

Responses to Novel Odors Mediate Maternal Behavior and Concaveation in Gerbils

MERTICE M. CLARK, CHERYL A. SPENCER AND BENNETT G. GALEF, JR.¹

Department of Psychology, McMaster University, Hamilton, Ontario, Canada, L8S 4K1

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CLARK, M. M., C. A. SPENCER AND B. G. GALEF, JR. *Responses to novel odors mediate maternal behavior and concaveation in gerbils.* *PHYSIOL. BEHAV.* 36(5)845-851, 1986.—In a series of three experiments we examined: (Experiment 1) responses to novel odors by early- and late-maturing not-pregnant, pregnant, nursing and postweaning female Mongolian gerbils, (Experiment 2) the response of the same eight groups of female gerbils to unfamiliar pups, and (Experiment 3) the rate of induction of maternal behavior by concaveation in early- and late-maturing nulliparous gerbils. We found: (1) that those females that responded relatively positively to novel odors in Experiment 1 were more likely to retrieve and less likely to attack unfamiliar pups in Experiment 2 than those females responding relatively negatively to novel odors in Experiment 1, and (2) that early-maturing nulliparous gerbils both responded more positively to novel odors and exhibited more rapid induction of maternal behavior by concaveation than late-maturing nulliparous gerbils. The results both confirm and extend Fleming and Rosenblatt's (1974) hypothesis that differences in response to novel odors mediate individual differences in maternal responsiveness.

Maternal behavior Concaveation Sexual maturation Infanticide Neophobia Gerbils

FEMALE Mongolian gerbils (*Meriones unguiculatus*) encountering unfamiliar gerbil pups may behave maternally, ignore the young, or attack and kill them [5, 6, 7]. As is the case in rats, mice and other rodents (for reviews see [12, 13, 14]), response to conspecific neonates in female gerbils varies with reproductive state: nulliparous gerbils and those in early or mid-pregnancy frequently kill young [5,6]; recently parturient females tend to respond maternally toward them, while female gerbils more than 11 days postpartum again exhibit increasing levels of infanticide [7]. Female gerbils in the same reproductive condition also show considerable variability in their response to pups. Some parturient female gerbils exhibit little maternal behavior, while others are consistently maternal [1,15].

Fleming and her co-workers [8, 9, 10] have presented evidence consistent with the hypothesis that some of the variation in response to pups exhibited by nulliparous and parturient rats is the result of hormonally induced changes in the tendency of parturient females to avoid novel olfactory cues. Induction of maternal behavior in nullipara can be accelerated by rendering them anosmic prior to concaveation [9]. Parturient rats are less timid or emotional in a variety of test situations than are nullipara [8,11]. On this model, the initial reluctance of nulliparous female rats to contact pups is seen as the result of avoidance of the constellation of cues emitted by pups and the willingness of parturient dams to exhibit maternal behavior is seen as reflecting a reduced level of emotional response to that constellation of cues.

Given that differences in the degree of maternal behavior

exhibited by nulliparous and parturient rats is to be at least partly understood in terms of differences in the extent to which rat pups elicit emotional response from them, it seemed possible that differences in behavior towards pups exhibited by female gerbils might be similarly mediated. If gerbils differ in their response to novel odors, on the Fleming hypothesis, one would expect those gerbils showing greatest relative avoidance of novel odors to show reduced levels of maternal behavior. Conversely, one would expect those female gerbils exhibiting low levels of maternal behavior to exhibit greater reluctance to contact novel olfactory stimuli than those female gerbils exhibiting relatively high levels of maternal behavior. For example, we have recently reported that differences in behavior toward own young exhibited by female gerbils correlates with their ages at vaginal introitus. Those nursing females that had exhibited vaginal introitus before reaching 25 days of age (early-maturing) were less likely than those that had exhibited vaginal introitus after reaching 25 days of age (late-maturing) to keep their pups gathered in the nest, nurse their young, or retrieve displaced young [3,4]. On the Fleming hypothesis, one might expect early-maturing lactating gerbils to be more timid or emotional than their late-maturing sisters. In general, support for a role of emotional response to pups in mediating differences in levels of maternal responsiveness could be provided by demonstration of negative correlations between the levels of maternal behavior exhibited by gerbils of different maturational histories and in different reproductive states and their relative levels of avoidance of novel olfactory stimuli.

