

Establishment and Maintenance of Preference for Natural and Artificial Olfactory Stimuli in Juvenile Rats

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The role of sensory-affective bias and of two types of experience (simple exposure to an odor and exposure to an odor in association with conspecifics) in the establishment and maintenance of preference of rat pups for odorants was investigated. (a) Simple exposure of pups to a mildly aversive odorant (peppermint extract) from birth to 21 days of age was sufficient to establish a preference for that odorant in 21-day-olds as strong as their normal preference for maternal excreta. (b) Simple exposure of pups to peppermint extract for 33 days following birth was not sufficient to maintain preference for peppermint extract to 33 days of age. (c) Exposure of pups to peppermint extract painted on the dam for 33 days following birth was sufficient to maintain pup preference for peppermint extract to 33 days of age. (d) Pups reared artificially, with very limited contact with conspecifics, exhibited robust preferences for conspecific odors. Taken together, the data suggest that a variety of mechanisms play complementary roles in the development and maintenance of preference for olfactory stimuli.

Both adult and juvenile rats emit odors attractive to normally reared weanlings of their species (Alberts & Brunjes, 1978; Galef & Muskus, 1979; Leon, 1978). These olfactory stimuli play a central role in directing young rats to conspecifics serving as sources of warmth, milk, and other requisites of pup survival and growth (Alberts, 1976; Alberts & Brunjes, 1978; Galef & Heiber, 1976; Leon, 1978). While the importance of odors emitted by conspecifics in eliciting and directing the behavior of juvenile rats is well established, relatively little is known of the mechanisms underlying development and maintenance of appetitive responses to conspecific odors.

In the studies described below we consider three mechanisms, each of which could contribute to the observed tendency of

weanling rats to respond positively throughout the juvenile period to odors emitted by members of their species. First, rat pups might be born with sensory-affective systems (Cabanac, 1979; Young, 1959) that bias them toward displaying a preference for the odors of other rats. Alternatively, either of two different types of experience, simple exposure to conspecific odors (Hill, 1978; Zajonc, 1968) or the learning of associations between conspecific odors and primary reinforcement provided by other rats (Cairns, 1966), might underlie the preference of young rats for odors of their own kind. The three mechanisms mentioned above are clearly not mutually exclusive, and all three might well be expected to interact in the ontogeny and maintenance of appetitive responses to the smells of other rats.

The results of a recent series of studies by Leon, Galef, and Behse (1977) provide evidence of robust effects of simple exposure to odors early in life on subsequent preference for those odors. Leon et al. found, for example, that rat pups isolated from their dams and siblings for 3 hr/day, and exposed during these periods of isolation to a mildly aversive odor (peppermint extract), subsequently exhibited a strong tendency to approach sources of that odor during a single brief preference test. In fact, these pups,

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simply exposed to peppermint extract for 3 hr/day, were as likely to approach peppermint extract as were normally reared pups to approach odors of their dam. These data, taken together with other findings in the report of Leon et al., are consistent with the hypothesis that simple exposure to conspecific odors during maturation may be sufficient to cause pups to exhibit appetitive responses to those odors at weaning.

It seemed to us possible that more extensive and potentially more sensitive testing procedures than those employed by Leon et al. (1977) might reveal evidence of effects of associative learning and of inherent sensory-affective biases in the ontogeny and maintenance of attraction to various olfactory cues in young rats.

Experiment 1 examines the effects of simple exposure to an odorant and of exposure to the same odorant in association with conspecifics on the response of 19-33-day-old rat pups to that odorant. Experiment 2 examines the olfactory preferences of juvenile rats artificially reared in isolation from conspecifics for evidence of an appetitive response to conspecific odors in individual animals having very limited experience of those odors during maturation.

General Method

Subjects

Subjects were litters of Long-Evans rat pups born in the McMaster colony to dams purchased from the Canadian Breeding Farms, St. Constant, Quebec. Each litter was culled to eight pups shortly after birth, and each was maintained with its dam on ad lib Purina Laboratory Chow and water in a 35 x 30 x 15 cm polypropylene cage until completion of experiments on Day 33 postnatally. Subjects were tail painted for individual recognition at the start of testing at 19 days of age.

