Journal of Comparative and Physiological Psychology
1979, Vol. 93, No. 4. 708–716

Olfactory Mediation of Mother–Young Contact in Long-Evans Rats

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Twenty-one-day-old Long-Evans rat pups, unlike 16-day-old pups of the Wistar strain, (a) find the odors emitted by adult virgin females of their strain attractive, (b) find the odor of the anal excreta of adult virgin females of their strain attractive, (c) find the anal excreta of virgin female rats as attractive as those of lactating rats of their strain, and (d) are less attracted by the odor of the anal excreta of a lactating rat than by the odor of the lactating rat itself. The results indicate that descriptions in the literature of olfactory communication between Wistar rat dams and their young cannot be generalized to rats of other strains or ages.

Leon and his co-workers recently completed an extensive series of studies the results of which are consistent with the view that the olfactory cues synthesized and emitted by lactating Wistar rats (from 14 to 27 days postpartum) are far more attractive to their 14–27-day-old young than are the olfactory cues synthesized and emitted by virgin female Wistar rats (Leon, 1978). Leon's data suggest that this difference in the attractiveness of Wistar females in various reproductive states is due primarily to differences in the quantity of cecotrophe in their anal excreta. In essence, Leon proposed that the odor of virgin Wistar rats is not attractive to Wistar pups because virgin rats tend to ingest the cecotrophe that they synthesize and, in consequence, produce an anal excreta unattractive to Wistar young. In contrast, 14–27-day postpartum Wistar females fail to ingest the large amounts of cecotrophe that they synthesize, and in consequence, both the odor of the females themselves and of their anal excreta are highly attractive to Wistar young.

The results of a recent study in our laboratory (Galef & Heiber, 1976) indicate that female rats of the Long-Evans strain may be quite different from those of the Wistar strain in the conditions under which they synthesize and excrete olfactory cues attractive to their 16–23-day-old young. Galef and Heiber found evidence that the excreta of virgin Long-Evans females were attractive to young Long-Evans rats and found no evidence of a difference in the attractiveness of the anal excreta of virgin and lactating females of that strain. Moreover, Galef and Heiber's data suggested that some of the attractive olfactory cues that are produced by adult Long-Evans rat are not contained in their anal excreta.

In the experiments presented below we address five related issues concerning the olfactory cues emitted by virgin and lactating Long-Evans rats and the attractiveness of those cues to Long-Evans pups: (a) Are the olfactory cues synthesized and emitted by virgin Long-Evans rats attractive to pups of their strain? (b) Are the olfactory cues contained in the anal excreta of virgin Long-Evans rats attractive to Long-Evans pups? (c) Are the olfactory cues emitted by lactating Long-Evans rats more attractive

This research was supported by National Research Council of Canada Grant A0307 and a McMaster University Research Board Grant to the first author. We thank Robert Shepherd and Sue Johns for their assistance in the collection and analysis of data, and Mertice Clark and Barbara Woodside for their useful discussion of earlier drafts of this manuscript. We especially thank Michael Leon who contributed generously to the interpretation and presentation of these data. The present manuscript owes much to his patient clarification and discussion of issues. Some of the experiments reported here represent a portion of a thesis submitted by the second author to the Faculty of Arts and Sciences of McMaster University in partial fulfilment of the requirements for the master's degree.

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than those emitted by virgin Long-Evans rats? (d) Is there any difference in the attractiveness of the anal excreta of virgin and lactating Long-Evans rats? (e) Are there any olfactory cues emitted by lactating Long-Evans rats, not present in their anal excreta, which make lactating Long-Evans rats attractive to pups of their strain?

General Method

Subjects

Subjects were Long-Evans (L-E) hooded rats descended from stock obtained from the Canadian Breeding Farms, St. Constant, Quebec. All animals were maintained ad lib on Purina Laboratory Chow and water in a colony room on a 14:10 hr light/dark cycle. Breeding stock was housed individually and virgins in pairs in 36 × 30 × 16 cm polycarbonate cages. Litters were culled to eight pups within 2 days of birth and left with their dams until testing at 21 days of age. It was necessary to use 21-day-old subjects in our apparatus because many younger subjects were reluctant to move freely in the alley.