¹Requests for reprints should be addressed to Dr. Mertice M. Clark.

In the present series of experiments, we examined the response of female gerbils both to novel odors and to unfamiliar pups. The issues we addressed were the relationship between avoidance of novel odors and maternal responsiveness of gerbils both of different maturational histories and at different stages in the reproductive cycle. In Experiment 1, we determined the relative aversion to novel olfactory stimuli of female gerbils with different rates of sexual maturation and in different reproductive states. In Experiment 2, we examined the relationship between individuals' preferences for novel odors, as determined in Experiment 1, and their probability of retrieving or attacking unfamiliar pups. In Experiment 3, we examined, in virgin gerbils, the relationship between responses to novelty, as determined in Experiment 1, and rates of induction of maternal behavior by concaveation.

GENERAL METHOD

Multiparous breeding pairs of Mongolian gerbils (*Meriones unguiculatus*) acquired from Tumblebrook Farm (Brookfield, MA) served as the source of all subjects. Breeding pairs were housed in polypropylene cages (35×30×15 cm) with hardware-cloth (1.27-cm) lids. Each cage was carpeted with a thin layer of woodchip bedding (Betta-chip, Northeastern Products Corp., Warrensburg, NY). The colony was maintained on ad lib Purina Laboratory Rodent chow and water in a single, temperature-controlled colony room illuminated on a 12-hr light/dark cycle (lights on at 0700 hr). Breeding pairs were examined daily and, when a female was visibly pregnant (third trimester), her mate was removed from her cage. Cages containing pregnant females were examined twice daily (1000 and 1700 hr) to determine dates of parturition.

Pups in each litter were toe-clipped for individual recognition on the day of their birth (Day 1) and were weaned to a cage separate from their dam on Day 25. During the period from birth to sexual maturation, each female was examined daily to determine her age at vaginal perforation. Examination for vaginal perforation was accomplished by applying gentle pressure just below the vagina.

Females exhibiting vaginal introitus before weaning on Day 25 were classified as early-maturing (EM) and those achieving vaginal perforation after weaning, as late-maturing (LM). As we have shown previously [4], age at vaginal opening is bimodally distributed in domesticated gerbils. There is no overlap in the ages at which EM females (mean=16.5±0.7 days) and LM females (mean=37.1±0.8 days) exhibit vaginal introitus. Because we weaned our gerbils at 25 days of age, it was convenient to use a criterion of vaginal patency at Day 25 to discriminate EM from LM females.

EXPERIMENT 1

The present experiment was undertaken to determine the relationship between reproductive state and response to novel odors in early-maturing (EM) and late-maturing (LM) female gerbils. Independent groups of EM and LM nulliparous, pregnant, nursing and 7-day postweaning females were tested for their tendency to investigate a novel odor in a choice situation.

METHOD

Subjects and Rearing Condition

Subjects were 81 EM and 71 LM female Mongolian ger-

bils selected from 85 litters born in the McMaster colony and reared as described in the General Method section.

Independent groups of females were tested for their responses to novel odors when not-pregnant (EM, n=25; LM, n=25), pregnant (EM, n=25; LM, n=25), nursing (EM, n=16; LM, n=11) or after weaning of their litters (EM, n=15; LM, n=10). Not-pregnant females had been mated at Day 25 but had failed to conceive (at the time of testing they were not visibly pregnant and they did not produce litters in the next 30 days). Pregnant females were visibly pregnant at the time of testing and each delivered a litter within 7 days of testing (mean=4.8±0.40 days). Nursing subjects were tested on Day 10 postpartum, and postweaning females 7 days after removal of their litters on Day 25 postpartum.

Subjects were selected from within our colony so that within each reproductive condition mean ages of EM and LM females were roughly equated at testing. Individual subjects ranged from 75–182 days of age at testing, with mean ages of 122.0±7.9, 107.0±5.8, 118.0±5.2, and 135.2±7.6 days for, respectively, not-pregnant, pregnant, nursing and postweaning groups.

