Male Copulatory Behavior and Female Maternal Behavior in Neonatally Bulbectomized Rats

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ALTHOUGH the rat is typically considered a macrosmatic species, bilateral olfactory bulbectomy or peripherally induced anosmia have been found to induce relatively mild deficits in the male's copulatory behavior [2, 5, 13, 16, 17]. These findings may be contrasted with the virtual abolition of sexual behavior following neonatal or adult bulbectomy in the male hamster [24, 33] and adult bulbectomy in the mouse [10, 26, 27]. Several lines of evidence suggest, however, that while the effects of adult bulbectomy may be relatively minor in the rat, disruption of the olfactory system during development may have more dramatic consequences.

Studies performed by Marr and his colleagues have indicated that the odor to which pups are exposed during the prepuberal period may influence the animal's sexual and social preferences in adulthood [21,22]. Such a process of olfactory imprinting [9] would require the rat to possess a functional olfactory system at an early age. Schapiro and Salas [28] have presented evidence that the rat pup is capable of responding to odors as early as day 2 postpartum and Leon and Moltz [18] have found that the lactating rat emits a maternal pheromone between days 14 and 27 postpartum. Despite these suggestions that olfactory stimulation early in life might be important for the development of normal adult sexual and maternal behaviors [21] few studies have examined the effects of neonatal bulbectomy in the rat. This appears to be due, at least in part, to the high mortality rates among young rats subjected to surgical interference with the olfactory system [15, 30, 31].

Kling [15] examined the effects of various neonatal brain lesions on the development of both male and female rats. He reported that four males subjected to bilateral transection of the olfactory stalk (at an average age of 5.7 days) failed to copulate during adulthood. The presence of a seminal plug was used as the criterion for successful copulation. The testes wt/body wt. ratios were unaffected in these animals, an indication that disruption of the hypothalamic-gonadal axis was not responsible for the absence of sexual activity. Unfortunately, no observations of copulatory behavior were reported, and Beach [3] has criticized the use of plug counts as a possibly misleading index of sexual vigor.

It is well known that olfactory bulbectomy may precipitate a variety of behavioral alterations similar to those following damage to a number of other limbic structures [20]. To test for these presumably nonolfactory effects of bulbectomy, Orbach and Kling [25] attempted to induce anosmia in 6–10 day old rat pups by destruction of the olfactory mucosa by injection of a drop of 10% Formalin into the nostrils, or by electrical coagulation or aspiration of the mucosa. When tested as adults, only 7/32 treated males (as compared to 6/9 control animals) were found to

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have impregnated females. The results of this study are somewhat difficult to assess. The olfactory mucosa is capable of rapid regeneration [29], suggesting that Orbach and Kling's animals may not have been anosmic when tested as adults.

In a recent investigation, Wilhelmsson and Larsson [32] reported that male rats socially isolated from day 10 and bilaterally bulbectomized at day 30 (prepuberally) exhibited no sexual activity as adults. When the surgical procedure was not combined with social or sexual deprivation, a large proportion of the subjects still failed to mate. In contrast, Bermant and Taylor [5] reported that almost all postpuberally bulbectomized (but previously sexually inexperienced) males would initiate copulation. The trend thus appears to be for lesions produced relatively early in ontogeny to exert the strongest deleterious effects on adult sexual behavior, possibly as a result of disrupting an activation of the olfactory bulbs on the hypothalamus and limbic system [16,19].

Experiments 1 and 3 of the present report assessed the effects of bulbectomy on the sexual behavior of male rats when the operation was performed during the neonatal period. Our initial expectations were that severe copulatory deficits would follow such a procedure. Instead, the sexual behavior of neonatally bulbectomized males was found to be essentially normal.

Experiments 2 and 4 examined the consequences of neonatal bulbectomy on maternal behavior in the female rat. Studies of Beach and Jaynes [41] and Herrenkohl and Rosenberg [14] suggested only minor effects of bulbectomy when performed on the lactating or late pregnant female. Fleming and Rosenblatt [11,12] have reported that 50% of bulbectomized rats will cannibalize their own or foster litters if the operation is performed on the virgin female. Bathing the olfactory epithelium with a zinc-sulfate solution induces anosmia by coagulation necrosis of the olfactory receptors. The advantage of such a procedure lies in the fact that the olfactory bulbs themselves are spared. Zinc-sulfate treatment, unlike olfactory bulbectomy, does not potentiate cannibalism in the virgin rat [11,12]. The contribution of the olfactory bulbs to maternal behavior therefore appears to involve more than the mediation of olfactory information.

