Recognition of Food by Individual, Food-Naive, Weaning Rats (Rattus norvegicus)

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To control and observe first feeding experiences, pups were reared without access to food. At weaning age, individual pups received simultaneous access to a palatable, noncaloric diet and a similar diet containing starch. Each diet contained a flavor cue. Within 20 min of sampling both diets pups preferentially ingested the caloric alternative. Further tests indicated that pups learned a preference for flavor cues paired specifically with ingestion of starch. In caloric discrimination tests in which the diets were not distinguished by artificial flavors, pups did not show the rapid preference for the caloric diet seen in earlier experiments. We suggest that recognition and preference for the caloric diet is based on its rapid postingestive effects rather than readily preferred sensory features of the starch. Our findings demonstrate the abilities of individual, food-naive pups to rapidly recognize food and indicate a role for associative learning in the onset of independent feeding.

Mammalian development involves invariant sequelae. One of these is the weaning process, the offspring's shift from nutritional dependence on mother's milk to ingestion of solid food (Galef, 1981). Intake of solid food (feeding) involves novel behavioral and physiological capabilities in the offspring (Henning, 1981). Recognition of food is the fundamental precursor to reliable ingestion and use of nonmilk nutrients and is a key to the weaning process. Thus, the mechanisms of food recognition are important and special problems in the study of mammalian development.

Under natural or seminatural conditions, Norway rats begin to ingest solid food in the context of conspecifics. Adults transmit information about a colony's diet to juvenile conspecifics, and such information influences pups' choice of diets at weaning (Galef & Clark, 1971; Galef & Wigmore, 1983). Thus, to observe the individual pup's abilities to recognize food, one must separate the pup from its social context. In a rare study on this topic, Booth, Sloloff, and Nicholls (1974) reared litters without access to solid food in the nest area but provided the pups access to various diets in a compartment separate from the dam. After several days of feeding, the pups ingested primarily rat chow and a starch-rich diet but very little of a nonnutritive diet. However, the entire litter had access to the diets, and the maternal diet (Purina Rat Chow) was one of the choices. Thus, it was impossible to separate maternal influences on diet selection from individual recognition of food.

By 20-30 days of age, pups can discriminate among various nutrients, such as proteins and starches (Blake & Henning, 1986; Blake, Okuhara, & Henning, 1984; Booth et al., 1974; Overman & Yang, 1973), and they preferentially ingest diets that contain flavor cues previously paired with starch-rich and protein-rich diets (Booth et al., 1974; Hayward, 1983). The animals in these studies had substantial feeding experience before testing, or the effects were obtained over several days to a week of experience with the experimental diets. Thus, it is unclear whether feeding experience served to permit or facilitate recognition of the nutrients. The Booth et al. study suggested that weaning-age rat pups do not immediately recognize a nutritive diet; the pups initially ingested equivalent amounts of nutritive and nonnutritive diets. A short period of sampling food and nonfood items also appears necessary before recognition of food in chicks (Hogan, 1984), guinea pigs (Reisbick, 1973), and fledgling birds (Davies, 1976; Marler, 1956).

Our research was designed to investigate the abilities of individual, food-naive rat pups to recognize and preferentially ingest food at weaning. Can pups discriminate a caloric diet (containing starch) from another palatable but nonnutritive diet? Does associative learning mediate recognition of the caloric diet? Finally, what are the roles of the oral and post-ingestive cues of the caloric diet in the pup's recognition of food?

Experiment 1: Development of Caloric Discriminations

Norway rats engage in a substantial range of oral exploration before and throughout the weaning period (Galef, 1979; Melcer & Alberts, 1985). They appear to indiscriminately mouthing food and nonfood items. The presence of the mother does not prevent rat pups from mouthing nonfood items;
Indeed, portions of the mother's body are among the nonfood items in the pups' oral world. Maternal feces, under some circumstances, are ingested (Galef, 1979). These observations suggest that pups must make nutritive discriminations at weaning.

Harris, Clay, Hargreaves, and Ward (1933) developed a dietary choice procedure to study the ability of vitamin-deficient rats to select vitamin-rich diets. We investigated the ability of food-naive pups to sample two distinct, palatable substances and recognize the caloric one. In pilot studies food-naive rat pups ingested the novel, nonnutritive diet (Diet NONCAL; see Method) and showed temporal patterns of feeding similar to pups that received access instead to a similar diet containing starch (Melcer, 1987).

Polycose was the caloric additive. This starch has been studied extensively by Sclafani and his colleagues (Nissenbaum & Sclafani, 1987; Sclafani, 1987; Sclafani & Nissenbaum, 1987). They found that adult rats readily detect and prefer Polycose in solution and argued that its taste is distinct from other carbohydrates. This is an important methodological and interpretive issue that we address throughout this article.

