

Development of Olfactory Control of Feeding-Site Selection in Rat Pups

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The results of the present experiments provide two lines of evidence consistent with the view that development of olfactory control of feeding-site selection in rats depends on experiences during ontogeny. First, normally reared pups ate at a feeding site at which either an anesthetized conspecific or conspecific excreta were present in preference to a clean site, whereas pups reared without contact with conspecifics were not influenced in their choice of feeding site by these social stimuli. Pups allowed contact with conspecifics for only the 5 days immediately prior to testing exhibited, like normally reared pups, a strong preference for feeding sites marked with social stimuli. Second, exposure of pups to an arbitrarily selected odor rendered that odor subsequently capable of influencing feeding-site selection. Comparison of the results of the present experiments with those of similar studies, in which a different measure of pup olfactory preference was used, revealed that the factors affecting development of olfactory preference vary as a function of test situation.

During weaning, young rats are profoundly influenced in their selection of both feeding sites and diets by interaction with adult conspecifics (Galef, 1977). If given the choice, rat pups will utilize a feeding site at which conspecifics or their excreta are present rather than an alternative site lacking such social markers (Galef & Clark, 1971, 1972; Galef & Heiber, 1976).

While there is considerable evidence that olfactory cues typical of conspecifics play an important role in orienting the feeding behavior of juvenile rats, as they influence pup orientation in other contexts (Alberts & Brunjes, 1978; Brunjes & Alberts, 1979; Galef & Muskus, 1979; Leon, 1978), nothing is known of the processes underlying development of olfactory control of juvenile feeding-site selection.

Galef and Kaner (1980) investigated the effects of postnatal experience with an odorant on the amount of time that pups spent in contact with an airstream carrying that odorant. They found evidence of three distinct processes contributing to the development of olfactory preference in pups. Simple exposure to an olfactory cue (Leon, Galef, & Behse, 1977), experience of an olfactory cue in association with sources of primary reinforcement, and species-characteristic sensory-affective olfactory biases were each found to influence olfactory preference as measured by a choice between clean and odor-bearing airstreams.

The index of olfactory preference used by Galef and Kaner (1980), while having a number of practical advantages, was not clearly related to any biologically meaningful use to which rat pups might put olfactory cues. While results obtained in an "arbitrary" test situation, such as that employed by Galef and Kaner, may provide useful heuristics for analyzing behavior in more functionally defined situations, it is an empirical question whether extrapolation from arbitrary situations to other more natural or more meaningful ones is justified (Seligman, 1970).

The present experiments were undertaken, first, to examine the role of experience in

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the ontogeny of olfactory control of feeding-site selection and, second, to determine whether those developmental processes found by Galef and Kaner (1980) to influence olfactory preference in an arbitrary setting also influence use of olfactory stimuli in a feeding situation. More broadly, the present experiments address the issue of the generalizability of results obtained with arbitrary measures of olfactory preference to biologically meaningful contexts.

Experiment 1

Before initiating study of processes underlying development of the response of juvenile rats to olfactory cues in feeding situations, it was necessary to devise an experimental situation in which to examine the relevant behavior. In the present experiment, food-deprived pups of two ages were presented for 2 hr with two feeding sites, each containing the same diet. One of the two sites was socially marked, either with an anesthetized adult conspecific (Study 1) or with a sample of feces from an adult conspecific (Study 2). If, as the results of previous experiments in my laboratory indicate (for a review, see Galef, 1977), the presence of social markers at a feeding site attracts pups to that site, then one would expect pups to exploit the socially marked feeding site more vigorously than the unmarked one.

Method

Subjects. Twelve litters of Long-Evans rat pups born in the McMaster colony to females acquired from the Canadian Breeding Farms (St. Constant, Quebec) served as subjects. Each litter, culled to eight pups within 48 hr of birth, was left undisturbed with its dam in a 35 × 30 × 15 cm polypropylene cage until initiation of testing. Prior to testing, all litters were allowed free access to food (powdered Purina Laboratory Chow) and water.