Kling [15] reported that 3/6 female rats sustaining bilateral transactions of the olfactory stalk (at an average of 5.7 days of age) failed to rear young successfully. Females sustaining only unilateral or incomplete stalk transactions were not deficient in this capacity (4/4 rearing their young to weaning). Due to the small number of subjects this difference was not statistically significant, but the results do suggest a severe disruption of maternal behavior following damage to the olfactory system in infant rats. While confirming Kling's report of delayed sexual development, Experiments 2 and 4 of the present report found no evidence of an impaired maternal responsiveness in neonatally bulbectomized female rats.

**EXPERIMENT 1**

**Method**

Six Long-Evans female rats (Blue Spruce Farms, Altamont, N.Y.) were mated with males and then housed in individual plastic cages. All females were permitted to give birth normally, and the litters were not disturbed until day 6 postpartum, at which time female pups were discarded and each male pup subjected to one of the following treatments: (a) bilateral olfactory bulbectomy (n = 14); (b) sham olfactory bulbectomy (n = 10); and (c) unoperated control (n = 10). Each litter contained animals belonging to each of the conditions.

All surgery was carried out with the aid of a dissecting microscope. Pups were anesthetized by cooling in crushed ice. A small hole was opened in the skull overlying each of the olfactory bulbs (which are clearly visible through the skull of pups of this age). A blunt 20-gauge hypodermic needle was then inserted and the olfactory bulbs removed by aspiration. To minimize the possibility that some olfactory fibers remained intact, the posterior aspect of the cribiform plate of the ethmoid bone was thoroughly scraped. Sham operations were subjected to the same procedure except that the aspirator was not activated and no neural tissue was damaged. Unoperated pups were separated from their mothers for the same length of time as were their operated littermates but were subjected to neither surgery nor anesthesia. All wounds were closed with sutures and covered with a protective antiseptic covering (Nowskin). Pups were returned to their mothers only after complete recovery from anesthesia. At 21 days animals were housed singly in wire mesh cages.

Beginning at 56 days, all animals received four, biweekly, 15-min tests for sexual behavior. Subjects were allowed 15 min to adapt to the 26 x 50 x 30 cm aquarium which served as a test chamber. At the end of this period a female stimulus, previously ovariectomized and implanted with a 15-mg pellet of estradiol benzoate, was introduced. The occurrence of mounts, intromissions, and ejaculations were scored on an event recorder. All testing was administered during hours 2–5 of the 12-hr dark phase (lights out at 1200 hr). The weight and age at which an animal's first intromission and ejaculation occurred were noted and, in addition, the weight of each animal was recorded when 70 days old.

**Results**

Only 4/14 bulbectomized and 1/10 sham bulbectomized pups died prior to weaning. At this time, bulbectomized males were found to be significantly retarded in somatic development as indicated by body weight (F = 22.46; df = 2,26; p<0.001). While unoperated pups weighed 57.2 ± 1.56 g (mean ± S. E.), bulbectomized pups weighed only 37.6 ± 3.23 g. Sham bulbectomy produced no significant decrement in weaning weight (54.9 ± 1.4 g). The weaning weight differences between bulbectomized and unoperated and sham operated groups were significant beyond the 0.01 and 0.025 levels, respectively (Scheffé's test). These relationships were virtually unchanged when body weight at 70 days was considered. The mean weights for bulbectomized, sham bulbectomized, and unoperated animals were 308 ± 10.4, 381 ± 8.4, and 392 ± 7.3 g respectively.

Table 1 indicates that no significant differences existed in the mean age at which the first intromission or ejaculation was observed among animals that did achieve intromission or ejaculation in the three groups. Although the differences in body weight at the time of first intromission and ejaculation were not statistically significant, the former measure did approach significance (p<0.10). In addition, there were no significant differences among the three groups in the percent of subjects achieving intromission or
TABLE 1

<table>
<thead>
<tr>
<th></th>
<th>At First Intromission</th>
<th>At First Ejaculation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Age (days)</td>
</tr>
<tr>
<td>Bulbectomized</td>
<td>10</td>
<td>84.1 ± 6.28</td>
</tr>
<tr>
<td>Sham-operated</td>
<td>7</td>
<td>73.1 ± 5.72</td>
</tr>
<tr>
<td>Unoperated</td>
<td>10</td>
<td>82.5 ± 6.46</td>
</tr>
<tr>
<td>F ratio</td>
<td>0.76</td>
<td>2.50</td>
</tr>
</tbody>
</table>

*Only data from males that gained intromission or ejaculation are included. †p<0.10

EXPERIMENT 2

Method

Animals were the female offspring of six Long-Evans rats mated in our laboratory and treated as described in Experiment 1, except that at 6 days of age male pups were discarded. Female pups were then assigned to one of two groups: (a) bilateral olfactory bulbectomy (n = 29); and (b) sham bulbectomy (n = 8). Each litter contained animals in both conditions. Surgical procedures were identical to those described in Experiment 1, as were housing conditions and age at weaning.