Apparatus

Individual subjects were tested for their response to odorants in one of two identical (11 x 21 x 17 cm) transparent Plexiglas test enclosures, each housed in a light- and sound-attenuating freezer chest. Two 2.5-cm diam. circular apertures (6 cm center to center) were located in one 11 x 17 cm wall of each chamber.

A light source mounted between each pair of apertures activated a photocell at the distal edge of each. Each aperture opened onto a separate stimulus chamber through which flowed an airstream (see Figure 1). Insertion by the subject of its nose into either stimulus

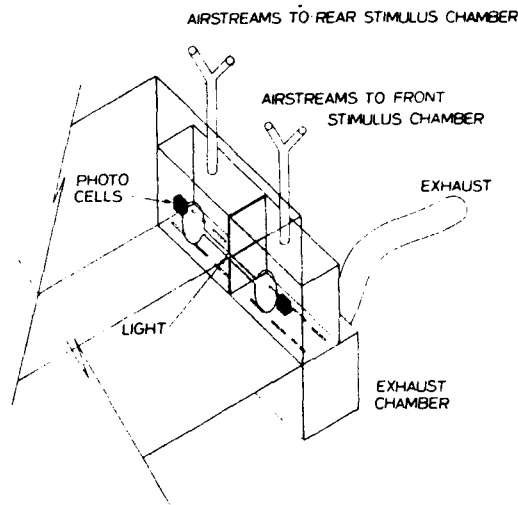


Figure 1. Test chamber of the olfactory preference apparatus.

chamber broke the beam of light activating the photocell mounted on the edge of the aperture leading to it. Deactivation of a photocell in turn activated two counters; the first counter recorded a single event each time its associated photocell was deactivated, and the second recorded a single event for each second its photocell was deactivated (see Figure 2).

Deactivation of a photocell also caused an associated solenoid valve (Skinner Precision Industries, New

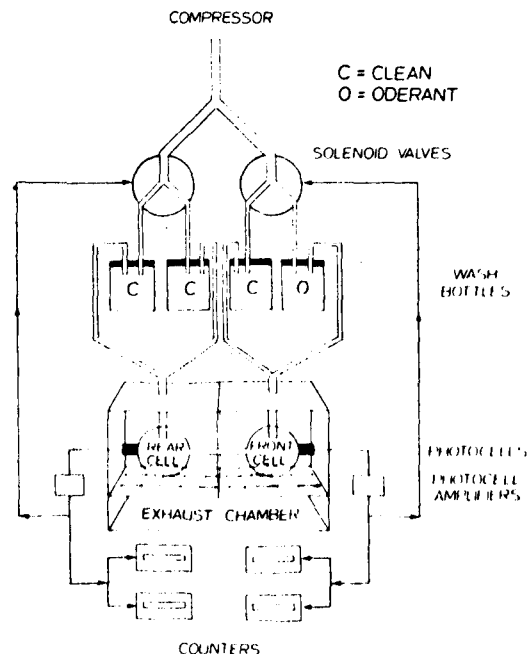


Figure 2. Schematic diagram of the olfactory preference apparatus.

Briton, Connecticut, Model V52DB2100) to close and remain closed until its photocell was reactivated. Valve closure redirected the airstream entering a stimulus chamber from one channel to another. Throughout most of each test session, a filtered airstream entered each stimulus chamber after passing through a clean wash bottle. When the subject placed its nose into a stimulus chamber, the filtered airstream was redirected either through a second clean wash bottle (rear stimulus chamber) or through a wash bottle containing an odorant (front stimulus chamber). After passing through a stimulus chamber, each airstream exited through an exhaust chamber to the building exhaust system.

