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Research report

Fasting increases and satiation decreases olfactory detection for a neutral odor in rats

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Abstract

Olfaction plays a fundamental role in feeding behavior, but changes in olfactory acuity according to feeding states have never been precisely demonstrated in animals. The present study assesses the olfactory detection performance of fasted or satiated rats placed under a strictly controlled food-intake regimen. We did this using a conditioned odor aversion (COA) protocol which induced in rats an almost total aversion to an ISO-odorized drink at 10^{-5} (1 μl in 100 ml of water). The rats (either fasted or satiated) were then presented with different concentrations of ISO-odorized water to compare their ability to detect and so avoid the ISO drink. In both states, the rats consumed significantly larger volumes of ISO at 10^{-10}, 10^{-9} and 10^{-8} than at 10^{-5}, suggesting lower detection at these three concentrations, although the fasted rats consumed significantly less ISO drink than did the satiated ones, showing better ISO detection at these concentrations.

These experiments provide original data demonstrating the expected fact that olfactory sensitivity increases in fasted animals. Since these results were obtained using a neutral odor, we suggest that olfactory acuity increases during fasting, enabling animals to more easily detect both food and environmental odors such as those of predators. This would have an obvious eco-ethological role by increasing the relevance of olfactory inputs when seeking food.

Keywords: Olfaction; Odor; Feeding; Behavior; Rat; Olfactory aversion

1. Introduction

Olfaction is a sensory dimension that is an integral part of food intake. Many animals rely on odor to determine the location of their food sources and to discriminate and identify them. Although odors are not contingent on the nutritive properties of food, they are always associated with them, and are the major determinant of the palatability of food items [29,31] and essential to control of food intake [23,24,27,28,30,43a]. The question of the effect of the nutritional state of an organism on odor perception (olfactory sensitivity) gave rise to several studies on humans at the beginning of the 20th century. The question is once more of interest because of the increased public health concerns regarding obesity. Since satiety towards a specific odor can be obtained only by smelling or chewing a food without swallowing it [40], it appears crucial to determine the implications of olfaction in the control of food intake. Some pathophysiological feeding behavior may be partly related to differences in the olfactory perception of foods, and thus in evaluating their palatability [34,46].

In humans, olfactory sensitivity has been shown to change extensively after lunch [15–18,23,26,50,52]. However, because these studies utilized experimental paradigms that focused on different parameters, their results are highly discrepant and do not allow definitive conclusions. For example, in the most recent of these studies, Koelega [26], studying the olfactory sensitivity of subjects to a neutral odor, concluded that there are no consistent changes in sensitivity related to food intake. He however chipped away at his conclusion by underlining that his experiments may have had some drawbacks attributable to a non strict

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control of the diet composition and size, to a lack of real knowledge of the internal nutritional status of his subjects, and to the fact that changes in olfactory sensitivity linked to feeding states could be very subtle.

In animals, the interactions between olfaction and food intake have been known for decades but the mechanisms underlying modifications of olfactory activity with the nutritional state remain unknown. The neural processing of olfactory information has been shown to be closely linked to the physiological and nutritional status of the organism. The olfactory system is more reactive to odors under starvation conditions, and its activity is reduced after satiation [1,37]. Moreover, olfactory bulb reactivity is selectively increased by an odor known to be palatable [36]. To our knowledge the changes in olfactory detection ability caused by the food status have never been precisely studied in animals using a specific paradigm focusing on olfactory performance dissociated from food intake. Obtaining such information in strict experimental conditions is an essential prerequisite for initiating further research dealing with the neural communication processes occurring between the hypothalamic feeding centers and the olfactory system. Knowledge of the natural modulation of the olfactory function by nutritional states will be especially useful for assessing the respective roles in odor processing of neuropeptides like orexin, leptin, or insulin (for a review see Ref. [32]), which are described as neurochemical signatures of the fasted and satiated states. This is why the question of whether odor sensitivity changes with the nutritional state was studied using a conditioned odor aversion (COA) protocol. This behavioral paradigm was devoted to comparing the olfactory detection abilities of fasted and satiated rats made aversive to a neutral odor.

2. Methods

2.1. Animals

Experiments were carried out in accordance with the European Community Council Directive of November 24th, 1986 (86/609/EEC) for the care and use of laboratory animals. Experimental protocols were approved by the Comité d'Expérimentation Animale de l'Université Claude Bernard–Lyon1.

Ten male Wistar rats were used in each COA based experiment and eight as controls of fluid intake during the COA protocol. They were purchased from Charles River. They were 2-months old and weighed 250–260 g at the beginning of the experiments. On arrival, they were housed individually in Plexiglas chambers at constant temperature and relative humidity ($22 \pm 0.5\,^{\circ}C$ and $50 \pm 5\%$). All rats were kept under a 12-h light:12-h dark cycle and were weighed daily at 09:00 a.m.