Apparatus

We tested individual pups for their tendency to remain in contact with olfactory stimuli, using a forced-choice paradigm (forced approach–avoidance paradigm; Doty, 1975) in order to avoid some of the statistical and interpretive problems posed by animals failing to leave the start box in approach paradigms (Doty, 1975).

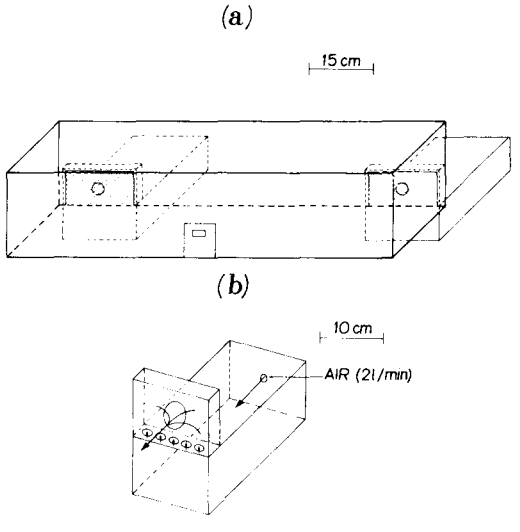

Figure 1. Schematic drawing of (a) the assembled apparatus and (b) a stimulus container.

Individual test subjects were introduced into a 92 × 17 × 20 cm straight alley (illustrated in Figure 1a), through a 12 × 8 cm guillotine door centered in the alley's front wall. Olfactory stimuli were introduced into the alley through two hardware-cloth-covered windows (15 × 9 cm) located 2.5 cm from each end of the alley's back wall. The floor of the alley was covered with paper toweling, and its top with a transparent Plexiglas cover on which was marked the alley's midline. The experimenter observed the behavior of subjects in the alley by closed-circuit television from an adjacent room.

Two 2-l/min airstreams from a common source carried olfactory stimuli into the alley. Each airstream passed through an opaque Plexiglas stimulus container, designed to prevent physical or visual contact between sources of olfactory stimuli and test subjects (see Figure 1b). Each airstream entered the rear of the lower part of a stimulus container, passed over the stimulus (if any), then passed from the lower to the upper portion of the container through five small holes (.3 cm), and finally exited the upper portion of the container through a 3.2-cm hole in its front wall. The 3.2-cm hole in the front wall of each stimulus container was centered in one of the windows of the alley.

Procedure

Before the beginning of testing of each olfactory stimulus, both stimulus containers were washed with detergent and water, and dried. The stimuli to be tested were then placed in the lower portion of the stimulus containers, and both containers were positioned facing the windows in the alley. Prior to the testing of each subject fresh paper toweling was placed on the alley floor.

A particular olfactory stimulus (e.g., Virgin Female 8) was presented to several individual littermates at the same end of the alley. Equal numbers of stimuli of a given class (e.g., virgin females) were presented to an equal number of subjects at each end of the alley.

The experimenter recorded the amount of time spent by each subject in each half of the alley during three successive 5-min intervals.

Data Analysis

The difficulties in conducting experimental studies so as to be able to determine the relative attractiveness of two classes of natural stimuli are not widely understood. The frequently employed statistical procedure of treating each of the subjects tested with a single pair of targets as providing an independent measurement of the relative attractiveness of targets belonging to the two classes of stimuli fails to take into account possible variability in attractiveness among targets within a class. Clearly, if in a simple choice situation each of 20 rat pups prefer a single lactating rat to a single virgin rat, it is not the case that the pups have demonstrated a significant preference for lactating over virgin rats. A larger sample of members of the two classes of stimuli is required to determine their relative attractiveness. The more important n is the number of pairs of targets examined, not the number of pups tested with each pair.

Brunswik (1947), in discussing the design of experimental studies of human social perception, reached similar conclusions: "Statistical sampling of objects—social objects to be sure—along with traditional sampling of 'judges' (the 'subjects' in the narrow sense of the word) is thus forced upon the researcher in perception for the first time" (Brunswik, 1947, p. 25; see also pp. 36–38). Generality of results depends, in Brunswik's terms, "on a kind of sampling-of-objects reliability" as well as the normal sampling of subjects, adequate in experiments in which relevant variability among "objects" is absent.