Pups normally begin to mouth food about 17 days after birth (Galef, 1979; Melcer & Alberts, 1985). In Experiment 1, 17-day-old pups received a series of caloric-discrimination tests. Individual pups received a simultaneous choice between a nutritive and a nonnutritive diet, each containing a distinctive artificial flavor cue. After caloric-discrimination training, all pups received simultaneous access to two noncaloric diets, identical except for the artificial flavor cues. This extinction test indicated whether the pups acquired a preference for the flavor previously associated with calories.

We measured intakes and videotaped feeding behavior. If pups could recognize the caloric alternative, they might ingest greater amounts of the caloric diet than the noncaloric diet. The development of the caloric discrimination within and between sessions might indicate whether recognition of food is based on its taste or postdigestive consequences.

Method

Subjects The subjects were seventeen, 17- to 23-day-old Sprague-Dawley rats (Rattus norvegicus) pups born in the Indiana University Animal Behavior Laboratory, outbred from SPF stock originally purchased from Charles River Inc. The colony rooms were maintained at 22°C and lighted on a 16:8 hr daily light/dark cycle.

Rearing. Pregnant dams were housed in standard polypropylene maternity cages (20 cm wide × 48 cm high × 26 cm deep) in which they had constant access to Purina Rat Chow and water. Births were recorded until 5 p.m. daily. Three days after birth (day of birth = Day 0) each litter was reduced to 8 pups (4 male and 4 female); the pups remained in the maternity cage with the dam until 14 days of age.

Rat pups had no ingestive experience with solid food before experimental testing. Under typical conditions rat pups do not sample solid food or water until Days 15 or 16 (Galef, 1979; Melcer & Alberts, 1985). Therefore, on the afternoon of Day 14 each litter and its dam were transferred to special rearing cages designed to prevent pups from encountering solid food. These cages had a maternal feeding compartment (30.5 × 25.4 × 33.0 cm) separated from a nesting compartment (30.5 × 30.8 × 33.0 cm) by a sheet metal wall (28.0 × 33.0 cm). The dam rapidly learned to transverse the 33-cm wall and gain free access to either compartment.

The dam's feeding compartment contained a bowl of powdered Purina Rat Chow and a graduated cylinder that provided water. Each compartment was covered with a wire mesh lid. A metal sheet (30.5 × 28.0 cm) was placed on the lid of the nesting compartment to ensure that the dams nested in that area. The pups did not climb the wall and remained confined to the water- and food-free nest chamber, the floor of which was blanketed with wood shavings. Thus, the pups were reared without access to solid food and lived solely on mother's milk until testing.

Nonnutritive base diet. The experimental diets were derived from a noncaloric mixture palatable to weanling rat pups (Galef, personal communication, November 11, 1984; Lewis, 1973; Maloney, 1972). The base diet (Diet AC) was prepared by mixing alpha cellulose (Sigma Chemicals), calcium carbonate, sodium chloride, heavy mineral oil, petroleum jelly, and water. (Table 1 provides a quantitative description of the experimental diets.) The resultant mixture was a moist, somewhat greasy paste.

Two variations of Diet AC were used in these experiments. The noncaloric diet (Diet NONCAL) used in all experiments consisted of Diet AC sweetened with saccharin (0.1% by weight).

Nutritive addition. The caloric additive in the nutritive diet (Diet CAL) was powdered Polycose (Ross Laboratories, Columbus, Ohio). Polycose consists of glucose polymers derived from hydrolysis of corn starch (2% free glucose, 5% maltose, and 93% polysaccharides). The caloric density (3.8 kcal/g) and absorption rates of Polycose are equivalent to those of glucose. In humans the serum concentrations of insulin and glucose peak 30 min after ingestion of Polycose and then decrease rapidly (Ross Laboratories, 1984). Adult humans report that Polycose has a bland, minimally sweet taste. The caloric diet consisted of Diet AC with Polycose (Diet CAL; 1 kcal/g diet).

Flavor cues. In Experiments 1 and 2, the diets were flavored with either artificial peanut or artificial bread flavoring (100 μl/25 g; International Flavors and Fragrances, Trenton, New Jersey). All dietary mixtures were sealed and refrigerated; they were used only for 72 hr after they were mixed.