At the time of weaning, each pup was weighed and housed in a wire mesh cage containing 4–5 animals belonging to the same experimental group. Beginning at 30 days of age, each animal was examined daily for the occurrence of vaginal opening. Both the weight and age of the subjects at the time of vaginal opening were noted.

At 60 days, seven sham-operates and six bulbectomized females were placed individually in clear plastic maternity cages. Two weeks later, each female was presented with one, 1–2-day-old female pup for a period of 4 hr. At the end of this period, the pups were removed and examined for evidence of mutilation or cannibalism.

At 100 days of age, each of the animals was mated and returned to the home cage. Following parturition, pups were examined daily for the presence or absence of milk in the stomach and for evidence of cannibalism. On day 21 postpartum, all pups were weighed.

Results

One sham-operated and eight bilaterally bulbectomized animals died prior to weaning. There were no other mortalities during the course of the experiment. Table 2 indicates that at the time of weaning, the mean body weight of bulbectomized females was significantly below that of sham-operated females. At the time of vaginal opening, this difference persisted even though vaginal opening was delayed an average of 4.4 days in the bulbectomized group.

During the 4-hr exposure to the two strange pups, no animal in either group mutilated or otherwise harmed those pups. Following the delivery of the female’s own litter, milk was observed in the stomachs of all pups by day 2 post partum. At the time of weaning, bulbectomized females had an average of 11.2 ± 0.40 pups/litter weighing an average of 42.9 ± 0.80 g each. The comparable figures for the litters of sham operated females were 11.4 ± 0.43 and 43.1 ± 0.89. The number of pups per litter noted at weaning was identical to the number of pups recorded within 24 hours of parturition. If any cannibalism did occur, it was apparently minimal and occurred within 24 hr of delivery.

As in Experiment 1, the animals were sacrificed following the completion of the study and their brains examined in situ. Of the 21 surviving bulbectomized females, bulbectomy was virtually complete in 16; no neural tissue was observed anterior to the frontal poles. Slight damage to the frontal cortex was observed in 3 animals. The remaining two females had complete destruction of one bulb, but only half of the contralateral bulb had been removed. In all of these cases, however, the ventral surface of the bulbs had been severely damaged, indicating that the olfactory deficit must have been, at the very least, severe.

EXPERIMENT 3

Experiment 1 provided evidence that olfactory bulbectomy performed early in life exerts little effect on the development of the capacity for sexual behavior in the male rat. Experiment 3 was performed in an attempt to determine the nature of any more subtle deficits in copulatory
behavior that might have been induced by the experimental procedure but which we were unable to ascertain due to the brief (15 min) tests. Tests of olfactory capacity provided behavioral confirmation of the surgically induced anosmia.

Method

Two litters of pups served as experimental animals in the present study. Six male pups (2 pups selected at random from each of 3 litters at the time of weaning) served as unoperated controls. Bilateral olfactory bulbectomies were performed on day 6 postpartum on the 9 males provided by the 2 experimental litters. The female littermates were not discarded but received the same surgical intervention. Data concerning the females will be presented in Experiment 4.

Animals were weaned at 21 days and housed 3 animals per 17 × 40 × 17 cm wire mesh cage until 77 days of age, at which time the animals were housed singly in 17 × 24 × 17 cm mesh cages. Beginning at 90 days of age, each male was given the first of 2 1-hr tests for sexual behavior. Stimulus females for these tests were implanted with a 5 mg pellet of estradiol benzoate. Seven days separated the two test sessions. Mounts, intromissions, and ejaculations were transcribed on an event recorder.

