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Analysis of the Sensory and Hedonic Impacts of Sweet and Bitter Tastes in Perinatally Underfed Rats

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Abstract

Newborn rats discriminate tastes and generate gustofacial response (GFR) because the neuronal substrate is already operating. The oral application of sucrose or quinine hydrochloride produces a specific GFR. We analyzed the effects of perinatal undernutrition on the GFR development of rats at two cue concentrations. In the undernourished group, pregnant dams received different percentages of a balance diet. After birth, prenatally underfed pups continue the undernourishment by remaining for 12 h with a foster dam, and for 12 h with a nipple-ligated mother. Cues were presented as a single droplet of sucrose, sodium chloride, or quinine at low or high concentrations onto the lips at postnatal days (PDs) 1 and 3, and mouth-opening (MOF) and lip-licking frequencies (LLF) were noted. On PD 1 the undernourished group showed smaller MOF increases in response to low salt and quinine stimuli than the controls but no differences at high concentrations. On PD 3, both low and high concentrations of the sucrose and quinine cues significantly increased the MOF in the underfed compared to the control group. Low but not high salt decreased LLF on PD1 in the underfed compared to the control group. On PD 3 the undernourished pups showed significant increases of LLF with low quinine compared with the control rats, but the reverse was observed with high quinine. These data suggest that perinatal undernutrition affects the development of the sensory and hedonic aspects of taste causing changes in GFR expression.

Keywords

Undernutrition, Gustofacial Responses, Gustatory System, Development, Rats

1. Introduction

In the rat the gustatory system is important for the preference-aversion function that is critical for the food proc-

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ess of feeding behaviors. The adult rat responds to direct infusion into the oral cavity of sucrose and quinine, which are the classical taste stimuli that evoke stereotyped lingual, masticatory, and face-pulling movements. The sucrose elicited rhythmic orofacial movements, is systematically followed by lateral tongue movements and accompanied by subsequent tongue protrusion. By contrast, aversive quinine stimuli produce oral-rejection responses (gaping) and a sequence of flexor-extensor body movements, chin rubbing, head-shaking, face washing, flailing of the forelimbs, and paw pushing [1] [2]. Based on electrophysiological studies the orofacial motor activities induced by taste stimulation might be integrated between the forebrain structures and a neuronal locus located in the caudal parts of the brain stem [3]-[5].

The orofacial responses are not only reflexes in response to gustatory stimulation, but they also reflect the affective impact of the stimuli [5] [6]. The hedonic impact results from the integration of gustatory information throughout the sensory and limbic relays that contribute to food selection [7]-[9]. The positive hedonic impact of food taste can enhance its acceptance by acting as a sensory reward; conversely, the negative hedonic impact may result in an aversive response [10]. The orofacial movements reflect the hedonic aspect of the stimulus, and they are also related to the palatability of tastes at different concentrations.

In the rat development of the gustatory system begins during gestation, and 1 to 3 days old rat pups reject quinine solutions, showing aversive responses accompanied by gaping and forelimb flailing. By contrast, sucrose solutions produce rhythmic mouth opening and lateral tongue protrusions [11]. However, as the animal matures, its nervous system develops and becomes more organized in order to integrate taste cues and allow appropriate ingestive behavior necessary for survival [11]-[13]. Altricial mammals dramatically change their feeding behavior in the first week of life, and taste is an important determinant of the ingestive behaviors of adult mammals [12]. Thus, sensory experience initiates when the fetus can shape food preferences because the tastants are transmitted from the maternal diet to the amniotic fluid [14]. Additionally, clinical and experimental evidences indicate that adverse foetal environment may interfere with the development of specific food preferences, and to develop chronic disorders in adulthood [15]. The current study analyses if perinatal underfeeding has adverse effects upon GFR expression in the newborn rats.

On the other hand perinatal undernutrition affects the normal development of pups as evidenced by body and brain weight reductions; dendritic branches are also diminished with neuronal hypoplasia in some structures such as the solitary tract nucleus, olfactory bulb, facial motor nucleus, and insular cortex [16]-[19]. Additionally, some responses, like maternal care and social play behaviors, are significantly disturbed [20] [21]. Each member of the same hedonic category elicits similar GFR responses, even at different concentrations however, it is not yet known if the responses in the normal and early underfed pups are graded in accord with the concentration of the gustatory cues. In the present study we investigate the newborn GFR of undernourished and control rat pups elicited by low or high concentrations of sweet, salt, and bitter taste stimuli during the first postnatal days.

