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Memory-dependent effects on palatability in mice

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HIGHLIGHTS

- Consumption in mice is maximal with intermediate concentrations of sucrose.
- Lick cluster size increases monotonically as a function of sucrose concentration.
- A successive negative contrast procedure reduced lick cluster size.
- Flavour habituation led to an increase in lick cluster size.
- Memory has effects on palatability similar to altering the sweetness of a solution.

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ABSTRACT

While palatability depends on the properties of particular foods, it is also determined by prior experience, suggesting that memory affects the hedonic value of a substance. Here, we report two procedures that affect palatability in mice: negative contrast and flavour habituation. A microstructure analysis of licking behaviour was employed, with the lick cluster size (the number of licks made in quick succession before a pause) used as a measure of palatability. It was first confirmed that lick cluster size increased monotonically as a function of sucrose concentration, whereas consumption followed an inverted U-shaped function. In a successive negative contrast procedure it was found that when shifted from a high sucrose concentration (32%) to a low sucrose concentration (4%), mice made smaller lick clusters than a group that only received the low concentration. Mice exposed to flavours (cherry or grape Kool Aid) mixed with sucrose (16%) made larger lick clusters for familiar flavours compared to novel flavours. This habituation effect was evident after short (5 min) and long (24 h) test intervals. Both successive negative contrast and flavour habituation failed to affect levels of consumption. Collectively, the results show that prior experience can have effects on lick cluster size that are equivalent to increasing or decreasing the sweetness of a solution. Thus, palatability is not a fixed property of a substance but is dependent on expectation or familiarity that occurs as a result of memory.

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1. Introduction

Palatability reflects the hedonic value of foods and is a key determinant of feeding behaviour. Although it is determined by the properties of the food, it is also moderated by prior experience (e.g., [17]). While the level of intake of a particular food may reflect its palatability, it has been shown that measures of palatability are dissociable from measures of consumption. For example, dopaminergic manipulations affect levels of consumption, but not necessarily the orofacial taste reactivity responses [24] that are taken to reflect palatability responses [13,20]. Similarly, there are manipulations that affect consumption, but have different effects on taste reactivity. For example, Pelchat, Grill, Rozin, and Jacobs [21] found that rats would avoid consuming flavours that had previously been paired with sickness and shocks to a similar extent, but only flavours that had been paired with sickness elicited negative taste reactions such as gaping and head shaking.

Given the distinct role of palatability in feeding behaviour it is important to understand both the psychological and neurobiological processes underlying palatability. Crucially, understanding of the neurobiological processes requires the use of animal models. Due to the prevalence of genetically modified mouse lines there is a benefit in identifying valid behavioural manipulations of palatability in mice. Currently, there are well-established behavioural procedures for examining palatability in rats, but there are fewer successful demonstrations in mice. Therefore, a purpose of the current study was to determine behavioural factors that affect palatability in mice by testing the effect of prior experience on consumption of sucrose solutions.

In order to assess palatability in mice we used a microstructure analysis of licking behaviour during consumption of sucrose. Rodents drink,

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typically, by making a series of licks in quick succession (a lick cluster) before a pause (e.g., [3,5]). In rats the mean number of licks in a cluster increases monotonically as a function of sucrose concentration, whereas consumption follows an inverted U-shaped function [7,23]. Therefore, lick cluster size has been proposed to provide a measure of palatability that is independent of levels of consumption (see [9], for a discussion). Consistent with this proposal, lick cluster size decreases with increasing concentration of unpalatable tastes (e.g., [14]). In the present study we used the mean lick cluster size as an alternative measure of palatability to the orofacial taste reactivity responses. While taste reactivity measures have been used to measure changes in palatability as a consequence of experience (e.g., [11]), the method requires human coding of the behaviours and surgery to enable the administration of substances directly into the oral cavity of rodents. Therefore, the measurement of lick cluster sizes avoids the use of those procedures.

We have previously demonstrated in mice that lick cluster size is affected by sucrose concentration, but this was with only a limited range of concentrations [1]. In addition it has been suggested that the monotonic effect of sucrose concentration on lick cluster size in mice is observed only when using a particularly large pause criterion (>1 s) to determine the end of a lick cluster [15]. In order to validate the use of lick cluster size as a measure of palatability in mice Experiment 1 assessed consumption of a range of sucrose concentrations using a range of inter-lick cluster interval criteria.

The effect of memory on palatability was assessed using procedures that should either decrease or increase palatability. Experiment 2 examined a detrimental effect on palatability using a successive negative contrast procedure in which one group of mice was preexposed to 32% sucrose and another group was preexposed to 4% sucrose. Both groups were then allowed to consume 4% sucrose. In rats it has been demonstrated that the shift from a high concentration of sucrose to a low concentration results in a reduction in palatability of the low concentration of sucrose compared to a condition in which animals only experience the low concentration of sucrose [12]. In mice there are reports of negative contrast effects on levels of consumption (i.e., a shift from high to low concentration of sucrose results in reduced intake compared to controls, [19]), but there are few reports of an effect on palatability (see [1]).