Apparatus. Testing the influence of social markers on feeding-site selection by individual subjects was carried out in 1 × 1 m enclosures like that schematized in Figure 1. Each test enclosure was constructed of angle-iron and hardware cloth, with a floor of galvanized sheet metal covered to a depth of 1–2 cm with pine shavings. A 30 × 30 cm nest box, with two 5 × 5 cm entrances, present in each test enclosure, provided a refuge for subjects.

Food (powdered Purina Laboratory Chow) was available in each enclosure in two food bowls located approximately .7 m apart. Water was provided through

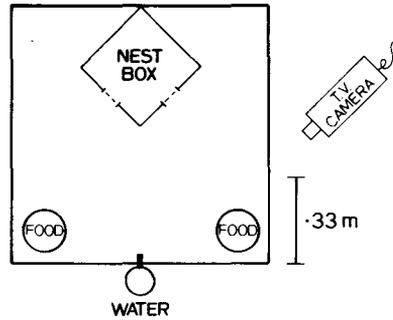


Figure 1. Overhead schematic of the test enclosure in which experiments were carried out.

a drinking spout placed midway between the food bowls. Each test enclosure was housed in a sound-attenuating room and was illuminated by a single 20-W red light bulb suspended 2 m above the enclosure. The experimenter observed the behavior of each subject on closed-circuit television.

Procedure. Four pups from each of the 12 litters serving as subjects were tested early in weaning (at 19 days of age) and four late in weaning (at 25 days of age). Nineteen hours prior to initiation of testing of a subject, it was removed from the cage containing its dam and littermates, placed in isolation, and food deprived.

At the start of testing, a pup was placed in the nest box of a test enclosure. During the next 2 hr, the experimenter recorded the number of times the pup approached to within 10 cm of each of the two food bowls (number of approaches) and the number of times the pup ate from each food bowl (number of meals). The amount of food eaten from each food bowl (amount eaten) was determined by weighing each bowl before and after each 2-hr test session.

Study 1 (six litters): For determining the effects of the presence of an adult conspecific at a feeding site on pup preference for that feeding site, prior to introduction of each subject into its test enclosure an adult (200–250 g) virgin female Long-Evans rat was anesthetized (.22 ml of Equi-Thesin/100 g of body weight, injected ip), and its head and forepaws were draped over the rim of one food bowl.

Study 2 (six litters): For determining the effects of the presence of an olfactory cue associated with conspecifics on feeding-site selection, a 100-ml-capacity screw-top jar containing a 6–8-g sample of fresh feces collected from the cages of 16–20-day postpartum Long-Evans dams (other than the subjects' own dam) was placed in one food bowl. The sample of feces rested on a bed of cotton batting which filled the bottom two thirds of the jar; the lid of the jar was covered with hardware cloth to prevent pup entry. An identical jar, containing a wad of cotton batting but no feces, was placed in the second food bowl.

Data analysis. To determine the effects of the presence of a social marker on each of the three measures of feeding-site selection (number of approaches, number of meals, and amount eaten), I first determined the percentage of that behavior directed toward the socially marked bowl by each pup. To control for litter

effects, I determined the mean of the percentage scores of the four pups from a litter tested at any one age and used that mean value as a single data point in all graphic presentations and statistical analyses.

Results and Discussion

The main results of Experiment 1 are presented in panels A and B of Figure 2 which show, respectively, data describing the behavior of pups 19 and 25 days of age at testing. Illustrated in these panels is the mean percentage of the total amount of food eaten at the two feeding sites that was eaten at the socially marked feeding site. As is clear from inspection of the panels and as statistical tests confirmed, both 19- and 25-day-old rat pups ate more at a socially marked feeding site than at an unmarked one (sign tests, all $n_s = 6$, all $x_s = 0$, all $p_s = .032$, two-tailed). In the interest of brevity, I have not presented data describing either the relative number of approaches to or the relative number of meals taken from socially marked and unmarked feeding sites. However, both of these measures correlate highly with the measure of percentage eaten at the socially marked feeding site (see results of Experiment 2 below) and support the conclusion that social markers strongly affect pup feeding-site selection.