Table 1  Percentage concentration (by weight) of various substances in each of the experimental diets

<table>
<thead>
<tr>
<th>Substance</th>
<th>Diet AC</th>
<th>Diet NONCAL</th>
<th>Diet CAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cellulose</td>
<td>19.0</td>
<td>99.9</td>
<td>75.0</td>
</tr>
<tr>
<td>Petroleum jelly</td>
<td>26.7</td>
<td></td>
<td>5.0</td>
</tr>
<tr>
<td>Calcium carbonate</td>
<td>13.7</td>
<td></td>
<td>0.1</td>
</tr>
<tr>
<td>Water</td>
<td>28.4</td>
<td></td>
<td>25.0</td>
</tr>
<tr>
<td>Mineral oil</td>
<td>10.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salt</td>
<td>1.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Diets contained either artificial peanut or artificial bread flavoring (100 μl/25 g diet).
We selected the artificial flavors on the basis of the results of pilot tests conducted with ground samples of chocolate, unsalted peanuts, graham crackers, wheat bread, and cheddar cheese. Pups showed more feeding bouts with bread and peanuts than with the alternative choices.

Apparatus and tests. Two test situations were used. Some pups (n = 6) were tested individually in standard wire hanging cages (19.0 x 24.1 x 7.8 cm). The testing room was dimly illuminated. A preweighed ration of the appropriate diet was placed in metal food cups (5.6 x 5.7 cm). Each cup was secured to a food tray (5.6 x 12.8 x 8.8 cm) provided to collect spillage from individual food cups. Two trays, each with one food cup, were placed 7.5 cm apart against the wall directly opposite the water spout. Each food cup was weighed before and after testing as a measure of food intake. Tests during which pups ingested less than 0.25 g were eliminated from the data analyses.

Additional pups (n = 11) were tested in glass compartments (24.0 x 48.0 x 30.5 cm aquaria) that permitted clear visibility for videotaping. The length of the compartment was half by a metal partition (30 x 24 cm) so that two pups could be tested simultaneously and independently. For each pup, two plastic food cups (1.9 x 5.0 cm) containing experimental diets were fastened to the floor against the glass wall (30.5 x 24.0 cm) and a cup of water was secured against the opposite wall.

Video analysis. The timecourse of feeding was obtained by time-lapse videography (6:1 record/playback, Gyyr Model TLC 2001). It was possible to discern a pup's approach, contact, manipulation, and ingestion of the experimental diets. Feeding was recorded when a pup made oral contact with a diet. The pups rarely removed diets from view, and data for such pups were discarded. An observer recorded the onset and offset of feeding from a keyboard interfaced to a computer (LSI-II, MDB Systems Inc., Orange, California).

The total time spent feeding on each diet during consecutive 10-min intervals was calculated, beginning with the onset of the pup's first feeding bout. Feeding bouts less than 5 s in duration were excluded from data analysis. Intraclass reliability was assessed on the feeding behavior of 11 pups, and the mean correlation coefficient was 0.97.

Procedure. Experiment I consisted of a series of caloric discrimination tests. Each test was a two-choice discrimination between a palatable, nonnutritive diet (Diet NONCAL) and a similar diet that contained the carbohydrate Polycose (Diet CAL). Pups (n = 9) were tested on Days 17, 18, and 19.

On Day 17, the pups were separated from the dam about 9 a.m. and deprived of the opportunity to nurse for 4 h. All pups then received a simultaneous choice between Diet CAL and Diet NONCAL for 2 h. The artificial flavors added to the diets (peanut or bread) were counterbalanced across the caloric and noncaloric diets.

Pups were returned to the dam in the home cage for 2 h immediately after this initial test (Session 1). Pups were then separated from the dam for 4 hr before a second, identical caloric-discrimination test (session 2) at about 9 p.m. Similar tests were repeated on the next two days (Sessions 3–6). Thus, each pup received a simultaneous choice between a caloric diet and a noncaloric diet twice each day for 3 days.

All pups received an extinction test, a choice between Diet NONCAL flavored with peanut and Diet NONCAL flavored with bread, on the 4th day. All other procedures during the day of extinction testing day were the same as those described on previous days.

We repeated these tests with 20- and 23-day-old pups and found the same pattern of results shown by 17-day-old pups. Because older pups were more likely to eat, we included some 20- and 23-day-old pups as subjects in videotaped analyses of feeding behavior. These pups (n = 11; three 17-day-olds, six 20-day-olds, and two 23-day-olds) were tested in the aquaria and videotaped in Session 1 to determine the initial time course of the caloric discrimination. A subset of these pups (n = 6; two 17-day-olds, two 20-day-olds, and two 23-day-olds) were also videotaped from Sessions 2 through 6.

Design and analysis. Pups that ingested less than 0.25 g in Session 1 were excluded from data analysis. The intake percentage of the Polycose diet was calculated for each pup (g Intake Diet CAL x 100 / g Intake Diet CAL + g Intake Diet NONCAL). Also, we calculated from videotapes the percentage of time feeding on each diet during 10-min intervals across the session (i.e., Seconds Spent Eating Diet CAL x 100/600 s).