Procedure

Immediately before testing each female, other gerbils if any in her cage (her mate or litter) were removed. The lid of her cage was then replaced with an experimental lid. The experimental lid, constructed of (1.27 cm) screen, had two circular holes (5 cm) cut in it 14.1 cm apart, equidistant from the sides of the lid and 5.4 cm from one end. Attached to the lid, over the holes, were two L-shaped, 5-cm diameter, cylindrical metal tubes. These tubes were attached to the lid, with the long arm of the "L" at right angles to it and the short arm parallel to the cage floor. Removable closures at the end of the short arm of each "L" permitted stimuli to be introduced into each cylinder.

The experimenter placed a 0.5 g ball of cotton batting, wrapped in screen (to prevent subjects from shredding the stimulus), and moistened with 2.5 ml (0.5 tsp) of lemon extract (Club House Foods Ltd., Toronto, Ont.) in the short arm of one L-shaped cylinder and 0.5 g of material (wrapped in screen) from a subject's own nest in the short arm of the other cylinder.

In the 15 min following placement of stimuli in the apparatus, an observer, unaware of the location of the two stimuli and unaware of the reproductive state of the subject, recorded the number of sec each subject spent investigating each stimulus. A subject was considered to be investigating a stimulus when its head was inside the long arm of the L-shaped cylindrical metal tube holding that stimulus. A novelty preference score was calculated for each subject by dividing the number of sec a subject spent investigating the scented stimulus by the number of sec it spent investigating both scented and unscented stimuli.

After testing, nursing subjects were given back their litters and allowed to rear them to weaning on Day 25.

RESULTS

The main results of Experiment 1 are presented in Fig. 1 which shows the mean novelty preference scores of both EM (left-hand panel) and LM (right-hand panel) females in various reproductive states at testing.

Novelty Preference as a Function of Reproductive State

Reproductive state had a significant effect on response to

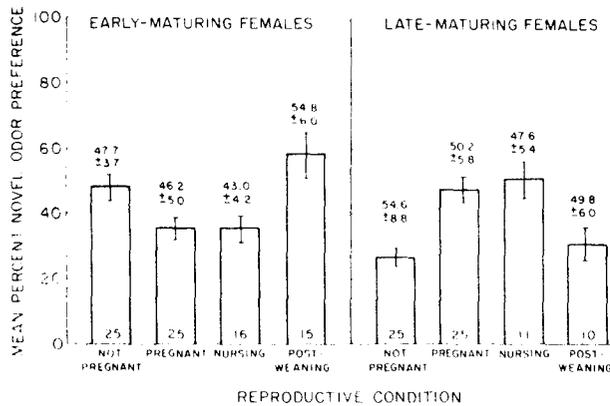


FIG. 1. Novel odor preference scores of early-maturing (left-hand panel) and late-maturing (right-hand panel) females in various reproductive conditions. Numbers in bars = N's per group. Numbers above bars = mean total number of sec subjects spent investigating both the familiar and the novel olfactory stimuli. Flags = ± 1 SEM.

the novel olfactory stimulus of both EM, $F(3,77)=7.22$, $p<0.01$, and LM, $F(3,67)=7.90$, $p<0.01$, females. Early-maturing reproductively active females, (i.e., those pregnant or nursing) spent less time investigating the novel stimulus than those EM females not reproductively active (i.e., either not-pregnant or postweaning) (protected t tests [16], all 4 t 's >3.01 , all p 's <0.01). In contrast, LM females responded more positively to the novel olfactory stimulus when reproductively active than when reproductively not active (protected t tests, all 4 t 's >3.17 , all p 's <0.01).

There were no significant differences in novelty preference scores either between not-pregnant and postweaning or between pregnant and nursing females in either the EM (protected t tests, both t 's <0.74 , both p 's >0.20), or LM groups (protected t tests, both t 's <0.72 , both p 's >0.20).

Novelty Preference as a Function of Age at Sexual Maturation

Comparison of the data presented in the left- and right-hand panels of Fig. 1 revealed that not-pregnant and postweaning EM females responded more positively to a novel odor than LM females in the same reproductive conditions (two-tailed t tests, both t 's >3.98 , both p 's <0.001). Early-maturing females that were either pregnant or nursing responded less positively to a novel odorant than LM females in comparable reproductive conditions (two-tailed t tests, both t 's >2.46 , both p 's <0.05).