The results of Experiment 1 indicate that the procedures described above are adequate to reveal the effects of both olfactory and more global social markers on the orientation of pup behavior in feeding situations.

Experiment 2

The results of Study 2 of Experiment 1 indicate that olfactory cues contained in the feces of adult rats are sufficient to direct feeding-site selection by weanling rat pups (Galef & Heiber, 1976). These data, of course, give no indication of the processes responsible for the development of olfactory control of pup behavior in feeding situations.

Data presented in Galef and Kaner (1980) indicate that rat pups may develop a preference for an odor as the result of either of two types of postnatal experience. Both simple exposure to an arbitrary odor and experience of that odor in association with the dam were found to be sufficient to establish a preference for it. Simple exposure to an odor rendered that odor attractive to pups at about the time of initiation of weaning; pup experience of the same odor in close association with the dam established and maintained a relatively long-lasting preference for the odor.

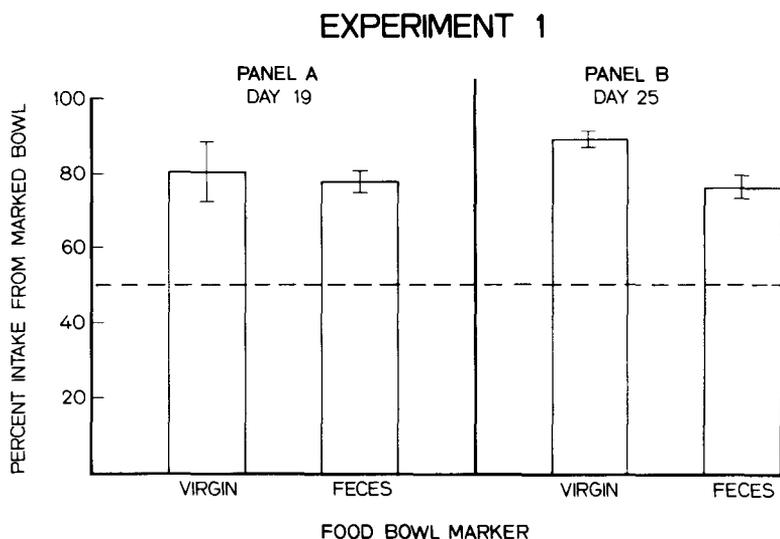


Figure 2. Mean amount eaten from the socially marked food bowl as a percentage of total amount eaten from both food bowls by 19- (panel A) and 25- (panel B) day-old pups. (Flags indicate ± 1 SE.)

The present experiment was undertaken to determine whether the same postnatal experiences, sufficient to produce a preference in an arbitrary test situation for an olfactory stimulus, are also adequate to produce olfactory control of feeding-site selection. Replication of the Galef and Kaner (1980) findings in a totally different test situation would indicate both the robustness and generality of the previous result. Failure to replicate, on the other hand, would provide evidence of a test specificity of the factors important in the development of olfactory control of behavior.

Method

Subjects. Subjects were 18 litters of Long-Evans rat pups obtained from the same source and maintained under the same conditions as subjects in Experiment 1.

Apparatus and procedures. The procedures employed in the present experiment were identical to those of Experiment 1 except with respect to (a) the olfactory experiences of pups during ontogeny and (b) the olfactory markers used in test enclosures during test periods. In the present experiment, subjects were reared under conditions providing (a) simple exposure to an arbitrarily selected odorant ("Pure Mint and Peppermint Extract"; Club House Foods Ltd., London, Ontario), (b) experience of that odorant in association with their dam, or (c) no experience of the odorant. Independent groups of pups from each condition were then tested at

19 and 25 days of age to determine the extent to which the presence of peppermint extract at a feeding site increased utilization of that site.