Procedure

A sample of odorant, either 2 ml of Club House Pure Mint and Peppermint Extract (Club House Foods Ltd., London, Ontario) or 6–8 g of fresh anal excreta taken from a postparturient rat¹, was placed in the wash bottle of the airstream entering the front stimulus chamber of a test enclosure. After the wash bottle was placed in position, a pup was introduced into the test enclosure and left there undisturbed for 1 hr. Each subject was tested under identical conditions once every 24 hr for either 3 or 15 consecutive days.

Upon completion of a test session the experimenter returned the subject to its litter, recorded both the number of times the pup had introduced its nose into each stimulus chamber and the number of seconds it had spent with its nose in each stimulus chamber, and placed fresh samples of odorants in the appropriate wash bottles.

Data Treatment

Pilot work revealed that occasional equipment failure, experimenter error, or lack of cooperation by subjects would make it impossible to acquire useful data from each subject in each 1-hr test session. To exclude misleading data from consideration, we first calculated for each animal, on each test day, an odor-preference ratio. The odor-preference ratio was defined as the number of seconds spent by a subject with its nose in the odor-containing stimulus chamber divided by the total number of seconds spent by a subject with its nose in either stimulus chamber. We then determined the median odor-preference ratio for each 3-day block of trials and used the data of the median day to represent that 3-day block. By using nonparametric measures of preference, the actual observed values of two thirds of the data collected were excluded from direct consideration, but, as a result, we were able to reject any spurious data values in a nonarbitrary fashion.

Experiment 1

The present experiment was undertaken to determine the preference of 19–33-day-old rat pups for each of two odorants (maternal excreta and peppermint extract) relative to

clean air. Comparison of the preferences of pups reared (a) without exposure to peppermint extract, (b) simply exposed to peppermint extract, (c) exposed to peppermint extract painted on their dam, and (d) exposed to peppermint extract painted on their dam and siblings allowed assessment of the contribution of both simple exposure to an arbitrary odorant and exposure to that odorant in association with sources of primary reinforcement to the establishment and maintenance of preference for that odorant.

Method

Subjects. Subjects were 40 litters of Long-Evans rat pups assigned to one of four rearing conditions on the day of birth.

Rearing conditions. At birth 10 litters were assigned to a control group and 10 to each of three peppermint-exposure groups. The peppermint-exposure groups differed from one another with respect to the locus of the peppermint extract to which pups in each group were exposed.

Simple-Exposure group (S-E group): On the day following 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 9:00 a.m. and 1 ml at 4:30 p.m., until completion of the experiment 32 days later.

Mother-Exposure group (M-E group): 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 dorsal surface of the dam of each litter twice daily instead of placing the peppermint extract in bottles in each litter's home cage.

Mother-Pup-Exposure group (M-P-E group): Litters in the M-P-E group were treated identically to those in the M-E group until Day 14 postnatally. On Day 14 and thereafter, 1 ml of peppermint extract was painted on the dorsal surface of the dam and 1 ml on the dorsal surface of the pups in each litter twice daily.

Control group: Pups in the Control group were reared by their dams without any exposure to peppermint extract in a colony room separate from the one in which litters in the three peppermint-exposure groups were maintained.

Testing conditions. Table 1 presents the testing

¹ Whenever possible the sample of excreta presented to a subject was taken from a dam (other than the subject's own dam) that had given birth within 24 hr of that subject's own dam. However, occasional failures of contribution by dams necessitated taking approximately 10% of excreta samples from females that had given birth from 24 to 72 hr before or after a subject's own dam.