DISCUSSION

The results of the present experiment indicate that the response to novel odors exhibited by female gerbils is affected both by their reproductive state and by their ages at sexual maturation. In general, EM females responded more positively to a novel odorant when they were not reproductively active, while LM females responded more positively to a novel odorant when they were reproductively active.

In order to be sure that the results of the present experiment were not peculiar to lemon extract, we tested an additional four groups of 16 subjects each (EM pregnant and not-pregnant, LM pregnant and not-pregnant) using almond

extract rather than lemon extract as the novel olfactory stimulus. The pattern of results paralleled those found in the main experiment (mean novelty preference for almond extract: EM pregnant, 27.9 ± 3.1 percent; EM not-pregnant, 44.3 ± 5.9 percent, LM pregnant, 44.9 ± 5.4 percent, LM not-pregnant, 17.1 ± 3.8 percent).

EXPERIMENT 2

If Fleming and her co-workers [8, 9, 10] are correct in asserting that the response exhibited by female rodents to unfamiliar pups is, at least in part, a reflection of their reaction to novel odors, then the results of Experiment 1 should predict the response to unfamiliar pups of EM and LM female gerbils in various reproductive states. In general, one would expect those groups of females exhibiting a relatively positive response to the novel odorant in Experiment 1 to retrieve unfamiliar pups more frequently and attack them less frequently than females in those groups tending to avoid contact with a novel odorant. In particular one would predict (see Fig. 1):

(1) That EM not-pregnant and postweaning females should be more likely to retrieve and less likely to attack unfamiliar pups than LM not-pregnant and postweaning females.

(2) That EM pregnant and nursing females should be less likely to retrieve and more likely to attack unfamiliar pups than LM pregnant and nursing females.

(3) That not-pregnant and postweaning LM females should be less likely to retrieve and more likely to attack unfamiliar pups than pregnant and nursing LM females.

(4) That not-pregnant and postweaning EM females should be more likely to retrieve and less likely to attack unfamiliar pups than pregnant and nursing EM females.

(5) That, independent of reproductive condition, females retrieving unfamiliar pups should have exhibited higher novelty preference scores in Experiment 1 than those females not retrieving them.

(6) That the time females spend in contact with unfamiliar young should correlate positively with their novelty preference scores in Experiment 1.

In the present experiment we tested each of these six predictions.

METHOD

Subjects

The 81 EM and 71 LM females that were tested in Experiment 1 also served as subjects in Experiment 2. Forty-three EM and 53 LM experimentally naive females, selected from 44 additional litters reared in the McMaster colony as described in the General Method section, were also used to bring our total N's to 124 EM and 124 LM females.

Procedure

The 152 subjects from Experiment 1 were tested for their response to unfamiliar pups either 2 hr before or 2 hr after they were tested for their response to a novel odorant. Each of the 96 experimentally naive subjects was tested only once for her response to unfamiliar pups at an appropriate point in her reproductive cycle.

Immediately before testing any female for her response to strange pups, her mate, if present, was removed from her cage. Nursing females were tested with their litters present in their cages.

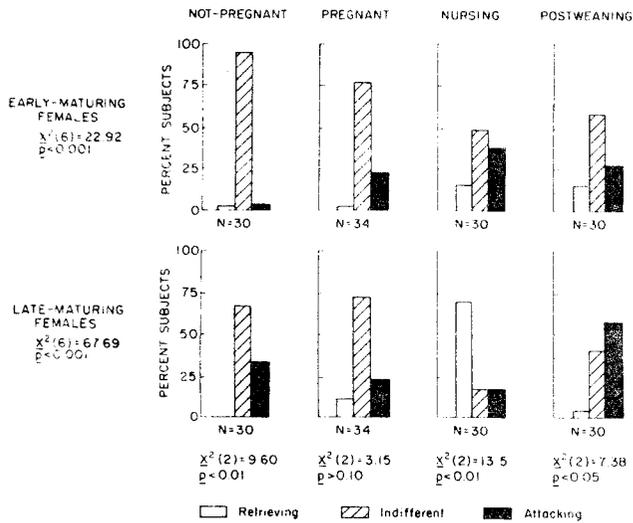


FIG. 2. Percentage of early-maturing (upper panel) and late-maturing (lower panel) females in various reproductive conditions retrieving, indifferent to, and attacking strange pups. χ^2 in left-hand margin are comparisons across reproductive conditions. χ^2 along the bottom of the figure are comparisons between EM and LM females in each reproductive condition.