Rearing conditions. Simple-Exposure (S-E) group (six litters): On the day following the pups' birth, two 100-ml-capacity glass jars, lidded with hardware cloth and filled with cotton batting, were placed in the cage of each litter assigned to the S-E group. Two milliliters of peppermint extract were added to each jar daily, 1 ml at 0900 and 1 ml at 1630 hours, until completion of the experiment when subject pups were 25 days of age.

Mother-Exposure (M-E) group (six litters): Litters in the M-E group were treated identically to those in the S-E group except that the experimenter painted 2 ml of peppermint extract onto the back of each litter's dam twice daily instead of placing the peppermint extract in jars in each litter's home cage.

Control (C) group (six litters): Litters in the control group were reared by their dams without any exposure to peppermint extract, in a colony room separate from that in which litters in the two peppermint-exposure groups were maintained. Two 100-ml glass jars, lidded with hardware cloth and filled with cotton batting, were left in the cage of each control litter.

Testing conditions. Testing conditions were identical to those of Study 2 of Experiment 1 except that the cotton-batting-filled screw-top jar placed in the marked food bowl contained 1 ml of peppermint extract rather than a 6-8-g sample of feces.

Results and Discussion

The main results of Experiment 2 are presented in panels A and B of Figure 3. Shown in these panels is the mean amount of food eaten from the peppermint-marked

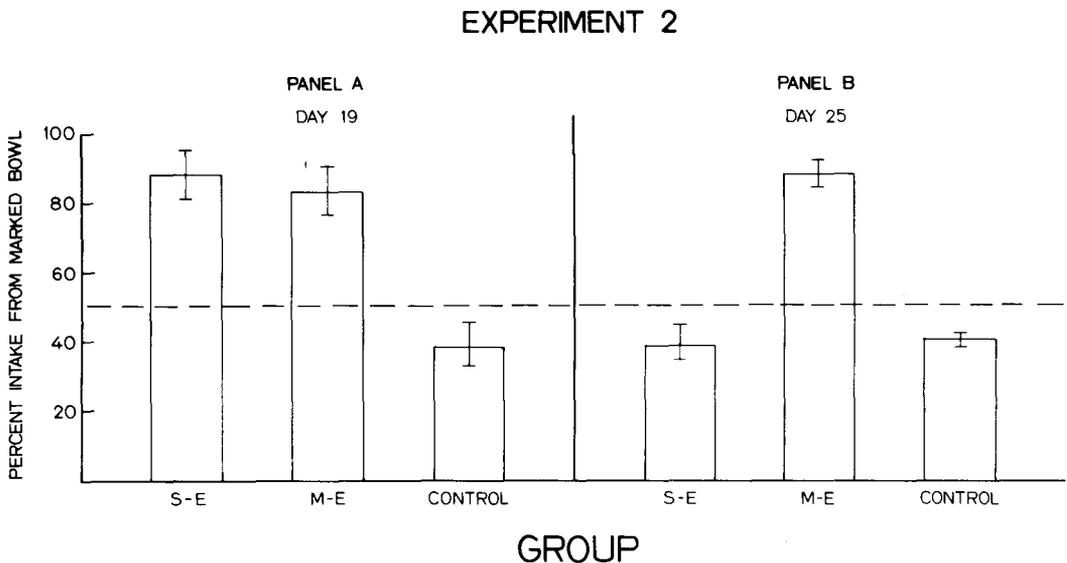


Figure 3. Mean amount eaten from the food bowl marked with peppermint extract as a percentage of the total amount eaten from both food bowls by 19- (panel A) and 25- (panel B) day-old pups. (S-E = Simple-Exposure—exposure to peppermint from day after birth onward; M-E = Mother-Exposure—peppermint painted on mother's back. Flags indicate $\pm 1 SE$.)

food bowl, as a percentage of the total amount eaten from both food bowls, by 19- (panel A) and 25- (panel B) day-old rat pups. Data describing the other two measures of pup behavior (number of approaches to and number of meals eaten from the peppermint-marked bowl) are not presented. Both of these measures correlated highly with the measure of amount eaten from the peppermint-marked food bowl (Spearman rank correlation coefficient on data from 25-day-old pups: percent approaches vs. percent eaten, $r_S = .90$; percent meals vs. percent eaten, $r_S = .88$) and provided little additional information.