Results and Discussion

The results of Experiment I establish that individual, food-naive weanling rats can sample novel, ingestible substances, readily detect the presence or absence of a usable caloric compound, and rapidly adjust their earliest independent feeding. Figure 1 illustrates the intake percentage of the caloric alternative for 17-day-old food-naive pups. In each of the six 2-hr tests (Sessions 1–6), there was a reliable preference for the caloric diet.

Amounts eaten. Total intake (g Diet CAL + g Diet NONCAL) during the caloric discrimination tests generally increased with the age of the pups. The pups that began testing on Days 17 or 18 steadily increased their total intake across tests (Session 1, M = 0.77, SE = 0.18; Session 6, M = 1.16, SE = 0.12, F(1,8) = 6.31, p < .001. In addition, pups showed a significant increase in the intake percentage of Diet CAL across tests (Session 1–6), F(1,8) = 4.76, p < .001. The increased preference for Diet CAL between sessions suggests that postigestive effects of Polycose were responsible, in part, for recognition of the starch.

![Figure 1](https://example.com/figure1.png)

Figure 1. Means (±SEs) for percentage of intake of the Polycose diet during each of the six 2-hr caloric discrimination tests. (Food-naive pups received a simultaneous choice between a caloric and noncaloric diet on Days 17, 18, and 19.)
Within-session discrimination. Figure 2 shows the percentage of time spent eating Diet CAL and Diet NONCAL during consecutive 10-min intervals of the initial caloric-discrimination test (Session 1). Food-naive pups spent equivalent time eating the caloric and noncaloric diets during the first 10-min interval but spent significantly more time feeding on the caloric diet during the second and third 10-min intervals, $F(2, 20) = 4.22, p < .05$. We also observed whether pups sampled each diet for at least 5 s during the first 10 min of feeding. Seven of 11 subjects (64%) sampled both diets. Thus, pups rapidly recognized the caloric alternative after an initial period of equal sampling of both diets. It is unclear whether sensory features of Polycose or its rapid postingestive effects mediated the initial discrimination process. These possibilities are considered further in Experiment 3.

The pups' retention of the caloric discrimination was robust; they showed immediate recognition of the caloric alternative during subsequent tests. Figure 3 shows that pups spent substantially more time feeding on the caloric alternative than on the noncaloric one during the first 10 min of Sessions 2 through 6, $F(1, 5) = 48.9, p < .001$.

Extinction testing. After the caloric-discrimination tests all pups received a choice between two noncaloric diets (Diet NONCAL), identical except for the artificial flavor cues (bread and peanut). The overall intake percentage of the flavor previously paired with calories ($M = 86.6, SE = 5.9$) was significantly greater than 50%, $t(8) = 6.18, p < .01$. During these extinction tests, the intake percentage of the caloric flavor (bread or peanut) did not change with repeated testing; pups maintained a strong flavor preference during the second extinction test conducted 6 hr after the first test. These data suggest that pups acquired a conditioned flavor preference on the basis of the taste or the postingestive consequences of the caloric diet. Pups appear to have acquired the flavor preference during the first caloric discrimination test (Session 1). At the beginning of the second discrimination test (Session 2), pups showed an immediate preference for the caloric diet without substantial sampling of the noncaloric diet (see Figure 3). Previous studies have indicated that weanling rats preferentially ingest flavors paired with nutritive diets (Booth et al., 1974; Hayward, 1983).

The food-naive rat pups recognized food following a very brief period of feeding experience (Figure 2). Booth et al. (1974) reported that pups required a day or two of feeding experience before they preferentially ingested a starch diet. In their study the pups were not tested individually, and rat chow, a starch-rich diet, and a nonnutritive diet were available simultaneously. In our experiment individual pups received access to two novel diets during discrete 2-hr tests. These procedures may have facilitated the rapidity of the discrimination process relative to the Booth et al. study.

Finally, it is interesting to compare these results with similar food discrimination experiments with the young of other species. Food-naive rat pups, like infant guinea pigs and chicks, initially sampled both nutritive and nonnutritive alternatives. However, in contrast to chicks (Hogan, 1984) and piglets (Reisbick, 1973), rat pups preferentially ingested food only 20 min after initial ingestive experience. Rat pups are relatively altricial and may have more extensive oral or ingestive experiences before independent feeding than chicks or guinea pigs. The ingestive experience of suckling mother's milk may facilitate recognition of food at weaning. However, Hall (1975) reared rats' pups with almost no suckling experience and reported no gross deficits in their initial feeding behavior. It remains unclear whether Hall's rearing procedure would affect pups' ability to recognize food in a discrimination test such as the one used in this experiment.