To initiate testing, two 1–3 day old pups, one male and one female, were placed in a female's cage in the corner diagonally opposite her nest. During the 5-min period immediately following introduction of the pups, an observer unaware of the design or purpose of the experiment categorized each subject as (1) attacking (if she caused one or both pups to bleed), (2) retrieving (if one or both pups were transported to the nest) or (3) indifferent (if the pups were neither harmed nor retrieved). Testing was terminated immediately by the observer if a female attacked pups. The observer also recorded the number of sec retrieving and indifferent females spent licking and nosing pups.

RESULTS

The main results of Experiment 2 are presented in Fig. 2 which shows the percentage of EM and LM females in various reproductive states retrieving, indifferent to, and attacking pups during the 5-min test. The data are discussed below with respect to the six predictions made in the introduction to the present experiment. In each of the analyses presented below, we first performed a Chi-square test across all relevant subject conditions and all three measures (retrieval, indifference and attack) to determine whether there were significant differences among groups in maternal behavior. We then partitioned the Chi-square table [2] to examine the effects of subject condition on the frequency of occurrence of retrieval vs. indifference and attack vs. not-attack.

Prediction 1

As predicted, EM not-pregnant and postweaning females were significantly more maternal than LM not-pregnant and postweaning females, $\chi^2(2)=13.54$, $p<0.01$. These differences in maternal behavior were the result both of EM females retrieving with greater frequency, $\chi^2(1)=3.87$,

$p<0.05$, and attacking with less frequency, $\chi^2(1)=9.65$, $p<0.01$, than LM females.

Prediction 2

As predicted, EM pregnant and nursing females were less maternal than LM pregnant and nursing females, $\chi^2(2)=12.97$, $p<0.01$. This difference was, in large measure, attributable to the greater frequency of retrieval exhibited by LM females, $\chi^2(1)=11.14$, $p<0.01$. Although there was no significant difference in frequency of pup attack by EM and LM females, $\chi^2(1)=1.57$, $0.15>p>0.10$, one-tailed test, there was a tendency for EM pregnant and EM nursing females to attack pups more frequently than LM pregnant and LM nursing females.

Prediction 3

As predicted, there were significant differences among LM females in different reproductive states in their response to unfamiliar pups, $\chi^2(6)=67.69$, $p<0.001$. Pregnant and nursing females were both more likely to retrieve, $\chi^2(1)=16.08$, $p<0.001$, and less likely to attack, $\chi^2(1)=10.13$, $p<0.01$, than not-pregnant and postweaning LM females. Confirmation of Prediction 3 is, of course, not very informative, as it would be predicted by any model of maternal behavior.

Prediction 4

In partial confirmation of Prediction 4, EM females in different reproductive states differed significantly in their response to unfamiliar pups, $\chi^2(6)=22.9$, $p<0.01$. This resulted from a lower frequency of attack by not-pregnant and postweaning EM females than pregnant and lactating EM females, $\chi^2(1)=3.12$, $p<0.05$, one-tailed test. The two groups of EM females did not, however, differ in their frequency of retrieval, $\chi^2(1)=0.01$, NS.

Prediction 5

As predicted, those EM and LM females examined in both Experiments 1 and 2 that retrieved pups had higher mean novelty preference scores (EM, mean=50.4±3.8%; LM, mean=51.1±4.6%) than those of EM and LM females attacking pups (EM, mean=35.8±3.3%; LM, mean=28.7±3.9%; two-tailed *t* tests, both *t*'s>2.32, both *p*'s<0.05).