There are three findings in the present data relevant to the question of the role of simple exposure and association learning in the development of olfactory control of feeding-site selection. First, control pups lacking experience of peppermint extract during maturation exhibited a weak avoidance of peppermint-marked feeding sites (Figure 3, panels A and B; sign tests, 19-day-olds, $n = 6, x = 1, p = .20$; 25-day-olds, $n = 6, x = 0, p = .032$). These data indicate that peppermint-naive pups are not attracted to a feeding site by the odor of peppermint extract.

Second, simple exposure to peppermint extract from 24 hr following birth until testing was sufficient to render peppermint extract highly attractive to pups 19 days of age (S-E group, panel A; sign test, $n = 6, x = 0, p < .032$, two-tailed) but not to pups 25 days of age (S-E group, panel B; sign test, $n = 6, x = 2, p = .688$). In fact, 25-day-old pups simply exposed to peppermint extract until testing (S-E group) behaved very much like subjects in the Control group which had never been exposed to peppermint extract.

Third, exposure of pups to the odor of peppermint extract painted on their dam (M-E group) was sufficient both to establish preference for the odor of peppermint extract (panel A) and to maintain that preference into the later stages of weaning (panel B; sign test, both $n_s = 6, x_s = 0, p_s = .032$).

Comparison of the results of the present experiment with those of Galef and Kaner (1980) reveal exact parallels. In both test situations, (a) peppermint extract was aversive to naive pups, (b) simple exposure to peppermint extract during maturation

produced a transient preference for peppermint extract, and (c) exposure to peppermint extract in association with the dam produced long-lasting preference for that odorant.

Experiment 3

Unfortunately, it cannot be inferred from the finding that exposure of young rats to an arbitrary odor is sufficient to establish a preference for that odor, that preference for rat-produced odors results from exposure to those odors during maturation. In fact, Galef and Kaner (1980) found that rat pups reared artificially, and hence without olfactory contact with conspecifics except during the first 48 hr postnatally, exhibited at 25 days of age as great a preference for the smell of conspecific feces as did their normally reared littermates. This finding is consistent with the hypothesis that sensory-affective biases, which develop relatively independently of postnatal experience, may underlie the preference that rat pups exhibit for some naturally occurring conspecific odors.

The present experiments were undertaken to determine whether pups reared with severely limited olfactory contact with conspecifics would utilize cues emanating from conspecifics in the selection of feeding sites during weaning.

Method

Subjects. Subjects were 21 Long-Evans rat pups from nine litters.

Procedure. Pups were taken from their dams at 36 to 48 hr of age, anesthetized, and implanted with chronic intragastric cannulas by the method of Hall (1975). Following implantation, each pup was individually maintained in a polystyrene cup in a 40 °C constant-temperature bath and fed an enriched milk diet by infusion through its cannula until it was 19 days of age (Hall, 1975). When pups were 19 days old, the intragastric cannulas were removed, and pups were weaned over a 2-day period (during which their voluntary intake was supplemented with forced feeding by gavage of enriched milk) to a highly palatable, nutritionally adequate diet.¹ Pups were maintained on this

¹ The diet was composed (in grams/kilogram) of 584.5 g of sucrose, 211 g of casein, 104.5 g of cellulose, 50.0 g of corn oil, 40.0 g of salt mix (USP XIV), and 10.0 g of Vitamin Fortification Mix (purchased as Fat Sufficient Diet from GIBCO, Madison, Wisconsin).

diet and water in isolation in individual cages until completion of the experiment when they reached 25 days of age.