Regresses were subsequently analyzed and the following measures of copulatory activity computed: mount latency (ML) – the latency from the introduction of the female to the first mount; intromission latency (IL) – the period from the introduction of the female to the first intromission; intromission frequency (IF) – the number of intromissions preceding ejaculation; interintromission interval (III) – the mean interval between successive intromissions within an ejaculatory series; ejaculation latency (EL) – the time from the first intromission of a series to the occurrence of ejaculation; postejaculatory intromission latency (PEI) – the duration of the period extending from ejaculation to the next intromission; and, ejaculation frequency (EF) – the number of ejaculations achieved during each 1-hr test.

Following the second test session, all animals were placed on a 23-hr food deprivation schedule and administered a series of tests to determine the extent of any olfactory deficit. The procedure (based on that described by Alberts and Galef [11]) involved placing a male in a plastic cage, the floor of which measured 21 × 43 cm and was covered with approximately 6–8 cm of wood shavings. The animal’s task was to locate within 5 min 1/3 of an Oreo cookie buried under the shavings. If the animal failed to locate the cookie in the allotted time, it was retrieved by the experimenter and placed on top of the shavings. Control males were tested until they had located the cookie on 5 successive days. Bilbectomized males were tested either until they found the cookie on 5 successive days or for 5 days longer than was required by the last control male to reach criterion.

At the completion of olfactory tests, the animals were again fed ad lib for two weeks, at which time they were given a lethal dose of Equithesin and perfused with 0.9% saline and Formalin. The bone overlying the olfactory bulbs was subsequently removed and the brains examined in situ to determine the extent of damage.

Results

Five of the nine bulbectomized males survived the surgical procedures and, of these, 3 failed to locate the cookie even once (Table 3). One male (No. 7) may or may not have been anosmic; he located the stimulus on Days 5 and 12 of the 15 days of olfaction tests. Microscopic examination revealed that although only about 1/2 of the bulbs (in an anterior-posterior plane) had been removed in this animal, there had been essentially complete destruction of the ventral surface of these structures. Male 11 demonstrated substantial retention of olfactory capacity, locating the stimulus on 6/15 days. This male was found to be essentially hemibulbectomized, one bulb being almost completely destroyed, while only minor damage to the anterior aspect of the second bulb was noted. A third male (No. 8) sustained complete destruction of the olfactory bulbs and in addition, massive damage to the frontal lobes. In the remaining 2 animals, bulbectomy was complete with negligible damage to the adjacent neocortex.

On the initial sex test, 2/6 control and 1/5 bulbectomized males achieved ejaculation. The single bulbectomized male displaying the response was the male (No. 11) with the least amount of bulb damage. Data from the second sex test are presented in Table 3.

The most striking feature of these data is the absence of differences between the groups. The single bulbectomized male sustaining massive damage to frontal lobe tissue is the only animal in this group for which some scores (ML, IF,
### TABLE 3
MEASURES OF MASCULINE SEXUAL BEHAVIOR OBTAINED FROM CONTROL AND NEONATALLY BULBECTOMIZED MALE RATS DURING THE SECOND 1 HR SEX TEST*

<table>
<thead>
<tr>
<th>Animal</th>
<th>ML (sec)</th>
<th>IL (sec)</th>
<th>IF</th>
<th>III (sec)</th>
<th>ELI (sec)</th>
<th>PEI (sec)</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>39</td>
<td>39</td>
<td>14</td>
<td>89</td>
<td>1245</td>
<td>460</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>140</td>
<td>252</td>
<td>10</td>
<td>153</td>
<td>1532</td>
<td>896</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>Noncopulator</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>163</td>
<td>1420</td>
<td>8</td>
<td>69</td>
<td>1420</td>
<td>548</td>
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<td>5</td>
<td>928</td>
<td>1201</td>
<td>13</td>
<td>110</td>
<td>1424</td>
<td>432</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>Noncopulator</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 (2)</td>
<td>6</td>
<td>189</td>
<td>13</td>
<td>153</td>
<td>1993</td>
<td>746</td>
<td>1</td>
</tr>
<tr>
<td>8 (0)</td>
<td>1010</td>
<td>1010</td>
<td>18</td>
<td>120</td>
<td>2164</td>
<td>815</td>
<td>1</td>
</tr>
<tr>
<td>9 (0)</td>
<td>308</td>
<td>308</td>
<td>8</td>
<td>143</td>
<td>1146</td>
<td>761</td>
<td>2</td>
</tr>
<tr>
<td>10 (0)</td>
<td>72</td>
<td>72</td>
<td>6</td>
<td>154</td>
<td>927</td>
<td>710</td>
<td>2</td>
</tr>
<tr>
<td>11 (6)</td>
<td>20</td>
<td>20</td>
<td>7</td>
<td>259</td>
<td>1816</td>
<td>693</td>
<td>1</td>
</tr>
</tbody>
</table>