Prediction 6

Consistent with prediction, as can be seen by comparing Fig. 1 with Fig. 3 (which shows the mean time those EM and LM females that did not attack pups spent in contact with them in the 5-min test in Experiment 2), the mean novelty preference scores of females in various reproductive conditions correlated well with their mean time spent in contact with pups. Rank order correlations between the percentage of time individual females not attacking young in Experiment 2 spent in contact with them and the percentage of time those same females spent in contact with the novel olfactory stimulus in Experiment 1 were significantly positive for both the 67 EM (Spearman's $\rho=0.28$, $t=2.35$, $p<0.02$) and 53 LM (Spearman's $\rho=0.40$, $t=3.08$, $p<0.01$) females. Although the values of ρ are not high, they are fairly impressive given that attacking females (not included in the

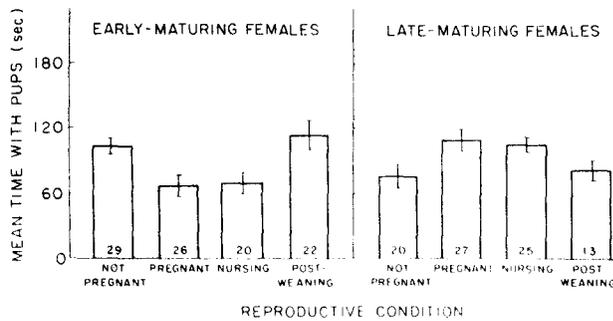


FIG. 3. Mean number of sec spent in contact with strange pups by those early-maturing (left-hand panel) and late-maturing (right-hand panel) females not attacking strange pups. Numbers in bars = N's per group. Flags = ± 1 SEM.

analysis) were responsible for most of the low novelty preference scores in Experiment 1 (see Prediction 5).

DISCUSSION

The results of the present experiment support the contention [8, 9, 10] that elicitation of maternal behavior in female rodents by unfamiliar young is influenced by a female's degree of aversion to novel odors. Five of the six predictions concerning the occurrence of retrieval and attack derived from the novelty preference scores of females in Experiment 1 are supported in the present experiment.

Obviously, the occurrence of maternal behavior in response to unfamiliar pups is not determined solely by a female's degree of neophobia. Thus, it is not too surprising that Prediction 4, that reproductively active EM females should be less maternal than those EM females not reproductively active, was not strongly confirmed. However, the finding in the present experiment of low levels of retrieval of unfamiliar pups by nursing EM females (that exhibited low novelty preference scores in Experiment 1) suggests that their tendency to avoid novel olfactory stimuli was inhibiting whatever other factors might have influenced them towards behaving maternally. Further, the finding of greater frequency of attack of unfamiliar pups by reproductively active than by reproductively inactive EM females (Prediction 4) is both counterintuitive and consistent with Fleming's [8, 9, 10] model.

It might be argued that high frequency of retrieval and low frequency of attack of unfamiliar pups in a 5-min test is not an adequate index of maternal responsiveness. To validate our measure of maternal responsiveness we examined the rate of loss of pups by nursing EM and LM females between birth and weaning (Day 25) as a function of their behavior towards unfamiliar pups in Experiment 2. As can be seen in Table 1 (which shows the mean number of own pups lost by females that retrieved, ignored, or attacked unfamiliar pups in Experiment 2), those females retrieving strange pups were more successful in maintaining their own litters than those females attacking unfamiliar pups (protected *t* tests, both *t*'s > 2.03, both *p*'s < 0.05).

Further, we found significant negative correlations between the novelty preference scores of pregnant and lactating EM and LM females in Experiment 1 and the number of pups they lost between birth and weaning (Spearman rank-

TABLE 1
MEAN NUMBER OF OFFSPRING LOST BY EM AND LM FEMALES RETRIEVING, INDIFFERENT TO, AND ATTACKING STRANGE YOUNG

	N	Retrieving	Indifferent	Attacking	F
Early-Maturing	30	0.6 \pm 0.3	1.1 \pm 0.3	2.6 \pm 0.5	F(2,27) = 4.38*
Late-Maturing	30	0.7 \pm 0.2	3.0 \pm 1.1	2.6 \pm 1.4	F(2,27) = 4.21*

**p* < 0.05.

order correlations: EM pregnant, $\rho = -0.34$, *p* < 0.05; EM nursing, $\rho = -0.53$, *p* < 0.01; LM pregnant, $\rho = -0.45$, *p* < 0.05; LM nursing, $\rho = -0.61$, *p* < 0.01). Thus, retrieval and attack during testing in Experiment 2 predicted behavior by a female toward her own young and response to a novel olfactory stimulus in Experiment 1 predicted a female's behavior toward her own pups as well as foreign ones.