Experiment 2: Learned Aspects of Food Recognition

In the extinction tests of Experiment 1, pups preferentially ingested a noncaloric diet that contained a flavor previously associated with calories. Any one of several distinct mecha-
nisms could account for this finding. Pups may have learned a positive association between the flavor and the postingestive consequences of the caloric diet. Alternatively, pups may have formed an aversive association between the flavor of Diet NONCAL and its postingestive consequences. A third possibility is that the flavor preference resulted from differential exposure to the flavors rather than a specific association. In the two-choice preference procedure, pups primarily ingested the caloric diet; they therefore received greater exposure to that flavor.

Galef and Kennet (1987) suggested that such simple exposure may be a general mechanism by which young animals acquire preferences for important species-typical stimuli. Similar ideas have been entertained and demonstrated by Sluckin (1964). In earlier studies in which weanling-aged pups showed preferences for flavor cues associated with nutritive diets (Booth et al., 1974; Hayward, 1983), there were no specific controls to evaluate the effects of exposure. It remains possible that the preferences observed in Experiment 1 are based on a general tendency to interact with familiar stimuli or avoid novel ones.

Experiment 2 was designed to examine these hypotheses. Two groups received equivalent flavor exposure but the flavor was paired with calories (Diet CAL) in one group and with no calories (Diet NONCAL) in the second group. Later, both groups received a choice between two noncaloric diets: One contained the flavor to which pups had been exposed, and the other diet contained a novel flavor. If pups associate dietary flavor with the taste or the postingestive effects of the caloric diet, then they ought to show greater preference for a flavor paired with calories than a flavor paired with ingestion of a noncaloric diet. If ingestion of the noncaloric diet is aversive, then pups in the noncaloric group ought to ingest significantly more of the diet with the novel flavor during the preference test. If exposure learning or familiarization can account for the formation of early flavor preferences, then the two groups ought to display equivalent preferences for the diet they experienced during training, regardless of its caloric content.

Method

Subjects. Nineteen 20-day-old rat pups were the subjects. All pups were food-naive before testing.

Procedure. On Day 20, all pups were separated from the dam at 10 a.m. and deprived for 4 hr of the opportunity to nurse and then tested in the hanging cages described previously. During Phase 1 (training), half of the pups in each litter received a cup containing 2 g of Diet CAL and the remaining half of the litter received a cup containing 2 g of Diet NONCAL. In this experiment, both diets were sweetened with saccharin (0.1% by weight). Thus, the diets were identical except for the addition of Polycose to Diet CAL. The bread and peanut flavorings were counterbalanced equally for pups in each group. Pups were trained for 4 hr per day for 3 days or until they had ingested at least 0.75 g. Nine pups in Group NONCAL were trained on 2 consecutive days, and 1 pup for 3 consecutive days in Phase 1. Seven pups in Group CAL were trained for 2 consecutive days, and 2 pups for 1 day in Phase 1. In Phase 2, all pups received a 4-hr-extinction test that involved a simultaneous choice between two noncaloric diets. One diet contained the flavor to which pups had been exposed in Phase 1 (Diet EXP). The other diet contained a novel flavor (Diet NOV). The intake percentage of Diet EXP was calculated for each pup: (g Intake Diet EXP x 100) / (g Intake Diet EXP + g Intake Diet NOV).

Results and Discussion

Following relatively limited feeding experience, food-naive rat pups acquired a flavor preference based specifically on the starch component of the caloric diet. During Phase 1, the two groups ingested equivalent amounts of either a flavored caloric diet or a similarly flavored noncaloric diet (Group CAL, M = 0.68 g, SE = 0.06; Group NONCAL, M = 0.58 g, SE = 0.06), t(17) = 1.04, p > .2. These groups later ingested equivalent amounts of the test diets during Phase 2 preference tests (Group CAL, M = 0.90 g, SE = 0.06g; Group NONCAL, M = 1.01 g, SE = 0.09), t(17) = 1.04, p > .2.

In the preference test (Phase 2), Group CAL pups preferentially ingested the flavor paired with the caloric diet, relative to the novel flavor. Pups that ingested Diet NONCAL during training showed no preference for either the familiar or novel flavor during the Phase 2 preference test. The mean percentage intake of Diet EXP by Group CAL (M = 90.4%, SE = 5.9) was significantly greater than for Group NONCAL (M = 57.9%, SE = 8.8), t(17) = 2.85, p < .01. Group NONCAL showed no significant preference or aversion for Diet EXP during the extinction test; 57.9% of their total intake resulted from ingestion of the Diet EXP, and this value did not differ significantly from 50%, t(9) = 1.04, p > .2. These data suggest that food-naive pups learned an association between the flavor and the caloric substance (Polycose) after ingestion of only 0.7 g (0.7 kcal) of the caloric diet.