For purposes of significance testing, we therefore, pooled data taken from a group of pups tested with a single olfactory stimulus (e.g., Virgin Female 8). This pooling was accomplished by first calculating the percentage of the 15-min test period each individual pup spent on the side of the alley into which a single olfactory stimulus (i.e., the odor of Virgin Female 8) was introduced and then determining the mean percentage of the 15-min period the group of pups tested with that olfactory stimulus spent near it. To determine whether a class of stimuli (i.e., the odor of virgin females) was attractive to pups, we performed a Wilcoxon one-sample signed-rank test (Gibbons, 1976) on those mean values associated with that class of stimuli, treating 50% as the expected mean value on the null hypothesis. Such pooling of the data from subjects tested with a single olfactory stimulus is conservative but does prevent overrepresentation of the number of independent samples taken and consequent miscalculation of p values in significance tests.

All statistical tests reported below are based on the mean percentage of the 15-min test period which groups of pups spent near the preferred end of the apparatus. Both for descriptive purposes and to provide a basis for comparison of our data with those of others, we also have reported the mean percentage of litters of pups spending more than 50% of the test period at the preferred end of the alley, the end near the more attractive of the two targets presented.

Data from pups failing to cross the midline of the alley at least once during the first 5-min of testing, and therefore perhaps failing to sample both stimuli, were discarded. Approximately 8% of subjects were excluded for this reason. We have not reported analyses of the three 5-min test periods separately because we found no additional information in such analyses.

Experiment 1

The present experiment was undertaken to determine whether the olfactory cues synthesized and emitted by virgin Long-Evans rats are attractive to 21-day-old pups of their strain.

Method

Subjects. Twelve virgin Long-Evans (L-E) rats, anesthetized to prevent defecation (verified by inspection), vocalizations, and so on, served individually as sources of olfactory stimuli. Four 21-day-old L-E pups from 1 of 12 litters were tested with each virgin.

Procedure. A single anesthetized (Equi-Thesin, Jensen-Salsbery, .25 ml/100 g of body weight), virgin L-E rat was placed in one of the stimulus containers, and nothing was placed in the other.

Results and Discussion

The main results of Experiment 1 are presented in Figure 2a which indicates both (a) the mean percentage of groups of pups exposed to each anesthetized virgin spending more than 50% of the 15-min test period on the side of the alley into which olfactory cues from the virgin were introduced (open bars) and (b) the mean percentage of the 15-min test period that groups of pups spent on that side of the alley (stippled bars). As can be seen in the figure, and as statistical test confirmed (Wilcoxon $T = 1$, $n = 12$, $p < .001$), olfactory cues from virgin L-E rats were highly preferred to a clean airstream by 21-day-old L-E pups. The results of the present experiment indicate that the olfactory cues synthesized and emitted by virgin

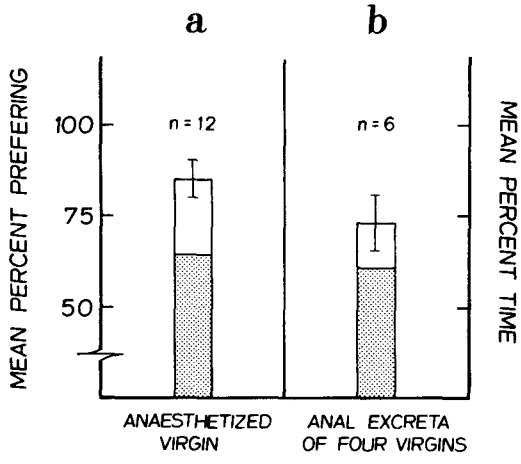

Figure 2. (a) Mean percentage of groups of Long-Evans rat pups preferring the odor of an anesthetized virgin L-E rat to that of a clean airstream (open bar), and mean percentage of the 15-min test period spent by groups of pups on the side of the alley in which the odor of the virgin was presented (stippled bar). (b) Mean percentage of groups of Long-Evans rat pups preferring the odor of the anal excreta produced by four L-E virgin females to a clean airstream (open bar), and mean percentage of the 15-min test period spent by groups of pups on the side of the alley in which the odor of the anal excreta was presented (stippled bar). (Flags indicate ± 1 *SE*, and the n refers to the number of anaesthetized virgins or samples of excreta tested.)