EXPERIMENT 3

On the Fleming [8, 9, 10] model, it should be more difficult to induce maternal behavior by concaveation in those virgin females responding negatively to novel odors than in those responding positively to novel odors. In the present experiment we compared the rate of induction of maternal behavior by concaveation in EM and LM nullipara. Because the results of Experiment 1 of the present series indicate that non-pregnant EM females respond more positively to novel odors than non-pregnant LM females, one would expect, on the Fleming hypothesis, that maternal behavior should be induced more easily in EM than in LM nullipara.

METHOD

Subjects and Rearing Condition

Subjects were 19 sister pairs of nulliparous gerbils from 19 litters reared in the McMaster colony as described in the General Method section. One member of each pair was early-maturing (EM) and the other late-maturing (LM). At weaning, on Day 25, sister pairs were placed together in cages separate from their dams and littermates. At 80 days of age, all 38 subjects were placed in individual cages (30 \times 18 \times 11 cm).

Procedure

Induction of maternal behavior was initiated 1 week after each female had been transferred to its individual cage. On each of 7 days, two pups, 1-3 days of age, were introduced into each female's cage in the corner diagonally opposite her nest site. During the 15-min period following introduction of the pups, an observer, unaware of the age of subject females at vaginal introitus, recorded: (1) retrieval (i.e., transport of one or both test pups to the nest), (2) contact (i.e., the number of sec a female sniffed or licked the test pups), and (3) nursing (i.e., a female assuming a nursing posture over

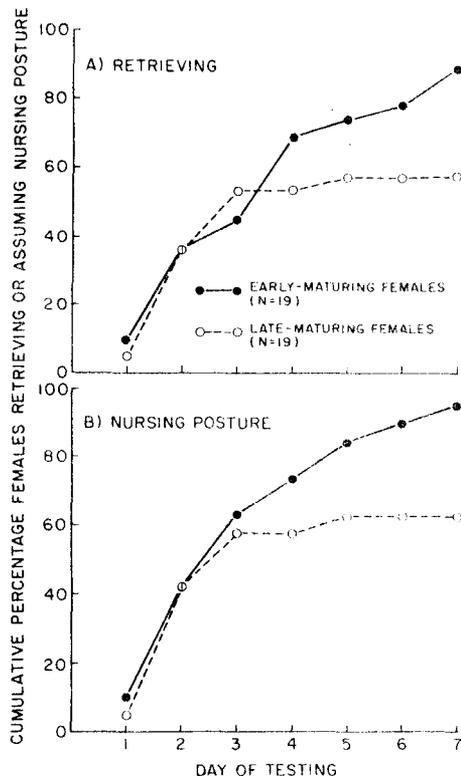


FIG. 4. Cumulative percentage of virgin early-maturing and late-maturing females (A) retrieving pups and (B) assuming a nursing posture on each of 7 days of testing for induction of maternal behavior.

the pups or lying on her side, exposing her nipples to the pups).

At the conclusion of each day's test, test pups were replaced with 2-4, 1-3 day-old young that were left with each female for the following 24 hr. At the end of each 24-hr period of exposure to pups, these pups were removed. One hr later, a 15-min test with two new 1-3 day-old pups was initiated.

RESULTS

The main results of Experiment 3 are presented in Figs. 4a and 4b which show, respectively, (4a) the cumulative percentage of EM and LM females retrieving pups or (4b) assuming a nursing posture during daily 15-min tests for induced maternal behavior. There were significant differences between EM and LM females in rate and probability of induction of maternal behavior. Early-maturing females required fewer trials to first retrieve (Wilcoxon matched-pairs signed-ranks test, $T=22$, $p<0.025$) and fewer trials to first assumption of a nursing posture ($T=28$, $p<0.025$) than their LM sibs. During the 7 days of testing, 17 of 19 EM females retrieved pups, while only 10 of 19 LM females did so (Fisher Exact Probability Test, two-tailed, $p<0.05$). Eighteen of 19 EM females exhibited nursing postures, while only 12 of 19 LM females did so (Fisher Exact Probability Test, two-tailed, $p<0.05$).

Those EM and LM females that did become maternal

differed neither in the number of trials on which they retrieved pups (two-tailed t test, $t(25)=0.51$, NS), nor in the number of trials during which they exhibited nursing postures (two-tailed t test, $t(28)=0.65$, NS).