A beneficial effect on palatability was examined using a flavour habituation procedure. A common finding in rats is that exposure to a novel flavour leads to a reduction in feeding that habituates with increased exposure [2]. In addition, measures of palatability increase as the flavour becomes familiar [16]. A flavour habituation effect on palatability was examined in Experiment 3 using a between-subjects procedure in which mice were exposed to a novel flavour and then after a short (5 min) delay half of the mice were exposed to the same flavour and the other half were exposed to a novel flavour. Experiment 4 examined the longer lasting effects of flavour habituation using a within-subjects procedure in which mice were exposed to one flavour over eight days and then given that flavour, and a novel flavour, 24 h after the last exposure.

2. Method

2.1. Subjects

Female C57BL/6 J/Ola mice obtained from Charles River, UK were used. Mice were caged in groups of four, in a temperature controlled housing room (light-dark cycle: 0800–2000). Mice in Experiment 1 were 10 weeks of age at the beginning of the experiment and weighed between 16.3 and 20.9 g (mean = 18.9 g). Mice in Experiment 2 were approximately five months old at the beginning of the experiment and weighed between 19.4 and 24.3 g (mean = 21.7 g). Mice in Experiment 3 were between 12 and 20 weeks of age at the beginning of the experiment and weighed between 14.1 and 25.7 g (mean = 21.4 g). Mice in Experiment 4 were between 16 and 27 weeks old and weighed between 17.4 and 24.5 g (mean = 20.0 g). Mice were initially allowed free access to food, but one week prior to training the weights of the mice were reduced, by receiving a restricted diet, and then subsequently maintained at 85% of their free-feeding weights. Mice were tested during the light period between 10 am and 4 pm. Throughout testing mice had ad libitum access to water in their home cages. All procedures were in accordance with the United Kingdom Animals Scientific Procedures Act (1986); under project license number PPL 70/7785.

2.2. Apparatus

A set of eight identical operant chambers (interior dimensions: 21.6 × 17.8 × 12.7 cm; ENV-307 W, Med Associates), enclosed in sound-attenuating cubicles (ENV-022 V, Med Associates) were used. The operant chambers were controlled by Med-PC IV software (Med Associates). The side walls were made from aluminium, and the front and back walls and the ceiling were made from clear Perspex. The chamber floors each comprised a grid of 24 stainless steel rods (0.32 cm diameter), spaced 0.79 cm apart and running perpendicular to the front of the chamber (ENV-307W-GFW, Med Associates). Retractable sippers (ENV-352AW, Med Associates) and a small hole in one wall of each chamber allowed graduated pipettes to be extended into, and retracted from, the chambers. The graduated pipette (0.1 ml) allowed measurement of consumption by comparing the volume before and after testing. Contact lickometer controllers (ENV-250, Med Associates) allowed contacts between the mice and the graduated pipettes to be recorded at a resolution of 0.01 s. A fan (ENV-025F, Med Associates) was located within each of the sound-attenuating cubicles and was turned on during sessions. Sucrose solutions were made weight/volume with commercially available sucrose in distilled water. For Experiments 3 and 4 the flavours used were cherry and grape Kool Aid (0.05% *w*/*v*, Kraft Foods USA, Rye Brook, NY, USA).

2.3. Procedure

2.3.1. Experiment 1: the effect of sucrose concentration on licking behaviour

Mice (N= 16) were allowed to consume 2.5%, 5%, 10% and 20% sucrose solution on four sessions, one session per day. Mice were presented with one of the concentrations per session, and the order in which the concentrations were presented was counterbalanced across mice. Specifically, half of the mice received the two low concentrations (2.5% and 5%) in the first two sessions and the remaining mice received the two high concentrations (10% and 20%). Within each of these groups the order of the concentrations in these first two sessions was counterbalanced. For the last two sessions mice received the two remaining concentrations in a counterbalanced order that across mice was also counterbalanced with respect to the order of the concentrations in the first two sessions. Sessions lasted 30 min and the pipette was extended into the chamber for the full duration of the session.

2.3.2. Experiment 2: the effect of negative contrast on licking behaviour

Mice were randomly allocated to either group Unshift (N= 8) or group Shift (N = 8). The groups did not differ in their free-feeding weights (Unshift: 22.0 g; Shift: 21.0 g; $F(1, 14) = 1.8$, $p = 0.21$). Mice received eight training sessions, consisting of one trial per session, one session per day, in which a sucrose solution was available for consumption. Each trial lasted 15 min; however, the pipette was only extended into the chamber for the final ten minutes of the trial (similar to the procedure used by Austen and Sanderson [1]). Group Unshift received 4% sucrose solution on each training session, and were subsequently given a single test session 24 h after the final training session, using the same procedure as during training, in which they were also given 4% sucrose. Group Shift received 32% sucrose during training and then 4% sucrose in the test session.

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