2. Material and Methods

2.1. Animals

Experiments were approved by local Animal Committees and were in accord with the NIH Guide for Care and Use of Laboratory Animals. Subjects were male Wistar rats (*Rattus norvegicus*), born and reared in the animal colony at the Institute of Neurobiology, University of Mexico. All animals were maintained in an automatically controlled room at 23˚C ± 2˚C, 50% humidity and a 12 h/12h light/dark cycle (lights on at 0700 h), with water and food (Purina chow) ad libitum. For mating, a male was placed in a plastic cage (60 × 32 × 20 cm^3) containing three females (200 - 250 g). Sperm-positive females were placed in individual plastic maternity cages (35 × 27 × 17 cm^3) with grill tops and wood shavings as nesting material one week before parturition. The day of birth was referred to as postnatal day (PD) 0, and 24 h later pups were randomly mixed, redistributed, and adjusted to 8 pups per mother (four males and four females). The redistribution was intended to balance possible genetic and prenatal biological differences between litters and give them equal probability of development. The presence of the bilateral thoracic and abdominal line of nipples and the shorter anogenital distance in the female were used as criteria for sex recognition [22].

2.2. Nutritional Treatments

2.2.1. Undernourished Group (UG)

The UG male and female pups in this group (n = 64) came from at least nine different litters. Pregnant dams

were fed from G6 to G12 with 50% (7.8 g/day) of a balanced diet (Purina chow) received by a normal dam; from G13 to G19 with 70% (10.9 g), and with the 100% (15.6 g) until parturition, to avoid cannibalism or resorption of pups. After birth, prenatally underfed newborns were nursed by a pair of gestationally underfed dams, in one of which the main galactophorous ducts had been subcutaneously tied [23]. To continue the neonatal underfeeding method, these two lactating dams were interchanged every 12 h between litters from PDs 1 to 3 (**Figure 1(a)**). This cross-fostering procedure reduces the effects on the newborn of maternal sensory deprivation that may interfere with the expression of GFR [23]-[25]. This underfeeding paradigm was chosen because the oromotor responses are regulated at the brainstem level and most of its neurogenesis occurs prenatally following first a rostrocaudal and then a mediolateral cytogenetic gradient. Moreover, the facial nerve efferent projections to the facial muscles and taste buds also develop during this period and continue during the early postnatal period [26] [27].

2.2.2. Control Group (CG)

The CG subjects consisted of 64 male and female pups obtained from nine, well-nourished litters, nursed by well-fed dams that had free access to water and balanced food (Purina chow) during gestation. After birth, CG pups were fed by two, normally lactating mothers, who were interchanged every 12 h between litters. To evaluate the effects of the nutritional treatment on physical growth, body weights of pups treated with different diets were also recorded after the gustatory test.

2.3. Gustatory Test Solutions

The animals labeled with different colors for each gustatory stimulus came from different litters. The CG and UG pups were exposed to the following gustatory stimuli: the water, and three different sapid solutions, each at low and a high concentration in distilled water: salt, 0.1 M and 0.3 M; sucrose, 0.1 M and 0.3 M; quinine hydrochloride, 0.01 M and 0.1 M.

2.4. Procedures and Experimental Groups

All GFR tests were performed between 10:00 and 12:00 h in a sound-proof chamber illuminated with red light (60 W) under controlled temperature (26˚C ± 2˚C) and separated from the ambient noise of the main laboratory. The GFR tests were carried out with a slight modification of the procedure previously described for neonatal rats [28]. A total of 4 males and 4 females from either CG or the UG were used for each taste test on PDs 1 and 3.

2.5. Behavioral Testing

Pups under the two dietary treatments were maintained with the mother in their habitat for at least 30 min before the gustatory test began. The taste stimuli were presented centrally on the pups' lips as a single droplet (about 8 µl) via a 2 cm length of polyethylene tubing (P.E. 160) attached to a blunted tip of a 2.0 mm plastic micropipette. A single micropipette was used for each taste during the recording tests.

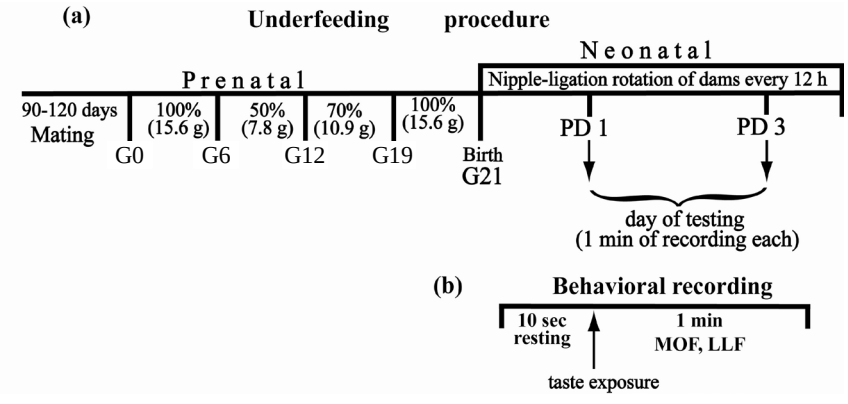

Figure 1. (a) Schematic representation of the underfeeding procedure; (b) Behavioral recording of MOF and LLF at PDs 1 and 3.