L-E rats are highly attractive to pups of their strain.

Experiment 2

The present experiment was undertaken to examine the attractiveness of the anal excreta of virgin L-E rats to 21-day-old L-E pups.

Method

Study 1. Using the procedure of Leon (1974), we restrained individual virgin L-E rats in stainless steel cages for 3 hr, removed any anal excreta with a clean glass slide, placed the excreta in a disposable polystyrene weigh-boat, weighed them, and presented the weighing tray and its contents to the 21-day-old young in a stimulus container at one end of the test alley; an empty weigh-boat was presented in a stimulus container at the other.

As can be seen in Figure 3, which indicates the amount of anal excreta deposited by virgin female rats during 3 hr of confinement, there is a problem in implementing this procedure. Forty-seven percent of virgin rats deposited no anal excreta at all during a 3-hr period of confinement, and those that did excrete often deposited only minute quantities of excretory material (see also Leon, 1978, p. 124). Because we wished to determine whether the anal excreta of virgin L-E rats were attractive, we felt it necessary, as a first step, to present pups with fairly sizable quantities of excreta. We, therefore, combined the anal excreta produced by four virgins during a 3-hr period and placed them in a single weigh-boat for presentation to pups. Pups were thus presented with a mean of 3.47 g ± .73 g (*SE*) of the anal excreta of virgin L-E rats. Six groups of four virgin L-E female rats served as sources of excreta, and six litters of eight 21-day-old L-E pups served as test subjects. An entire litter of pups was tested with each sample of excreta.

Study 2. The method of Study 1, while circumventing the problem of virgins failing to defecate during 3-hr of confinement, is questionable in that it presents both unusually large and randomly varying quantities of excreta to pups. In the present study, fixed amounts of excreta were presented to pups to determine a "dose–response curve" of pups to various quantities of excreta. One hundred thirty-six 21-day-old L-E pups from 20 litters served as subjects, and 96 L-E virgins served as the sources of 0, .25, .50, 1.0, 2.0, or 4.0 g of anal excreta. Two pups from each of 6–12 litters were tested with each weight of excreta at one end of the alley and nothing at the other. At least six different virgins provided samples of excreta at each value. The difficulty of collecting large quantities of anal excreta from virgins prevented preassignment of pups to conditions, and it was, therefore, not possible to run a completely counterbalanced design.

Results and Discussion

Study 1. The main results of Study 1 are presented in Figure 2b, which indicates both the mean percentage of groups of pups preferring the odor of pooled samples of virgins' anal excreta to the odor of a clean airstream (open bars) and the mean percentage of the 15-min test period that pups spent on the side of the alley from which the odor of virgins' anal excreta emanated (stippled bars). The odor of anal excreta of virgin L-E rats is clearly preferred to a clean airstream by L-E pups (Wilcoxon $T = 0$, $n = 6$, $p < .03$).

Study 2. The main results of Study 2 are presented in Figure 4 (open bars), which indicates both the mean percentage of groups of pups preferring the odor of various quantities of virgins' anal excreta to a clean airstream and the mean percentage of the 15-min test period that pups spent on the side of the alley from which the odor of virgins' anal excreta emanated (heavily shaded bars). While pups preferred all quantities

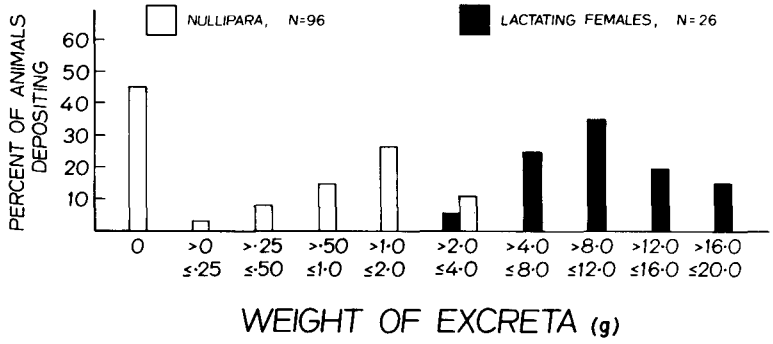

Figure 3. Percentage of 17–20-day postpartum and virgin female Long-Evans rats producing various amounts of anal excreta during 3-hr confinement.