Testing procedures were identical to those described in Method of Experiment 1, Studies 1 and 2. Pups in Study 1 were tested when 19-hr food deprived for their preference between two identical feeding sites, one of which was marked with an anesthetized virgin female; pups in Study 2 were tested for their preference between two identical feeding sites, one of which was marked with a jar containing a 6–8-g sample of excreta taken from a 16–20-day-postpartum conspecific dam.

While I would have preferred to test artificially reared pups at both 19 and 25 days of age, the difficulty my assistants and I experienced in inducing our artificially reared pups to wean to a diet of food and water caused us to delay initiation of testing until weaning had been successfully completed, and to test artificially reared pups only at 25 days of age. To ensure that any deficits in behavior we observed were not the result of gross nutritional deficits during artificial rearing, we tested only pups that weighed both 30 g or more at 19 days of age and 40 g or more at 25 days of age.

Results and Discussion

The main results of Experiment 3 are presented in the left-hand panel of Figure 4 which shows the mean amount of food eaten by artificially reared subjects from the socially marked feeding site as a percentage of the total amount eaten from both feeding sites.

Examination of the left-hand panel of Figure 4 reveals that, unlike dam-reared 25-day-old rat pups, artificially reared pups do not utilize social markers in the selection of a feeding site. This failure of artificially reared pups to exhibit a preference for a feeding site marked either with feces or with an anesthetized conspecific would not be predicted from Galef and Kaner's (1980) finding of a strong preference for a feces-odor-bearing airstream exhibited by artificially reared pups.

Unfortunately, the deficit in the social control of feeding behavior of artificially reared pups described above is not easily interpreted. Because the environment in which subjects in the present experiment matured differed in so many ways from that of dam-reared pups, the variable or variables responsible for the observed effect of artificial rearing cannot be identified on the basis of the present data. Discussion of the implications of the results of the present experiment is, therefore, deferred until after description of Experiment 4, which provides

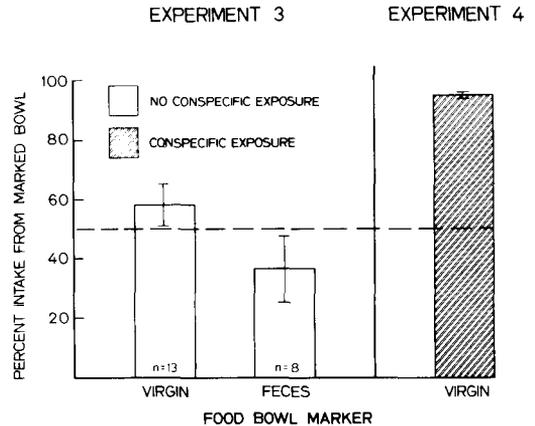


Figure 4. Mean amount eaten from the socially marked food bowl as a percentage of total amount eaten from both food bowls by artificially reared pups either exposed or not exposed to conspecifics from 20 to 24 days of age. (Flags indicate ± 1 SE.)

information sufficient to permit determination of the aspect of artificial rearing responsible for the failure of artificially reared pups to exhibit social stimulus control of feeding-site selection.

Experiment 4

The most interesting of the many possible causes of the failure of artificially reared pups to utilize social markers in feeding-site selection in Experiment 3 is the social isolation that artificially reared pups experienced during maturation. If lack of experience with stimuli emitted by conspecifics underlies the observed deficit in the behavior of artificially reared juveniles, then it might be possible to reinstate normal utilization of social cues in feeding-site selection by exposing artificially reared pups to conspecifics.

Method

Subjects. Subjects were seven Long-Evans rat pups from three litters.

Procedure. Subjects in the present experiment were treated identically to those in Experiment 3 until they were removed from artificial maintenance at 18 days of age. Following initiation of self-maintenance at 20 days of age, subjects in the present experiment were fostered in groups of four to dams whose young were of the same age as the subjects.

Subjects were removed from their foster dams, isolated, and food deprived 19 hr prior to testing at 25 days of age, with the method of Experiment 1, Study 1, used

to determine the effects of the presence of an anesthetized conspecific at a feeding site on utilization of that feeding site.