2.6. Recording System

These hand-held and relaxed, swaddled pups were observed and videotaped for a 10 seconds period of resting before exposure solution, and then under the effect of a tastant for a 1 min span until the droplet disappeared into the pup's mouth under red-lamp illumination (**Figure 1(b)**). Because the newborn rats produce reliable mimetic rhythmic facial, head, and body movements in response to oral gustatory stimulation, in each behavioral test the mouth opening frequency (MOF), and lip-licking frequency (LLF) of the pups were analyzed. These early mimetic responses have been shown to be a reliable index of taste sensitivity associated with the GFR [1] [28] [29]. To ensure blind observations with respect to taste stimulus presentation, the different dietary treatments and gustatory exposure sequences were randomly modified from one test to the other. Due to the small body size of neonatal rats and because a certain level of experience was required to record the GFR events, some experiments included data from naïve, partially experienced, and very experienced observers to assess the reliability of the measurements.

2.7. Statistics

The statistical package Statistica, version 6 was used to perform all comparisons of experimental data. For body weight measurements a two-way ANOVA, 2 (dietary treatments) × 2 (ages) was used. The MOF and LLF measurements in response to different gustatory stimuli were compared with a three-way ANOVA, 2 (dietary treatments) × 2 (ages) × 2 (taste concentrations), followed by the Fisher LSD *post hoc* test. The threshold level for significance was set at $p < 0.05$ for all analyses.

3. Results

3.1. Body Weight of Pups

Because statistical comparisons in body weight between male and female pups showed no significant differences, then they were treated as one group. Body weight comparisons showed significant differences by diet, $F(1,14) = 207.86$, $p < 0.001$ and age, $F(1,14) = 99.94$, $p < 0.001$ and an interaction diet × age, $F(1,14) = 6.41$, $p < 0.02$. *Post hoc* comparisons at each developmental age indicated consistent significantly lower ($p < 0.05$) body weights for the UG pups at PDs 1 and 3 compared to the CG subjects.

3.2. Effects of Water on the GFR

Water was used as a neutral stimulus to examine the GFR and also as a vehicle to dilute the sweet and bitter tastes. The ANOVA comparisons of the MOF were not modified by diet or by age. Moreover, the LLF comparisons yielded no differences by diet, but they were modified by age, $F(1,14) = 11.82$, $p < 0.003$, and there was a significant interaction between age × diet, $F(1,14) = 20.37$, $p < 0.0004$. *Post hoc* comparisons of LLF showed that in the CG the mean LLF was the same for the two ages, but in the UG rats the LLF increased significantly compared to the CG at PD 1 and decreased more than the CG at PD 3 (**Figure 2(a)**). Most of the comparisons of water with other gustatory stimuli showed negligible differences (data not shown).

3.3. Effects of Sodium Chloride on the GRF

Comparing the effects of salt on the MOF showed no differences due to the diet, but significant differences between the high and low salt concentration, $F(1,28) = 32.60$, $p < 0.001$, no interaction diet × concentration; significant differences by age, $F(1,28) = 126.86$, $p < 0.001$, with no interaction age × diet; significant interactions between age × concentration, $F(1,28) = 35.80$, $p < 0.001$, and age × diet × concentration, $F(1,28) = 4.46$, $p < 0.04$. *Post hoc* comparisons show differences only between salt concentrations at PD 1 for both experimental groups. The low concentration of salt induces significantly higher GFR values ($p < 0.05$) than the high concentration, with no differences at PD 3. The effects of salt on LLF showed no significant differences by diet and concentration, a significant interaction diet × concentration, $F(1,28) = 7.8$, $p < 0.009$; no differences by age but a significant interaction age × diet, $F(1,28) = 16.29$, $p < 0.001$, and a significant interaction age × diet × concentration, $F(1,28) = 6.31$, $p < 0.01$. *Post hoc* comparisons showed that the CG animals have higher values on PD 1 compared with the UG at PD 3; at high salt the UG pups have significantly higher LLF values ($p < 0.05$) than the CG animals (**Figure 2(b)**).