*BNumbers in parentheses indicate the number of days on which a bulbectomized animal located the stimulus during the 15 days of anosmia testing. Behavioral measures with the exception of EF are for first ejaculatory series. ML = mount latency; IL = intromission latency; IF = intromission frequency; III = interintromission interval; ELI = ejaculation latency from first intromission; PEI = postejaculatory interval; and EF = ejaculation frequency.

and ELI) fell outside the range of those for control animals. IL, III, PEI, and EF all were within the range exhibited by control animals. In considering the ML and IL, it should be remembered that if 900 s passed without intromission, a new female was introduced. This procedure was applied to the two noncopulating controls as well as to control male No. 5. Only male No. 8, among the operated animals, required this additional stimulation. The only difference between the groups that approached statistical significance was in III (t = 1.9; df = 7; 0.05 < p < 0.10). With the exception of male 8, there appeared to be virtually no relationship between any copulatory measure and the extent of damage to neural tissue.

The failure of bulbectomized animals to locate the stimulus during olfaction tests was not a consequence of a motivational deficit. All animals appeared to search actively during the tests. When the cookie was retrieved by the experimenter at the end of the last 8 tests and shown to the subject, it was invariably seized and eaten with 10 sec.

### EXPERIMENT 4

This experiment replicated the findings, reported in Experiment 2, of normal maternal behavior in adult female rats following bilateral olfactory bulbectomy in infancy and, in addition, provided behavioral data on the extent of the olfactory deficit induced by this procedure.

**Method**

Animals were the littersmates of the males described in Experiment 3. As in the previous study, 6 control females were selected at random from the 3 control litters. Thirteen female pups from the two experimental litters received bilateral olfactory bulbectomies. Housing conditions were as described previously until the animals were approximately 90 days of age. At this time, each female was transferred to a clear plastic maternity cage. Two weeks later, each female was presented with two foster pups 1–2 days old, and the occurrence of retrieving, crouching, and cannibalism were noted every 1/2 hr for 4 hr.

The day following these tests females were permitted to mate with males introduced into each cage for a period of 10 days. On the day of delivery of a litter the number of pups per litter and the weight of the litter were recorded. The number of pups surviving to weaning and the litter weight at the time of weaning were noted on day 23 postpartum.

Three weeks after the weaning of their litters, each female was placed on a 23 hr food deprivation schedule and 2 days later administered the first of the cookie tests to determine the extent of any olfactory deficit. The last control female to reach the criterion of locating the cookie on 5 successive days did so after 18 trials. Bulbectomized females were therefore tested for 23 trials. Following the last trial, all animals were fed ad lib for 2 weeks and then sacrificed. Histological procedures were as described in Experiment 3.

**Results**

Nine of thirteen experimental animals survived the neonatal bulbectomy. Of these, one female was found to retain substantial olfactory sensitivity, locating the stimulus on 10 successive days of the anosmia tests. Histological examination confirmed that in this female one of the bulbs sustained only minor damage while the other was completely
destroyed. A second female located the cookie on 2/23 (nonsuccessive) days of anosmia testing. Bullectomy was found to be virtually complete in this animal. The remaining 7 experimental females were classified as completely anosmic according to the criterion of this test. We had initially planned to ascertain the distance which the bulbs protruded from the frontal poles as an approximate measure of olfactory bulb damage in both Experiments 3 and 4.

3 In animals in the present study, however, it was noted that what appeared under gross visual inspection to be bulb tissue was in fact cortical tissue. Although in some instances, this tissue occupied almost all of the space normally occupied by the olfactory bulbs, there was no division between bulbs and cortex such as existed in the unoperated or sham operated animals. Serial sections of this tissue were made from the brain of one animal that exhibited this phenomenon most markedly. It was found that bullectomy had in fact been complete and that what appeared at gross examination to be olfactory tissue was in fact neocortical. This identification was made independently by three observers.

When the experimental females were presented with 2 foster pups each, 7/9 were found to retrieve and crouch over the pups within one hour. Of the remaining 2 experimental animals, one seemingly ignored the pups, leaving them scattered around the cage while the last subject devoured part or all of both pups. The attacks on the pups were initiated with a latency of less than one minute. The cannibalizing female was verified as completely bullectomized by both behavioral and histological criteria, except that the right frontal cortex completely filled the space normally occupied by the right olfactory bulb. No control females cannibalized the foster young and 3/6 females were observed to retrieve and crouch over the pups within 1 hr after the introduction of the stimulus pups.