2.2. Experimental procedures

This study comprised two experiments. The first was designed to test that the olfactory detection ability of ad libitum fed rats for an odorant diluted in their usual drinking water did not change when the same concentration was presented on 2 successive days. This is the "baseline experiment". The second was designed to analyze how the feeding state influenced the olfactory detection ability when the same odor concentration was presented to the same fasted or satiated rats. This is the "detection experiment".

Isoamyl acetate (ISO) was utilized in both experiments as a neutral odor with no food significance for the rats. The possible involvement of taste was ruled out by using ISO dilutions at concentrations for which ISO has been shown to be detectable only by smell and not by taste [44]. A concentration of 10^{-5} (corresponding to 1 μl in 100 ml of water) was used for establishing COA and stabilization (aversion retest) and at concentrations ranging from 10^{-10} to 10^{-7} for testing.

2.3. Common features of the experiments

The behavioral tests were conducted in parallel in groups of four rats in individual Plexiglas operant chambers (330 mm × 210 mm × 180 mm) in the laboratory. The chambers were set side by side so that the experimenter could observe the animals but the animals could not see one another. Two plastic tubes were mounted on opposite sides of the flat ceiling of each chamber. These tubes (made from 15 ml conical centrifuge tubes, CellStar) were cut and fire polished to give them a 0.5 mm spout which protruded about 5 mm into the chamber, allowing the rats to drink easily by raising themselves up on their hind limbs. Each tube was connected to a custom-made capacitance circuit which allowed the experimenter to measure the amount of liquid consumed by the rat and to record its licks using a CED 1401 interface (CED, Cambridge) connected to a computer.

The two experiments were based on a COA protocol, and the schedules are illustrated in Fig. 1. For the first 3 days the rats in the operant chambers were given tap water to drink (not shown). During the following days, corresponding to COA establishment, the rats only had access to water odorized with ISO at 10^{-5}, and were then given an intraperitoneal injection of LiCl (10 ml/kg at 0.15 M) 15 min later to make the animals sick. Then only those which drank more than 0.5 ml of ISO during any of the subsequent three sessions were injected with LiCl. Once COA was established, the aversion was tested by giving the animals the choice between tap water and water odorized with ISO 10^{-5}, on day 0 (D0) of each experiment. The test period then began by offering the rats the choice between tap water and water odorized with ISO at different concentrations. Lastly, to confirm the aversion, the choice between ISO 10^{-5} water and tap water was repeated (aversion retest) at the end of the two experiments. When the tubes contained two different drinks, their right-left position was systematically interchanged across sessions. At the beginning of each session, the rats were intentionally placed under the tube containing the ISO-odorized water.

Rat olfactory sensitivity for ISO was thus assessed using a forced-choice task, and not by using a simple choice task, since the thirsty rats were forced to smell the odorized tube first. This procedure was chosen to avoid the possibility that the rats, highly motivated by thirst, would go by chance to the pure water tube first, drink only water, and not sample the ISO tube.

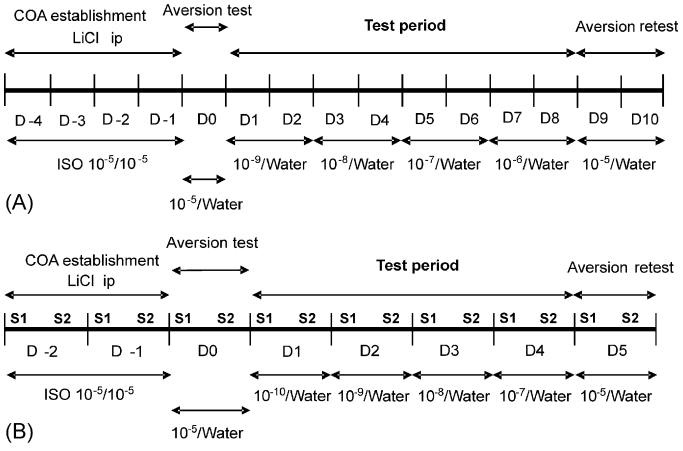

Fig. 1. Schematic representation of the overall course of the baseline (A) and detection (B) experiments. The two experiments are divided in four steps: COA establishment (Days before D0) during which ISO 10^{-5} presentation was paired with intraperitoneal (i.p.) injection of LiCl, the aversion test (D0) where the choice between ISO 10^{-5} and water was proposed, test period and aversion retest. One and two-daily sessions were performed in the baseline and detection experiment. In the baseline experiment (A), the test period ran from D1 to D8 and the same ISO concentration was presented on 2 consecutive days. In the detection experiment (B), the test period ran from D1 to D4 and the same ISO concentration was presented twice daily.