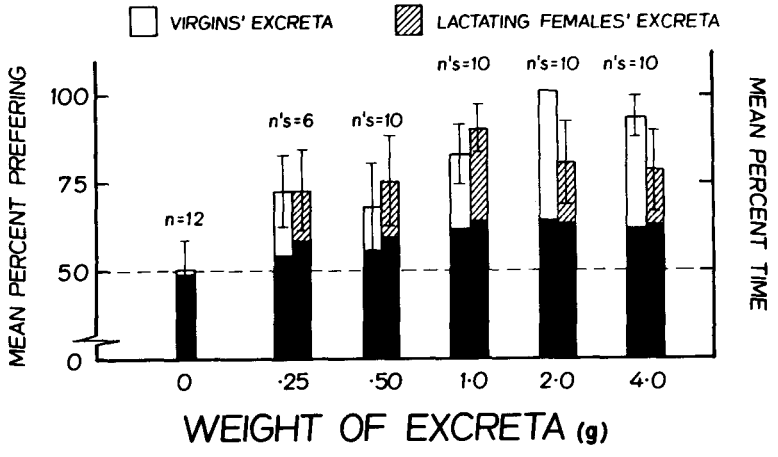

Figure 4. Mean percentage of groups of Long-Evans rat pups preferring the odor of various amounts of anal excreta to a clean airstream, and mean percentage of test periods groups of pups spent on the side of the apparatus in which the odor of each amount of excreta was presented (heavily shaded bars). (Flags indicate ± 1 *SE*, and the *n* refers to the number of samples of excreta tested.)

of virgins' anal excreta to a clean airstream, the preferences for .25 g and .50 g of anal excreta were not significant at the .05 level of confidence (Wilcoxon tests).

The results of Experiment 2, taken together with those of Leon (1974), are consistent with the view that the odor of the anal excreta of virgin L-E rats is sufficient to attract L-E pups whereas the odor of the anal excreta of virgin Wistar rats is not sufficient to attract pups of their strain. The results of the present experiment are also consistent with the view that Leon (1974) may have presented insufficient quantities of anal excreta from virgin Wistar rats to his pups to determine whether those excreta were attractive. (The mean amount presented by Leon was approximately 1 g [Leon, 1974, Figure 1], roughly the same mean amount of anal excreta produced by the 96 nulliparas whose excretatory behavior during 3-hr confinement [M = 1.1 g of anal excreta] is reported in Figure 3.)

The results of the present studies cannot be interpreted as providing evidence that the anal excreta of virgin L-E rats are the only source of olfactory cues rendering virgin rats attractive to pups. In fact, comparison of the absolute attractiveness of anesthetized virgins (Figure 2a) with that of their excreta (Figure 2b) suggests that the virgin herself is more likely to attract pups than are her excreta. Although this difference in attractiveness did not reach acceptable levels of significance (Mann-Whitney $U = 23$, $p > .05$), the tendency for greater numbers of pups to approach a single virgin than the excreta from four virgins suggests the existence of some attractive olfactory cue synthesized and emitted by virgin L-E rats, not contained in their anal excreta (see also Experiment 5 below and Galef & Heiber, 1976).

Experiment 3

In the present experiment, we explore the possibility that the anal excreta of lactating L-E rats are more attractive to L-E pups than the anal excreta of L-E virgins.