Results and Discussion

The main results of Experiment 4 are presented in the right-hand panel of Figure 4 which shows the mean amount of Purina Laboratory Chow eaten from the food bowl marked with an anesthetized virgin, as a percentage of the total amount eaten from both food bowls. Examination of Figure 4 reveals that exposure of artificially reared pups to conspecifics for 4 days immediately prior to testing was sufficient to restore normal utilization of a social marker in feeding-site selection.

The present finding strongly suggests both that absence of social interaction during maturation was responsible for the failure of artificially reared pups in Experiment 3 to utilize social markers in feeding-site selection and that the other unique aspects of artificial rearing do not preclude the development of normal social control of feeding-site selection. In comparison with artificially reared subjects tested with virgin females in Experiment 3, those in the present experiment showed a significantly greater preference for the socially marked bowl (Mann-Whitney, $U = 5$, $p < .002$, two-tailed).

General Discussion

The results of the present series of experiments provide two lines of evidence consistent with the view that the development of olfactory control of feeding-site selection in rat pups is dependent on experiences during ontogeny. First, pups deprived of contact with conspecifics during maturation fail to be influenced by social stimuli in selection of a feeding site, whereas pups given access to an adult for 4 days prior to testing are strongly influenced by social stimuli in the orientation of their feeding behavior. Second, pups exposed to an arbitrary olfactory stimulus during ontogeny are subsequently influenced by the presence of that stimulus in the selection of a location at which to feed.

The results of the present experiments also indicate that at different times during

ontogeny different types of olfactory experience are sufficient to render the experienced stimulus effective in orienting pup feeding-site selection. Simple exposure to an odor enables that olfactory stimulus subsequently to influence pup feeding behavior at 19 but not at 25 days of age. Exposure to the same stimulus in association with the dam has effects on orientation of the feeding behavior of both 19- and 25-day-old pups. The reasons why simple exposure to an olfactory stimulus has different effects on pups of different ages are unknown. It is possible that younger animals are more severely distressed by isolation during testing than their more mature siblings (Randall & Campbell, 1976) and are, therefore, more responsive to familiar olfactory stimuli in their environment.

Comparison of the results of Experiments 3 and 4 above, in which the response of artificially reared pups to natural odors was examined, with the data gathered by Galef and Kaner (1980) on the preference for natural odors of artificially reared pups reveals apparent inconsistencies. In the present experiments, I found no evidence of preference for a socially marked feeding site in pups reared in isolation (Experiment 3), whereas Galef and Kaner found that isolation-reared pups exhibited a normal preference for an airstream bearing a conspecific-produced odor.

The finding that species-typical olfactory stimuli that are attractive in one test situation fail to influence orientation of behavior in a second clearly indicates that considerable caution must be exercised in extrapolating the results of one measure of olfactory preference to another. This finding also suggests that conceptualization of given odors as "attractive" or "preferred" is inadequate to account for their effects on behavior. Variability across test situations in pup utilization of olfactory stimuli in behavioral orientation suggests that under some test conditions odors may function primarily as signals for the presence of primary reinforcers with which they have been previously associated but that in other situations olfactory control of behavior may result from acquired or inherent reinforcing properties of the olfactory stimuli themselves. In the former case, pup utilization

of olfactory cues in behavioral orientation depends upon congruence between a subject's deprivation state in a test situation and the signal value of the olfactory stimulus present there. In the latter, one might expect the olfactory stimulus to control orientation of behavior independently of subjects' deprivation state in the situation.

Determination of the conditions under which signal and reinforcing functions of olfactory stimuli predominate in orienting behavior remains a major challenge. The results of the present experiments, taken together with those of Galef and Kaner (1980), suggest that in feeding situations the signal value of olfactory stimuli is more important in controlling behavior than are their reinforcing properties but that in arbitrary test situations the converse may be true.

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