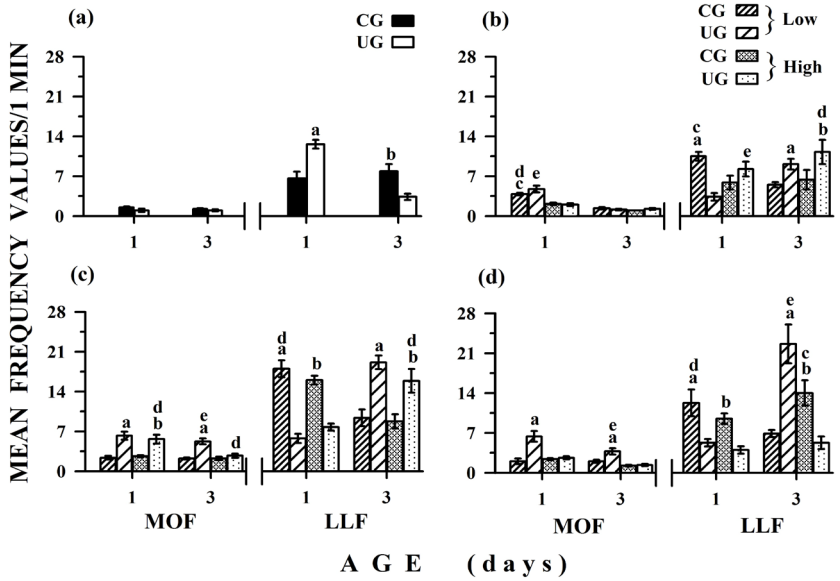

Figure 2. Mean (±EEM) of MOF and LLF at two ages evoked by different tastants: (a) water; (b) salt; (c) sucrose and (d) quinine, at low and high concentration in both CG and UG groups. Note in all the graphs of the panel that MOF measurements had lower values than the high LLF measurements. Letters above the pair of bars indicate statistically significant comparisons ($p < 0.05$) between different dietary and taste concentration groups: a: CG low vs. UG low; b: CG high vs. UG high; c: CG low vs. CG high; d: CG low vs. UG high; e: UG low vs. UG high respectively.

3.4. Effects of Sucrose on the GFR

ANOVA comparisons of the effects of sucrose concentrations on the MOF yielded significant effects of the diet, $F(1,28) = 44.77$, $p < 0.001$, without differences by concentration, and a significant interaction diet × sucrose, $F(1,28) = 11.39$, $p < 0.03$; significant differences by age, $F(1,28) = 15.85$, $p < 0.001$, and a significant interaction age × diet, $F(1,28) = 9.43$, $p < 0.001$. *Post hoc* comparisons showed significant reduced UG values vs. CG ($p < 0.05$) at PD 1; with significant lower values ($p < 0.05$) in the UG than CG for both concentrations; at PD 3 the UG exhibited significantly ($p < 0.05$) higher MOF values only at sucrose. The sucrose stimulation of LLF was not affected by the diet, age or by concentration; it only showed a significant interaction age × diet, $F(1,28) = 109.23$, $p < 0.001$. *Post hoc* comparisons indicated significantly higher ($p < 0.05$) LLF values in the CG compared to UG at P1 and the opposite in PD 3 (**Figure 2(c)**).

3.5. Effects of Quinine on the GFR

Statistical comparisons of the MOF elicited by the application of quinine showed significant reductions by diet, $F(1,28) = 31.65$, $p < 0.001$, and concentration, $F(1,28) = 31.65$, $p < 0.001$, with a significant interaction diet × concentration, $F(1,28) = 24.76$, $p < 0.001$; there was also a significant reduction by age, $F(1,28) = 12.25$, $p < 0.001$, without any interaction. *Post hoc* comparisons showed significantly increased MOF ($p < 0.05$) in the UG pups at low quinine on PDs 1 and 3. For the LLF, quinine showed no significant differences between the diets, but significant differences by concentration, $F(1,28) = 7.15$, $p < 0.01$, and a significant interaction diet × concentration of quinine, $F(1, 28) = 18.64$, $p < 0.001$. Additionally, there were significant differences by age, $F(1,28) = 14.26$, $p < 0.001$, with significant interactions age × diet, $F(1,28) = 17.21$, $p < 0.001$, and age × diet × concentration, $F(1,28) = 30.59$, $p < 0.001$. *Post hoc* comparisons showed differences at PD 1, with significantly increased LLF values ($p < 0.05$) in the CG at both concentrations. Additionally, at PD 3 the UG show significantly higher values than CG ($p < 0.05$) at low quinine, and lower values than the CG at high quinine (**Figure 2(d)**).