One procedure for exploring the relative attractiveness of the anal excreta of lactating and virgin L-E rats would be to compare directly the attractiveness of whatever excreta were produced by a virgin rat during a fixed period of time with those produced by a lactating rat during the same period of time. We have conducted such a study, and indeed, the anal excreta produced by lactating L-E rats (n = 8) during 3 hr of confinement are far more attractive to L-E pups (n = 32) than those produced by L-E virgins (n = 8) during a comparable period (Wilcoxon $T = 0$, $n = 8$, $p < .008$). However, such a procedure confounds three rather distinct possible causes of any observed

differences in the attractiveness of the samples of anal excreta taken from rats in the two reproductive states.

First, there could be a *qualitative* difference in the anal excreta of lactating and virgin rats, the anal excreta of lactating rats being more attractive than those of virgins. On this first hypothesis one would expect a given quantity of anal excreta taken from a lactating rat to be more attractive than the same quantity of anal excreta taken from a virgin rat.

Second, there could be a difference in the *quantity* of anal excreta produced by lactating females and virgins, and pups might be more attracted to large samples of excreta than small ones. On this hypothesis one would expect a large amount of anal excreta taken from a given animal to be more attractive than a small quantity of excreta from the same animal.

Third, there could be a difference in the *probability* of lactating and virgin rats' producing the minimum quantity of anal excreta necessary to attract pups. It is apparent from the data presented in Figure 4 that 1 g or more of the anal excreta from a L-E female is sufficient to attract pups and from the data presented in Figure 3 that more than 45% of virgin L-E females produce no anal excreta at all during 3 hr of confinement. Thus, if lactating female rats have a higher probability of producing 1 g of anal excreta during a 3-hr period of confinement than virgin rats, we would expect them to have more attractive anal excreta than virgins in a direct comparison of the attractiveness of the anal excreta produced by virgin and lactating rats in a 3-hr period.

Method

To determine whether there are qualitative differences in the anal excreta of virgin and lactating L-E rats which affect their relative attractiveness, we carried out two studies (1a and 1b). The quantitative and probabilistic explanations of the greater attractiveness of L-E lactating rats' anal excreta were tested, respectively, in Studies 2 and 3.

Study 1a. Eight virgin female L-E rats were confined in individual cages for 3 hr, and 6 g of their anal excreta were collected. Simultaneously, 6 g of anal excreta were collected from a pair of identically treated 17–20-day postpartum L-E females. Each of 12 groups of four 21-day-old L-E pups from 12 litters was presented in the test apparatus with a 6-g sample of anal excreta taken from 1 of 12 groups of virgin females and a 6-g sample of anal excreta taken from 1 of 12 pairs of lactating females.

Study 1b. The method was identical to that of Study 2 in Experiment 2 except that 45 Days 17–20 postpartum female L-E rats served as sources of .25, .50, 1.0, 2.0, or 4.0 g of anal excreta.

Study 2. To determine whether the quantity of anal excreta presented to pups influenced their probability of approaching a sample of excreta, we directly compared the relative attractiveness of 8-g and 1-g samples of anal excreta taken from the same animal. Each of eight 17–20-day postpartum L-E rats was confined in a cage for 3 hr. A sample of anal excreta was collected from the cage floor, and 8 g of the sample were placed in one weigh-boat and 1 g was placed in another. One of the two samples was then placed in each stimulus container. Thirty-two 21-day-old pups from eight litters served as subjects. Four pups from each litter were tested with excreta from a single female.

Study 3. To determine whether lactating L-E rats are more likely to produce attractive quantities of anal excreta during 3 hr of confinement than are virgins, we confined 26 Days 17–20 postpartum L-E females in individual stainless steel cages for 3 hr and then weighed any anal excreta produced. Data collected were compared with those collected from the virgin L-E rats, whose behavior, when identically treated, is presented in Figure 3.

Results and Discussion

Studies 1a and 1b. Long-Evans pups failed to exhibit a reliable preference between 6 g of anal excreta taken from virgin females and an equal quantity of anal excreta from 17–20-day postpartum females. Litters of pups spent a mean of 48.6% of the test period on the side of the alley from which the odor of a lactating female's anal excreta emanated (Wilcoxon $T = 42, n = 12, p = .85$), and only 54% of pups spent the majority of the test period on that side of the alley. This result extends the finding of Galef and Heiber (1976), who found no difference in the attractiveness to L-E pups of 1.58 g of the anal excreta of virgin and lactating L-E rats.