It is important to emphasize that the noncaloric diet group ingested equivalent amounts of the familiar and novel diets during the Phase 2 preference tests. This observation suggests that the pups did not acquire a conditioned aversion to the flavor of the noncaloric diet during Phase 1. Also, mere exposure to the noncaloric diet during Phase 1 did not produce a substantial preference for its flavor.

The present experiment indicates that the flavor preferences observed in the extinction tests of Experiment 1 resulted primarily from the formation of a specific association of the training flavor with some component of the starch contained in the training diet. We used mixtures designed to mask the taste of the starch (Polycose), but the possibility remains that the pups formed a positive association between the discriminative stimulus (bread or peanut) and the taste of the starch. Another possibility is that pups formed associations between flavor cues and postingestive events related to the intake of starch. These possibilities are addressed more directly in the next experiment.

It appears that the establishment of flavor preferences by ingestional experience is a more specific and narrowly tuned process than that by which social cues affect food selection in weanling rats (Galef & Kennet, 1987). Mere exposure to flavors during ingestive behavior is not sufficient to induce later flavor preference.
Experiment 3: Development of Caloric Discriminations Without Artificial Flavor Cues

The results of Experiments 1 and 2 demonstrated that food-naive rat pups rapidly recognized the starch component of the caloric diet. We intended noncaloric additives and the artificial flavor to mask the taste of the starch (Polycose). However, adult rats detect and readily show robust preferences for the taste of this starch (Selafani, 1987). Thus, the rapid preference for Diet CAL (Figure 2) could be based on the pups' detection and preference for orosensory features of Polycose in our experimental diet. Alternatively, the pups' preference for Diet CAL could be based on the formation of an association between the artificial flavor cues and rapid postigestive effects of the starch.

In Experiment 3, food-naive pups received a caloric discrimination test as in Experiment 1, but the diets did not contain the artificial flavor cues. If recognition of the caloric diet in Experiment 1 was based on the detectable and preferred taste of Polycose, then pups ought again to show a rapid preference for Diet CAL. Indeed, because Diet CAL in the present experiment contained no added flavor cue (bread or peanut), the salience of the sensory features of Polycose in the experimental diet should be enhanced. Thus, one might expect an immediate preference for Diet CAL. Alternatively, if the rapid recognition of the caloric diet in Experiment 1 was dependent on an association between the postigestive effects of starch and the artificial flavor, then pups ought to show a substantial delay before developing a preference for Diet CAL. We expected pups to eventually discriminate the diets because cues such as their location could be used as discriminative stimuli.

Method

Subjects. Twelve 20-day-old rat pups were the subjects. All were food-naive.

Procedure. All pups were tested in the aquariums and their feeding behavior was videotaped as described in Experiment 1. The procedures for the caloric discrimination test were identical to those described in Experiment 1 except that the experimental diets (Diets CAL and NONCAL) did not contain artificial flavors. Also, the pups were tested for 4 hr.

Results and Discussion

The pups that received a simultaneous choice between the Diets CAL and NONCAL without artificial flavor cues showed a substantial delay in recognition of the caloric alternative relative to Experiment 1. The overall amount of time spent feeding during the first 30 min was equivalent to that observed in Experiment 1. However, no significant preference for Diet CAL emerged during this period, *F*(1, 11) = 2.26, *p* > .15, as it did in Experiment 1 (see Figure 2). Exactly 6 of the 12 subjects spent more time feeding on Diet CAL than Diet NONCAL during the first 10-min interval. As in Experiment 1, we determined the number of subjects that sampled both diets during the first 10 min. Ten of 12 pups (83%) sampled both diets, a percentage that was slightly higher than that in Experiment 1. We also conducted *t* tests to compare the percentage of time spent feeding on caloric and on noncaloric diets during consecutive 10-min intervals. These tests revealed no significant preference for Diet CAL during any of the first four 10-min intervals (*p*s > .05). A significant preference for Diet CAL emerged during the fifth 10-min interval, *t*(11) = 2.32, *p* < .05 (Diet CAL, *M* = 6.8%, *SE* = 3.0; Diet NONCAL, *M* = 6.8%, *SE* = 0.6). Pups preferentially ingested Diet CAL thereafter, and their overall (4-hr) intake percentage of Diet CAL (*M* = 67.9%, *SE* = 7.04) was greater than 50%, *t*(11) = 2.54, *p* < .05.