Table 1
Test Conditions of Simple-Exposure, Mother-Exposure, Mother-Pup-Exposure, and Control Groups in Experiment 1

Condition no.	Age at testing (in days)	Test condition	
		Stimulus chambers	
		Front	Rear
1	19-21	P	C
2	19-21	E	C
3	25-27	P	C
4	25-27	E	C
5	31-33	P	C
6	31-33	E	C
7	19-33	P	C
8	19-33	E	C

Note. One of the eight pups from each of 10 litters in a given exposure condition was tested under each testing condition except for litters in the Mother-Pup-Exposure Group from which a pup was examined only in Conditions 5, 6, 7, and 8. P = peppermint extract, C = clean airstream, E = dam's excreta.

schedule of individual pups from each litter in Experiment 1. One pup from each of the 30 litters in S-E, M-E, and Control groups was randomly assigned to each of the eight test conditions described in Table 1. Problems of scheduling animals into the apparatus precluded testing subjects from litters in the M-P-E group in all test conditions. The behavior of one pup from each of the 10 litters in the M-P-E group was examined only in Conditions 5, 6, 7, and 8.

Assignment of only a single pup from a litter to each test condition and random assignment of litters to rearing conditions allowed both control for and identification of (a) the effects of repeated testing of single subjects, (b) age effects, and (c) litter effects, each of which was found to significantly influence behavior.²

Results

The main results of Experiment 1 are presented in Figure 3, which shows the mean odor-preference ratios of groups of subjects in peppermint-exposed and control groups in each of the eight testing conditions described in Table 1. Panels A, B, and C of Figure 3 present the behavior of groups of subjects tested for olfactory preference at, respectively, 19-21, 25-27, and 31-33 days of age. Panel D of Figure 3 presents the behavior of 31-33 day old pups from each of the four rearing conditions on their 13th-15th day of testing for olfactory preference.

There are five findings in the data pre-

sented in Figure 3 relevant to the question of the role of simple exposure and association learning in the formation of preference for olfactory stimuli. First, across all rearing conditions and test ages, pups reliably preferred the odor of maternal anal excreta to a clean airstream. These data indicate that conditions of normal maturation are sufficient for the establishment and maintenance of appetitive responses to maternal odors in pups from 19-33 days of age. Data describing response to maternal excreta by subjects in Groups S-E, M-E, and M-P-E further indicate that extensive exposure to other odors during maturation is not sufficient to interfere with development and maintenance of response to the odor of maternal excreta.

Second, at each test age, pups reared without experience of peppermint extract (Control groups) found a clean airstream preferable to the odor of peppermint extract. These data indicate that in the absence of previous exposure to peppermint extract, rat pups find its smell aversive.

Third, simple exposure to peppermint extract from 24 hr following birth until testing was sufficient to render peppermint extract as attractive as maternal excreta to pups 19-21 days of age (S-E group, panel A) but not to pups 25-27 or 31-33 days of age (S-E group, panels B and C). These data suggest that simple exposure is sufficient to establish a preference for an otherwise aversive odor but is not sufficient to maintain that preference through adolescence.

Fourth, exposure of pups to the odor of peppermint extract associated either with their dam (M-E group) or with their dam and siblings (M-P-E group) was sufficient both to establish preference for the odor of peppermint extract (panel A) and to maintain that preference through adolescence (panels B and C).

Finally, both 6 and 12 days of testing of

² Although litter effects are not directly relevant to the issues under investigation, our data revealed that they are present and must be controlled for in studies of this type. The combined results (Lehmann, 1975, p. 281) of separate Friedman tests (Siegel, 1956) for litter effects on odor preference ratios in each rearing condition were significant, $\chi^2(34) = 52.8, p < .025$.