When permitted to mate with stud males, 7/9 bullectomized and 5/6 control females became pregnant. Of these, all females successfully reared their litters to weaning. Data on the number and weight of pups are presented in Table 4. There were no significant differences in the number of pups observed either on the day of birth or day 23. Litter weights also did not differ significantly on either the day of birth or the day of weaning.

<table>
<thead>
<tr>
<th></th>
<th>Mean Litter Weight</th>
<th>Mean Number of Pups per Litter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day 0</td>
<td>Day 23</td>
</tr>
<tr>
<td></td>
<td>467.6 ± 32.78</td>
<td>10.0 ± 0.32</td>
</tr>
<tr>
<td></td>
<td>532.0 ± 32.10</td>
<td>9.5 ± 0.73</td>
</tr>
<tr>
<td></td>
<td>1.33</td>
<td>0.51</td>
</tr>
<tr>
<td>Mean</td>
<td>0.72</td>
<td>0.16</td>
</tr>
</tbody>
</table>

*Statistical analyses based upon 13 litters and 11 df; p > 0.10 in all cases.

DISCUSSION

The results of Experiments 1 and 3 clearly indicate that although somatic development may have been retarded, neonatal disruption of olfactory stimulation (at least after day 6) does not preclude the development of mating behavior in male rats. The efficacy of the surgical procedures used in these studies in producing permanent anosmia or severe hyposmia was confirmed in Experiments 3 and 4.

The results of Experiment 2 confirmed a previous finding [15] that disruption of the olfactory system delays the age of vaginal opening in rats. There was, however, no evidence that neonatal bullectomy inhibited the development of normal maternal behavior. Earlier reports have indicated that bullectomy induces cannibalism when performed on virgin, but not late pregnant or lactating, female rats [4, 11, 12, 14]. It is apparent that the effects of bullectomy on maternal behavior are strongly influenced by the age, hormonal condition, and previous maternal experience of the animal at the time of surgery.

The failure to find significant differences among the groups in the percentages of males copulating or on any of the various parameters of sexual activity (Tables 1 and 3) contrasts with the highly significant reduction in mating by prepuberally bullectomized rats reported by Wilhelmsson and Larsson [32]. Although they received opportunities for sexual experience prior to testing and were permitted 65 days to recover from nonspecific effects of the ablations, Wilhelmsson and Larsson's animals still exhibited severe deficits in copulatory activity. Our own animals received at least a 50 day surgery-test interval and were not permitted access to females from either 6 or 23 days of age until testing at 56 or 90 days. The apparently normal sexual behavior seen in these rats is, therefore, probably a consequence of the early age at which the ablations were performed rather than of the relatively long period of time allowed to elapse between surgery and subsequent sex behavior tests.

We observed an extremely high incidence of crouching and retrieving when both experimental and control virgin females in experiment 4 were tested with foster pups. For the 2 weeks prior to these tests, the females had been housed on a shelf occupied by other lactating females. The exposure of the virgin animals to the odors and sounds of
the nearby lactating females and their litters may have contributed to the extremely rapid induction of maternal behavior which we observed.

The present results suggest that olfactory stimulation after day 6 is not critical for the development of essentially normal sexual and maternal behavior in male and female rats respectively. The conclusion does not follow, however, that olfaction is unimportant in the normal development and expression of sexual and maternal responsiveness in this species. Male rats are known to use olfaction in discriminating between estrous and nonestrous female rats [6, 7, 8] and the odor to which males are exposed during the prepuberal period influences the choice of a given female for copulation [21]. In regard to maternal adequacy, Mena and Grosvenor [23] have demonstrated that olfactory stimuli are capable of eliciting the release of prolactin from the anterior pituitary of lactating female rats. In the absence of olfactory stimulation, however, prolactin release was triggered by cues from other sensory modalities. Our own neonatally bulbectomized females apparently suffered little or no difficulty with lactation since the weights of their pups were comparable to or greater than the weights of pups from sham-operated mothers.

The fact that a response is elicited by nonolfactory stimuli in the anosmic rat does not preclude the possibility that the response is under at least partial olfactory control in the normal animal. The absence of gross pathology in the sexual and maternal behavior of neonatally bulbectomized rats may reflect the availability of alternative developmental routes to essentially normal adult behavior.

REFERENCES