The results of Experiment 3 indicated that the pups had substantial difficulty in recognizing Diet CAL relative to Experiment 1. The absence of flavor cues retarded discrimination of the diet by 30 min, and the pups initially were more likely to sample both diets. These data are not consistent with the hypothesis that the pups used sensory features of starch to recognize the caloric diet in Experiment 1. The absence of artificial flavors ought to have allowed pups to detect and show a preference for oral cues of starch at least as rapidly as in Experiment 1. However, the pups showed no evidence whatsoever of such a rapid preference; their discrimination of the diets was impaired in this experiment.

We have considered one other source of oral detection of Polycose in our experimental diet. The delayed preference for Diet CAL in Experiments 1 and 3 might have resulted from the possible taste stimulation derived from the process of salivary degradation of the starch. Pups may have detected and preferred the component sugars because they tasted sweeter than did the intact Polycose substance. In a separate experiment (Melcer, 1987), one group of 20-day-old, food-naive pups (*n* = 7) received the caloric-discrimination test after surgical desalivation. A second group (*n* = 6) received the caloric-discrimination test after a sham surgical procedure that left the salivary glands intact. All pups received the extinction test described in Experiment 1 to test for flavor preference.

Desalivated pups spent more time feeding on the caloric diet than on the noncaloric diet during the first 20 min of feeding. Thus, desalivated, food-naive pups did not exhibit a delay in the timecourse of food recognition relative to sham-operated pups or similarly tested, normal pups. Both desalivated and sham-operated pups showed equivalent preference for the caloric-associated flavor during the extinction test. There was no evidence from analyses of the timecourse of feeding, intakes of caloric and noncaloric diets, or extinction tests that desalivation produced any deficit relative to the sham group. These results indicated that the process of caloric discrimination and preference for the caloric diet was not dependent on breakdown of starch into sweeter-tasting sugars by pepsin saliva.

The results of the Experiment 3 and the desalivation study strongly suggest that Polycose is not a preferred gustatory characteristic of the caloric diet for rat pups. These results suggest that the noncaloric additives in Diet CAL masked sensory cues of Polycose and that recognition of the caloric diet in Experiment 1 was based on the formation of an association between the artificial flavor and rapid postigestive effects of the starch.
General Discussion

The present research was restricted to one aspect of the weaning process, that of food recognition. It seemed clear that the social milieu at weaning (e.g., Galef & Wigmore, 1983) could obscure the individual pup's abilities to recognize food. We therefore controlled and observed the initial feeding behavior of single, weaning-aged animals.

Individual rat pups as young as 17 days of age that had never ingested solid food recognized a caloric diet (containing starch) within 20 min of initial ingestion. In our two-choice discrimination tests, the pups sampled both the caloric and noncaloric diets during the first 10 min of feeding and subsequently ingested almost exclusively the caloric alternative (Experiment 1). Thus, rat pups are capable of rapid recognition of food at about the same time that they are observed to begin mouthing food under standard laboratory rearing conditions (Galef, 1979; Melcer & Alberts, 1985).

The data indicate that food-naive pups learned a flavor preference on the basis of the starch component of the caloric diet (Experiment 2). We were particularly interested in evaluating whether taste or oral cues served to identify the starch as a nutritive substance. Several findings contradict hypotheses regarding such oral cues and indicate that postdigestional events signaled that food had been eaten. First the rat pups did not show an immediate preference for a diet that contained Polycose. Initially, animals spent equal time sampling both caloric and noncaloric diets. Recognition of real food (evidenced by preferential ingestion) developed subsequently and very rapidly. Moreover, the preference for the caloric alternative increased between the first and second test sessions; the pups showed an immediate and robust preference for the caloric diet at the beginning of the second test session (Figure 3). Also, the pups that received a choice between Diets CAL and NONCAL showed a substantial increase in percentage intake Diet CAL across the first several test sessions (Experiment 1).

Second, the results of Experiment 3 indicated that the pups did not, in fact, detect and prefer oral cues of Polycose in the caloric diet. The absence of artificial flavor cues retarded the development of the caloric discrimination. Thus, the pups could not rapidly distinguish the experimental diets on the basis of orosensory characteristics of Polycose alone (Sclafani, 1987). Finally, degradation of the starch into sweeter-tasting sugars by pup saliva was not necessary for rapid recognition of the caloric diet.

Food Recognition as a Developmental Phenomenon

We refer to most of the pups in this research as food-naive by virtue of their restricted rearing conditions; Food was available only to the mother at a remote site, and she was unable to bring hordage to her offspring. Nevertheless, even under the rarified conditions of the present experiment, the pups were demonstrably experienced with oral and postdigestional events prior to weaning.

Prenatal rats detect and respond to olfactory and gustatory stimulation (Pedersen & Blass, 1981) and regularly swallow amniotic fluid (cf. Smotherman & Robinson, 1988), which indicates that they have oral and ingestive experiences in utero.