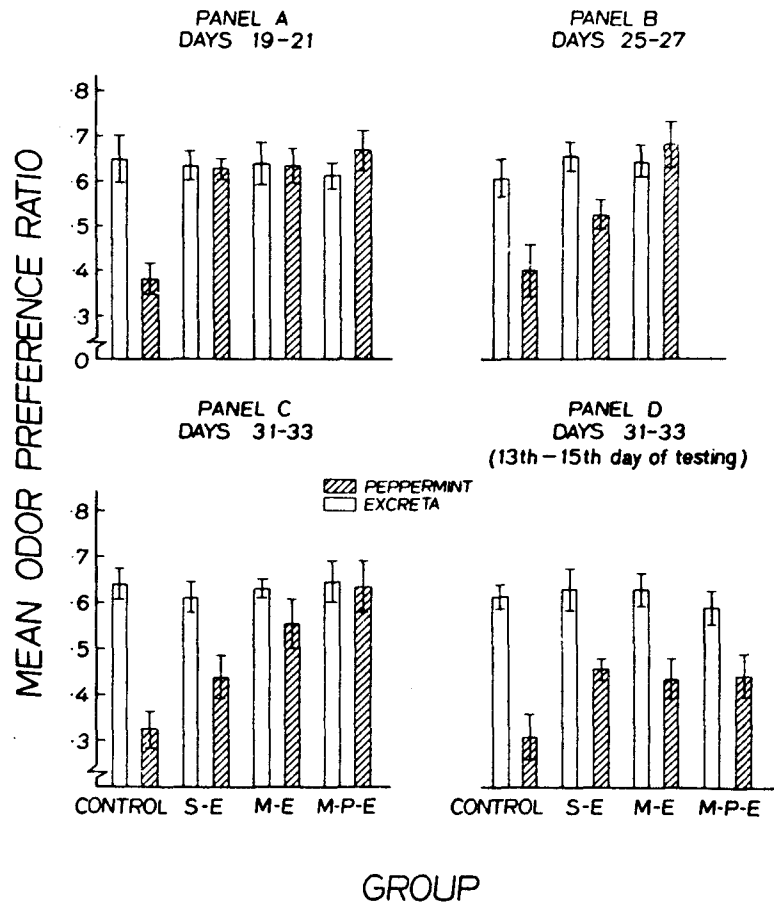


Figure 3. Mean odor-preference ratios for peppermint extract and maternal anal excreta in control and peppermint-exposed groups 19-21 (panel A), 25-27 (panel B), and 31-33 (panel C) days of age; panel D: Odor-preference ratios of 31-33-day-old pups on their 13th-15th day of testing. (Flags indicate ± 1 SE. Note that the data describing the behavior of pups in the M-P-E group in panel A are taken from the first 3 days of testing of M-P-E group pups tested for 15 consecutive days; they are presented only for purposes of comparison. S-E = simple exposure; M-E = mother exposure; M-P-E = mother-pup exposure.)

peppermint-exposed pups (Groups S-E, M-E, and M-P-E) for preference for peppermint extract produced a marked reduction of preference for peppermint extract. Comparison of the odor-preference ratios for peppermint of Groups M-E and M-P-E in panels C and D of Figure 3 reveals the robust effects on preference for peppermint odor of 12 days of testing for peppermint preference. (In 37 of the 48 possible comparisons between pairs of littermates tested for the first time on Days 25-27 or 31-33 and those tested for the 7th to 9th time on Days 25-27 or the 13th to 15th time on Days 31-33, pups

tested for the first time showed a greater peppermint-odor preference than their previously tested littermates (sign test, $p < .001$). The extinction of preference for peppermint extract was much stronger in Groups M-E and M-P-E (24 of 28 comparisons) than in Group S-E (13 of 20 comparisons) where it was largely masked by an age effect on preference for peppermint [see third point above].)

In contrast, testing of pups for either 6 or 12 days for preference for the odor of maternal excreta did not produce a reduction in preference for it. Comparison of the odor-

preference ratios for excreta of Groups S-E, M-E, and M-P-E in panels C and D reveals that 12 days of testing for preference for excreta did not affect preference for excreta. (In 27 of 48 possible comparisons between pairs of littermates tested for the first time on Days 25-27 or 31-33 and those tested for the 7th to 9th time on Days 25-27 or the 13th to 15th time on Days 31-33, pups tested for the first time showed a greater excreta-odor preference than their previously tested littermates.)

The finding that previous testing results in an extinction of preference for peppermint extract but not for anal excreta suggests that the processes maintaining pup response to odors produced by conspecifics may be different from those maintaining pup response to other odorants.