During the first test trial, when subjects were first exposed to pups, EM females spent a greater number of sec in contact with pups (mean= 217.8 ± 28.8 sec) than did LM females (mean= 150.3 ± 18.0 sec; correlated two-tailed t test, $t(19)=2.13$, $p<0.05$). Those LM females that subsequently exhibited retrieval or nursing behavior spent a greater percentage of the first test period in contact with pups (mean= 163.8 ± 26.1 sec) than did those LM females that did not become maternal (mean= 100.4 ± 10.8 sec; two-tailed t test, $t(17)=2.35$, $p<0.05$). A similar trend was apparent in EM females, with those females becoming maternal during the 7 days of testing spending more of the first 15-min test in contact with pups (mean= 228.6 ± 24.3) than the one female that never retrieved or assumed the nursing posture (164 sec).

Attack of pups was relatively infrequent and occurred only on the first day of concaveation when 4/19 LM females and 1/19 EM females exhibited aggressive behavior toward pups (Fisher Exact Probability Test, $p=NS$).

DISCUSSION

Results of the present experiment offer support for the hypothesis that in gerbils, as in rats [8, 9, 10, 11], rate of induction of maternal behavior by concaveation is, at least in part, mediated by response to novel stimuli emitted by pups and experienced by nullipara. Late-maturing nulliparous gerbils exhibited both higher levels of aversion to novel odors than EM nulliparous females (Experiment 1) and lower frequencies of induction of maternal behavior in the present experiment. Further those LM females that became maternal exhibited greater attraction to pups upon initial contact with them than those LM females that did not become maternal.

We were somewhat surprised to find that rate of induction of maternal behavior was equivalent in those LM and EM females that became maternal. It is perhaps relevant to note that although there were significant differences in novelty preference scores of EM and LM not-pregnant females in Experiment 1, there was overlap between the two groups in response to novel olfactory stimuli. Results of the present experiment, in which it was found that LM females exhibiting prolonged contact with pups upon initial exposure to them were more likely to exhibit induced maternal behavior, suggest that it is those LM females with the greatest initial aversion to novel stimuli presented by pups that were least likely to exhibit induced maternal behavior. Consistent with this interpretation is the finding that of those nine LM females below the median in time spent in contact with pups during the first exposure period, only two eventually retrieved, while seven of the nine females above the median in time spent with pups during initial contact retrieved (Fisher Exact Probability Test, $p=0.05$). Similarly, if one considers EM and LM females together, time spent in contact with pups on the first day of exposure to them predicted subsequent probability of induction of maternal behavior. Only 10 of 19 subjects below the median in time spent in contact with pups on the first exposure day exhibited retrieval during the 7 days of testing, while 17 of 19 of those subjects above the median did so (Fisher Exact Probability Test, $p=0.03$). Thus, response to novel stimuli both in Experiment 1 and in the present experiment were predictive of

probability of induction of maternal behaviors by concaveation in nulliparous gerbils.

GENERAL DISCUSSION

The results of the present series of studies indicate that the response of female gerbils to a novel odor is a predictor of individual differences in maternal responsiveness. The model Fleming [8, 9, 10] proposed to account for differences in the response of rats in different reproductive states to strange pups, is confirmed both in female gerbils maturing at different rates and those at different points in their reproductive cycles.

In Experiment 2, it was found that response of EM and LM female gerbils in various reproductive conditions to unfamiliar pups could, to some extent, be predicted on the basis of their previously determined tendency to investigate a novel olfactory stimulus. In general, those groups of gerbils tending to avoid contact with novel olfactory stimuli in Experiment 1 also exhibited lower frequencies of retrieval behaviour and greater frequencies of aggressive behavior

towards pups in Experiment 2. Further, in Experiment 3, it was found that relative probability of induction of maternal behavior by concaveation in EM and LM females corresponded to their relative aversion to a novel olfactory stimuli in Experiment 1.

In a previous paper [4], we described differences in the quality of maternal behavior early-maturing and late-maturing females directed towards their own young. In general, early-maturing females were less attentive to their young than were late-maturing gerbils. The results of the present studies suggest that such differences in maternal behavior may reflect differences in the emotional response of early- and late-maturing female gerbils to their own young.

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