Animals

Experiments were conducted on twenty-five male Long-Evans rats (Janvier Labs, Le Genest Saint Isle, France; 8 weeks old, 250–300 g at the start of the experiment). Rats were group-housed under environmental controlled conditions (temperature: 22 ± 1 °C; humidity: 55 ± 10%). They were maintained under a 12 h light-dark cycle (lights on from 6:00 AM to 6:00 PM) and experiments were conducted during the light period (between 9:00 AM and 1:00 PM). Food was available *ad libitum* but a water restriction was applied with water access provided only during each training session (15–30 min in the experimental cage) and for 60 additional minutes following the experimental training in home cages. Animals were weighed daily to ensure that their body weight was maintained to at least 80% of their body weight at the beginning of the experiment. It has to be noted that over time, no weight decrease was noticed and that the rats even gain weight during this training. All experiments were performed in accordance with Directive 2010/63/EU of the European Parliament and of the Council of the European Union regarding the protection of animals used for scientific purposes (Agreement #: DR2014-41, CEEA-55 University Lyon 1).

2.2. Experimental apparatus for sniff recording

As described by [26], a plethysmograph was used to measure different respiratory parameters in behaving animals. The material consisted of a whole body customized plethysmograph (diameter: 20 cm, height: 30 cm; EMKA Technologies, France) placed in a homemade sound-attenuating cage. It was divided in two independent airtight chambers: the animal chamber and the reference chamber. The pressure changes due to animal respiration were detected by a differential pressure transducer (Model dpt, EMKA Technologies, France) with one side exposed to the animal chamber and the other to the reference chamber. The signal was sampled at 1 kHz, amplified and recorded using a PC via an acquisition card (USB-2533, Measurement Computing, Norton, MA).

The plethysmograph was modified to be equipped with three ports (diameter: 2 cm, depth: 2.5 cm, see Ref. [30]). The three ports were placed 8 cm from the floor of the apparatus. The central odor port was bordered with two lateral reward ports placed 6 cm on each side. The central port was equipped with a capacitive sensor that allowed nose poke detection and it was connected to a homemade olfactometer (with a constant flow rate of 400 mL/min). The entry of the rat nose in the odor port triggered the odor delivery. Constant deodorized air also flowed through the top of the chambers at a constant flow rate of 1100 mL/min. In order to maintain a constant air flow and to preserve the respiratory signal, a ventilation pump was connected to the plethysmograph that vacuumed out the equivalent of the air pushed into the chambers at 1500 mL/min (400 mL/min + 1100 mL/min).

The two reward ports contained pipettes that were connected to water pumps. Each reward port was equipped with a capacitive sensor that allowed lick detection.

One camera (B/W CMOS PINHOLE camera) was placed in a corner of the cage in order to visualize the animal behavior.

2.3. Behavioral procedure

2.3.1. Odors

Odorants used (and their respective vapor pressures in mmHg at 25 °C, obtained from Chem Spider, ACD/Labs PhysChem Module) were p-cymene (1.7 ± 0.2), 1,8-cineol (1.6 ± 0.3), D-carvone (0.1 ± 0.5), L-carvone (0.1 ± 0.5), D-limonene (1.5 ± 0.2), heptanol (0.3 ± 0.7), methylbenzoate (0.3 ± 0.3), cumene (4.5 ± 0.1), and cyclooctane (4.6 ± 0.1). They were all obtained from Sigma Aldrich (St Louis, MO and Fluka, Germany). Odors were associated to form a pair to discriminate. We considered that the most reliable way to get odors with similar concentrations was to choose odors with similar or close vapor pressure in the same odor pair and use them pure. The different odor pairs are presented in Fig. 1B. The first pair (P1) animals had to

Download English Version:

https://daneshyari.com/en/article/4312086

Download Persian Version:

https://daneshyari.com/article/4312086

Daneshyari.com