4. Discussion

The current findings indicated that early in life, perinatal undernutrition interferes with the expression of the

GFR and also with the hedonic response elicited by sweet, salty or bitter tastes due to the chemical properties of substances at the two different concentrations employed here. In fact, the receptors excitability and response to gustatory stimuli can be affected by the size of the area stimulated, and by both the concentration and the volume of the taste solution used [30]. Previous studies in rats have used electromyography recordings of some masticatory muscles during the licking, such as the jaw closers (temporalis and masseter muscles) and the jaw openers during water, sucrose, and salt stimulation and the reciprocal relation between the jaw closers and openers. In the present study a characteristic of jaw opening (gaping) was observed during the lip licking after quinine stimulation. This finding suggests that licking patterns reflect the hedonic aspect of taste palatability (acceptance-rejection) rather than the taste quality (sugar, salt, acid, bitter, etc.) [4].

It is known that for humans, the sensory pleasure of sweetness is enhanced by hunger and suppressed by caloric satiety [31]. Moreover, the brain mechanism that mediates the aversive hedonic impact to the taste depends on the development of the opioid neurotransmitter system that elicits positive hedonic palatability [32]. Perinatal underfeeding may cause alterations in food-intake in adulthood; the UG rats showed larger increases in food consumption than the CG subjects, and they have a propensity to develop metabolic disorders. This behavior may be associated with age-related disruptions in the gustatory circuitry, that are related to the ontogeny of this opiod neurochemical system [2] [33] [34].

The present study indicated that during the sweet stimulation the pups maintained a continuous and rhythmic lips licking activity accompanied by a moderate secretion of saliva with negligible body movements. By contrast, during the quinine exposure the pups exhibited few LLF movements and they were immediately suppressed and changed to a gaping response with a profuse secretion of saliva that dilutes and ameliorates the gustatory cue stimulus [35]. Furthermore, current data also indicated that the reduced MOF elicited by the different taste concentrations are clearly different when compared to the increased LLF movements to the same gustatory cues. These findings suggest that the neuronal circuits underlying the MOF responses in the UG pups elicited by water and salt reflect different excitability or synaptic organization at this developmental period, because they maintain a relatively constant concentration in the amniotic fluid during gestation [11] [36]. Additionally, on PD1 the UG pups showed consistent LLF reductions in response to all tastants when compare to the CG animals; by contrast on PD3 most of the UG subjects displayed LLF movements in response to the same gustatory cues. These findings suggest that in the UG pups the undernutrition interfered more with the synaptic connectivity and the excitability of the circuit underlying the LLF movements [11] [33] [37].

Our findings revealed that, in addition to the GFR elicited by the gustatory stimulation some somatic and autonomic responses are produced at a neuronal locus located at the caudal brainstem level [3]-[5]. The neuronal timing of this impulse generator possibly was genetically coded early in life and is responsible for triggering the motor circuitries in the brain underlying the rhythmic jaw-tongue activity [2] [5]. According to previous studies, early undernutrition results in significant neuronal hypoplasia in the solitary tract nucleus, the first relay of the gustatory system; and particularly in the peripheral dendritic arbor branches and spines; these defects interfere with the integration of gustatory information [17]. Food restriction also similarly disrupts other gustatory relays, such as those of the parabrachial nuclei and the insular cortex of the rat. Thus, these brain stem and neocortical neuronal alterations may be generating different rhythms of motor activity, such as the excessive self-grooming bouts usually associated with early undernutrition [11] [38]-[40]. Giving support to these possibilities is the fact that the basic mechanisms that trigger the motor components of reactions to taste are generated by the brainstem, since anencephalic infants and decerebrate rats show the appropriate GFR in response to sucrose or quinine [1] [40]. Present GFR deficiencies may possibly be compensated through a balanced diet provided to the mother, by enhancing mother-litter bonds, physical contacts, and licking of pups to release different hormones (GH, T4-T3), and growth factors, all of which promote brain maturation and attenuate the neonatal stress responses [41] [42].

5. Conclusion

In summary the CG and the UG newborns are able to perceive the different types of taste stimuli early in life as revealed by the GFR in response to gustatory stimulation. Moreover, the findings obtained here are in line with the dietary treatments, and the general noxious effects of perinatal underfeeding on the central nervous system as previously reported in rats. The differences in the LLF and MOF patterns of facial expressions may be related to the early processes of learning to identify flavors, and with a long-term influence on the food selection habits

and healthy early conditions. However, further studies are needed to assess the excitability and responsiveness to taste stimulation and ingestive behavior during the pre weaning period.

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