Discussion

Taken together, the results of Experiment 1 not only confirm the finding of Leon et al. (1977) that simple exposure to an arbitrary odorant is sufficient to establish preference for that odorant in 21-day-old rat pups but also strongly suggest that experiences other than simple exposure (i.e., explicit association of the odorant with conspecifics) are required to maintain appetitive response to an arbitrary odorant through adolescence. Further, the finding that preference for an arbitrary odorant wanes with repeated testing, whereas preference for the odor of excreta does not, suggests that the processes maintaining preference for arbitrarily selected and conspecific-produced odors may differ.

Unfortunately, the data from the present experiment provide little evidence bearing on the question of whether the mechanisms underlying preference development are similar in the case of arbitrary and conspecific-produced odors. In the absence of evidence to the contrary, it is of course parsimonious to assume that the mechanisms responsible for the development of preference for arbitrarily selected and species-typical stimuli are similar. However, 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. The preference of rat pups for biologically important odors, such as those produced by conspecifics, might well be less dependent on experience than is the development of preference for odors of less biological relevance.

Experiment 2

The present experiment provides an initial test of the hypothesis that the role of exposure in the establishment of preference for an odorant is of less importance in the case of odors produced by conspecifics than other odors. If exposure to conspecific odors is necessary to establish preference for them, then one would expect rat pups reared artificially and without contact with conspecifics to exhibit indifference or aversion to conspecific odors. If, on the other hand, preference for conspecific odors develops independent of experience of those odors during maturation, then artificial rearing should have little effect on pup response to conspecific odors.

Method

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

Procedure. Pups were taken from their dams 36 to 48 hr after birth, anesthetized by ether inhalation, and implanted with chronic stomach cannulas by the methods of Hall (1975). Each pup was then maintained in a polystyrene cup kept in a 40 °C constant-temperature bath and was fed an enriched milk diet by infusion through its stomach cannula until it was 19 days old (Hall, 1975), at which time the stomach cannula was removed and the pup was weaned to a highly palatable diet, the main constituents of which were sucrose and casein³. Pups were maintained on this diet and water in individual cages until completion of the experiment when they reached 27 days of age.

Although we would have preferred to initiate testing of artificially reared pups at 19 days of age, the considerable difficulty we experienced in inducing our pups to maintain normal growth following weaning to solid

³The diet was compounded (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 Teklad Mills, Madison, Wisconsin). It is the same diet that Leon (1978) reported inhibited cecotrophe production in lactating Wistar rats.

food and water caused us to delay initiation of testing until weaning had been successfully completed at 25 days of age. Because many of our artificially reared pups grew slowly and because we wished to minimize differences between artificially and normally reared groups on dimensions other than their olfactory experience, we tested for odor preference only pups that both weighed 30 g or more at 19 days of age and weighed 40 g or more at 25 days of age.

Testing procedures were identical to those described in General Method. One pup from each artificially reared litter ($n = 9$) was tested for its response to the odor of peppermint extract, and one or two other pups ($n = 15$) from each litter were tested for their response to the odor of anal excreta of a dam of the same postpartum age as their natural mothers.

Results and Discussion

The main results of Experiment 2 are presented in Figure 4 (panel B) which indicates the odor-preference ratios of artificially reared pups in response to the odors of peppermint extract and maternal anal excreta. For purposes of comparison, data describing odor-preference ratios in response to peppermint extract and maternal excreta of 25–27-day-old pups in the Control group of Experiment 1 are presented in panel A of Figure 4. As is clear from examination of Figure 4, artificial rearing had no effect on the preference of rat pups for the odors of either peppermint extract or maternal anal excreta.