The main results of Study 1b are presented in Figure 4 (striped bars), which reports the two measures of pup behavior. The data, taken together with those of Experiment 2, Study 2, indicate that in comparison with a clean airstream, the various amounts of anal excreta from lactating L-E rats are no more attractive to 21-day-old L-E pups than are equal quantities of anal ex-

creta from virgin L-E rats (Mann-Whitney U tests, all $ps > .05$). As was the case with the odor of the anal excreta of virgin rats (Experiment 2, Study 2), L-E pups preferred the odor from all quantities of anal excreta to a clean airstream, but in the case of .25-g and .50-g samples the preferences were not statistically reliable (Wilcoxon tests).

The results of Studies 1a and 1b do not offer support for the hypothesis that qualitative differences in the anal excreta of virgin and lactating L-E rats are responsible for any difference in their attraction to pups.

Study 2. Long-Evans pups strongly preferred 8 g of anal excreta from a lactating female to 1 g of anal excreta from the same source. Litters of pups spent a mean of 62.4% of the test period on the side of the alley from which the odor of 8 g of excreta emanated (Wilcoxon $T = 3, n = 8, p < .04$), and 84% of pups spent the majority of the test period on that side of the alley. These data support the hypothesis that differences in the quantity of anal excreta produced by lactating and virgin L-E females might be responsible for observed differences in the attractiveness of their anal excreta collected in a fixed period of time.

Study 3. The main results of Study 3 are presented in Figure 3 (shaded bars), which indicates the amount of anal excreta produced by lactating L-E rats confined in individual cages for a 3-hr period. As is clear from examination of the figure, (a) Days 17–20 postpartum L-E females are more likely to produce measurable quantities of anal excreta during a 3-hr period than virgins of their strain, and (b) Days 17–20 postpartum L-E rats produce far more anal excreta than those virgins of their strain that do defecate during a 3-hr period of confinement.

Taken together, the results of Experiment 3 strongly suggest that there are two reasons why the anal excreta deposited by 17–20-day postpartum L-E rats during a fixed period are more attractive than those produced by L-E virgins under identical conditions. First, the probability of L-E lactating rats' producing the small quantities of anal excreta (1.0 g) sufficient to attract pups is roughly three times as great as the probability of virgin females' doing so. Second, even if a virgin and lactating female both produce some excreta, the lactating female will, with high probability, produce more excreta than the virgin. As the results of Study 2 indicate, large quantities of anal excreta are more attractive to L-E pups than small ones. We could find no evidence of qualitative differences in the attractiveness of the anal excreta of virgin and lactating L-E rats once the confounding effects of quantity and probability of emission were controlled.

We are not suggesting that there are no qualitative differences in the anal excreta of lactating and virgin L-E rats. Lactating L-E rats are more likely than virgins to produce a watery excreta (cecotrophe), the odor of which is very salient to humans. However, our data do not support the conclusion that the anal excreta produced by lactating females is qualitatively more attractive to L-E rat pups than the anal excreta produced by virgin L-E rats.

Experiment 4

The relative attractiveness of the anal excreta of lactating and virgin Long-Evans rats is, of course, in a sense a secondary issue. The important question is whether lactating Long-Evans rats are more attractive to pups than virgins of their strain. We found, as did Leon and Moltz (1971), that pups prefer the odor of a lactating Long-Evans rat to that of a virgin L-E rat when the two were presented simultaneously in our apparatus. In choosing between 12 virgin–lactating female pairs, 36 of 48 pups preferred the odors from the lactating female to which they were exposed to that of the virgin (Wilcoxon $T = 9, n = 12, p < .02$). In the present experiment, we examine the importance of anal excreta in producing this enhanced attractiveness of lactating Long-Evans rats.

Examination of lactating L-E rats reveals that some excreta cling to the fur of the female, especially in the vicinity of her anus, but the amount is invariably small, certainly less than 1 g. We found in Experiment 3, Study 2 of the present series that 8 g of a mother's anal excreta is far more attractive than 1 g of her anal excreta. If it is the anal

excreta that are responsible for the attractiveness of dams, then 8 g of a dam's excreta should be more attractive than the dam herself.