Soon after birth, the rat pup's behavior is organized around suckling. Milk delivery occurs in discrete episodes (Lincoln, 1983), and therefore, the infant experiences many hundreds of taste and postgestional pairings before weaning. With increasing frequency the developing rat pup orally explores its world by bringing into its mouth virtually every animate and inanimate element of its environment (Galef, 1979; Melcer & Alberts, 1985).

Though the weanling animal is not naive with respect to orogustatory stimulation and the aftereffects of ingestion (nutritive and nonnutritive), the developmental significance of most of these experiences remains unknown. Pups can acquire flavor preference from ingestion of mother's milk (Galef & Henderson, 1972; Galef & Sherry, 1973), and other experiences of suckling may contribute to the development of feeding behavior (Cramer, Pfister, & Blass, 1988). Yet pups deprived of suckling experience for virtually all of infancy exhibited apparently normal feeding behavior at weaning (Hall, 1975). However, Hall's pups received only a single nutritive diet and water during the test. Melcer (1987) found that food-naive pups ingested substantial amounts of a non-nutritive diet when it was the sole diet available. Therefore, it remains unclear whether deprivation of suckling experience would affect recognition of food in a discrimination test (e.g., Experiment 1).

Pups also sample maternal feces during weaning but this behavior does not appear to be a functional precursor to ingestion of solid food (Galef, 1979). Preweanling rat pups do ingest maternal feces before lab chow but in very small amounts. Moreover, 16-day-old rats did not prevent body-weight losses through ingestion of feces over 48 hr even if it was their sole source of nutrition. However, similarly treated 21-day-old pups did ingest sufficient feces to prevent some of their weight loss after 48 hr without an alternative food source (Galef, 1979), but by this age they were already experienced feeders.

The possible role of ingestion of maternal feces in our research can also be questioned because mothers are less likely to produce anal excreta that are attractive to pups when the offspring are not eating solid food (Moltz & Lec, 1983). In all, it seems unlikely that ingestion of maternal feces was necessary for the rapid recognition of food exhibited by our 17-day-old pups. We cannot rule out the possibility that ingestive experience with feces contributed to behavior of 20- and 23-day-old pups. However, their performance was essentially the same as 17-day-old pups.

Food Recognition as a Lifelong Challenge

Although we view food recognition as a special problem for the weanling animal, it also can be regarded as a lifelong challenge for the omnivorous and opportunistic Norway rat (Barnett, 1963; Galef, 1981; Rozin, 1976). Thus, it is appropriate to discuss how the processes described in this research may be general capabilities expressed throughout life as well as a specialization in the young animal as it makes its transition from monophagy at the nipple to omnivory as an adult.
Adult rats can form associations between flavors and the postigestive effects of nutritive solutions (Puerto, Deutsch, Molina & Roll, 1976; Tordoff & Friedman, 1986). Deutsch (1983) has hypothesized that there are nutrient receptors in the gut that can rapidly signal the arrival of food. Puerto et al. found that adult rats preferentially ingested flavored water that was conditionally paired with infusion of a nutritive solution (predigested milk) directly into the animal’s stomach. Moreover, the preference developed after only 10 min of sampling the alternative solutions. Animals that received stomach infusions of nonnutritive solutions after ingestion of similarly flavored water did not develop a flavor preference. Puerto et al. failed to find such conditioning after stomach infusions of glucose. However, it is interesting that the time course of postigestive conditioning reported by Puerto et al. is consistent with the rapid food preference exhibited by food-naive rat pups.

Concluding Remarks

The learning mechanisms present in weaning rat pups apparently contribute to their abilities to recognize solid food for the first time. Associations between oral and postigestive cues were established with remarkable rapidity after sampling a substance that contained starch. Little is known about such early responses to other nutrient elements.

It is compelling to suggest that we have discovered a learning mechanism normally used by pups near the nest as they begin to explore, sample their early environment, and discriminate food from nonfood. Subsequently, pups face more complex dietary challenges, namely, the selection of a nutritionally adequate diet from the range of food items sampled in the environment (Rozin, 1976). Indeed, Harris et al. (1933) found that rats had more difficulty in recognizing vitamin rich diets as the number of alternatives increased.

Learning to recognize, select, and ingest an adequate diet are milestones in the development of an omnivorous animal. Research with laboratory rats has already revealed relevant learning capacities in the prenatal, newborn, and weanling. Some of these capacities simply appear intact in the young animal and can serve its need on demand. Other capacities appear more precisely linked to the pup’s specific niche in life (cf. Alberts & Cramer, 1988; Galef, 1981; West, King, & Arberg, 1988).

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