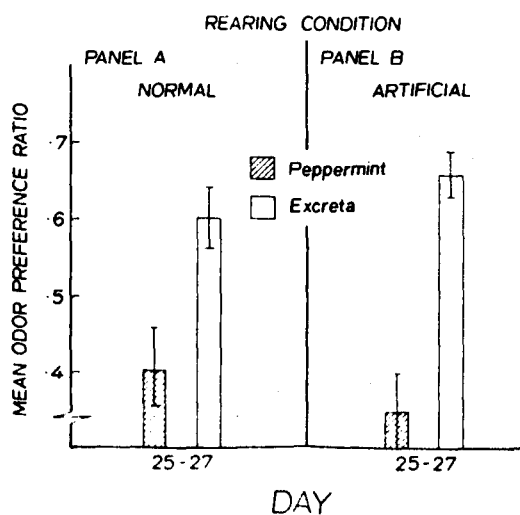


Figure 4. Mean odor-preference ratios of artificially and normally reared pups 25–27 days of age for peppermint extract and anal excreta. (Flags indicate ± 1 SE.)

The finding that rat pups reared with limited exposure to conspecifics exhibit strong preference for a conspecific-produced odor is consistent with the hypothesis that the establishment and maintenance of preference for conspecific odors may be relatively independent of postnatal experience. However, two methodological problems prevent the present experiment from providing unequivocal evidence of development and maintenance of pup preference for rat odors in the absence of experience of those odors during ontogeny.

First, although artificially reared pups were isolated from contact with conspecifics throughout most of their early development, they were constantly exposed to the odors they themselves produced. It is possible that such auto-exposure to rat odors during ontogeny is necessary for the development of normal preference for the odors of conspecifics. It is, however, important to note that artificially reared pups were maintained consecutively on milk and a sugar-casein-based diet and that excreta used as stimuli in the test situation came from adults maintained on Purina chow. Taken together with evidence in the literature suggesting that the diet on which a rat is maintained strongly affects the odor of its excreta (Leon, 1975), the different maintenance diets of artificially reared pups and of adults serving as sources of excreta in the test situation make it difficult to argue that pups in the present experiment exposed themselves to excreta similar in smell to those with which they were tested.

Second, during the first 48 hr of postnatal life, pups in our experiment were left with their dam and thus had some experience of the odor of excreta from females eating Purina chow. We are currently examining the possibility that brief exposures to odors early in life are sufficient to establish long-term preference for those odors by exposing pups to peppermint extract for the first 48 hr postnatally and testing them for preference for peppermint extract at weaning. Our preliminary data reveal no effects of exposure to peppermint extract during the first 48 hr postnatally on peppermint preference at weaning.

While technical problems may prohibit

the rearing of altricial mammals in total absence of exposure to species-characteristic odors, and thus prevent definitive testing of the hypothesis that rat pups exhibit a preference for conspecific odors without previous exposure to those odors, the present data do require that the possibility of experience-independent preference for conspecific odors be actively considered in future discussions of the mechanisms underlying the development and maintenance of response to species-typical olfactory cues.

General Discussion

The results of Experiment 1 indicate that establishment and maintenance of preference for at least one arbitrarily selected odorant are the result of two separable processes: (a) simple exposure and (b) associative learning. The results of Experiments 1 and 2 also provide two lines of evidence consistent with the view that preference for conspecific odors may result from inherent sensory-affective bias rather than postnatal experience. The finding of normal preference for conspecific odors in pups reared with limited contact with conspecifics and the absence of extinction of preference for conspecific odors are more easily interpreted as signs of experience-independent than of experience-dependent preference development. These data suggest that maternal excreta may be one of a class of rat-produced olfactory stimuli, including pup saliva, maternal saliva, and amniotic fluid (Teicher & Blass, 1977), to which rat pups respond appetitively in the absence of previous experience with those stimuli.

The data of the present experiments are consistent with the view that sensory-affective bias, simple exposure effects, and associative learning may all play significant roles in the response of rat pups to the variety of olfactory cues in their environment. The data also suggest that the experimental strategy of studying the development and maintenance of response to arbitrarily selected stimuli to uncover the mechanisms of development of response to species-typical stimuli may be inadequate. The present

data indicate that response to some species-typical stimuli may be less dependent on postnatal experience than is response to less biologically meaningful stimuli in the same modality.

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