Method

The method was essentially the same as that of preceding experiments except that 8 g of anal excreta, taken from one of fifteen 17–20-day postpartum L-E females, were placed in one stimulus presentation container and one of 15 anesthetized Day 21 postpartum L-E females was placed in the other. Four pups from one of eight litters chose between each of the 15 stimulus pairs used.

Results and Discussion

Long-Evans pups preferred the odor of an anesthetized lactating female to the odor of 8 g of her anal excreta. Litters of pups spent a mean of 57.6% of the test period on the side of the alley from which the odor of the dam herself emanated (Wilcoxon $T = 21$, $n = 15$, $p < .026$), and 70.2% of pups spent the majority of the test period on that side of the alley.

These data are not consistent with the view that the anal excreta of lactating L-E rats are a unique factor in the attraction of young to their dam. To the contrary, olfactory cues other than those in anal excreta appear to be more important in mediating adult–young interaction than are cues in anal excreta.

Given that pups of both the L-E and Wistar strains are known to exhibit a strong tendency to approach an arbitrarily selected odor to which they are exposed during ontogeny (Leon, Galef, & Behse, 1977; Muskus, 1978), it is not unreasonable to propose that pups of either strain would tend to remain in contact with any detectable familiar olfactory stimulus available in their environment. In this view, the odor of maternal anal excreta is only one of a functionally redundant class of stimuli (including respired gasses, saliva, various glandular secretions, urine, etc.) which pups might approach because of their familiarity.

General Discussion

The results of the present series of studies on the olfactory cues important in the attraction of Long-Evans rat pups to their dams suggest that such attraction is mediated very differently in 21-day-old Long-Evans pups than in 16-day-old Wistar pups. Although Long-Evans pups, like those of the Wistar strain, will approach a 17–20-day postpartum female in preference to a virgin female, unlike Wistar pups, Long-Evans pups (a) find virgin females of their strain highly attractive, (b) find the anal excreta of virgins of their strain highly attractive, (c) do not appear to respond differentially to any qualitative differences in the anal excreta of lactating and virgin females of their strain, and (d) are more attracted to olfactory cues not emanating from the anal excreta of a lactating female than to those emanating from a lactating female's anal excreta. In general, the interaction of 21-day-old Long-Evans pups and their dams does not seem to be mediated by olfactory cues similar to the maternal pheromone of Wistar rats.

Differences between strains in the nature of the olfactory cues mediating mother–young interaction could be due to differences in the olfactory sensitivity of their pups or to differences in the relative intensity of odor of the various excretions produced by lactating females. Leon (Note 1), for example, found rats of the ACI strain to differ markedly from Wistar rats in their production of olfactory cues attractive to their pups.

The design of our experiments does not, however, permit unequivocal attribution of the difference in results between the present studies and those of Leon and his co-workers (Leon, 1978) to differences in the strain of rat used. There are clearly further differences in ages of subjects, procedures, and experimental designs which may well be important in producing the different pictures of the olfactory mediation of mother–young interaction which emerge from the two sets of studies. We, for instance used 21-day-old pups, and Leon used 16-day-old pups as principal experimental subjects. As Landauer, Carr, and Marasco (Note 2) showed, the olfactory cues attractive to Wistar rat pups may change markedly during maturation. Further, the conservative statistical procedures employed in our studies, in which

the number of targets presented to groups of pups were treated as n, might have led us to different interpretations of some of Leon's data than those that he proposed.

The results of the present studies do, however, clearly indicate that the description of olfactory mediation of mother–young interaction in Wistar rats available in the literature (Leon, 1978) cannot be generalized to rats of other strains or ages. Our data also suggest that further examination of the role of various olfactory cues in mediating mother–young interaction under conditions in which the quantity of odoriferous material provided is controlled, conservative statistical procedures are employed, and subjects are tested at a variety of ages is required to complete our understanding of the range of olfactory cues important in mediating mother–young interaction.

Reference Notes

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Received September 25, 1978 ■