

THE DIFFERENTIAL EFFECT OF ANOSMIA ON MATERNAL BEHAVIOUR IN THE VIRGIN AND PRIMIPAROUS RAT

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(Received 26th October 1971, accepted 11th February 1972)

Following removal of their olfactory bulbs, virgin female rats consistently attack and kill rat young whereas non-lactating anosmic primiparous animals do not. The present studies were undertaken to compare the effects of bulbectomy on maternal behaviour in the parous and virgin female rat, and to analyse those experiences responsible for the marked behavioural differences towards young seen in these two groups.

Adult female Wistar rats, maintained by random breeding within a closed colony in the laboratory of M. X. Zarrow since 1949 (W/Z strain), were individually housed in 15 × 10 × 7 in. stainless steel cages under a 13-hr light/11-hr dark regimen (lights on at 07.00 hours), and at an ambient temperature of 70 to 74° F. Food and water were freely supplied. The virgin and non-lactating rats were screened for retrieval and cannibalism by placing three 1- to 2-day-old young into each cage for a 24-hr period. Observations were made for the first 20 min and again the next morning. All rats displaying retrieval or attack of young were excluded.

Bilateral bulbectomy was accomplished under ether anaesthesia by drilling a small hole in the skull just anterior and medial to the eyes. The membrane was then broken and the bulbs removed with suction. Gel foam was inserted to fill the space, and the incision was sutured. The same procedure was followed with animals subjected to sham operation, except that the bulbs were not disturbed following the breaking of the membrane. At the termination of testing, the animals were killed and their brains were macroscopically examined to determine the presence of olfactory bulb tissue.

In the initial experiment, the bulbs were removed from ten virgin and ten non-lactating primiparous rats. Bulbectomies were performed on the primiparous rats approximately 1 month after the litters were weaned. A comparable number of control rats were subjected to sham operation. Twenty-four hours later, three 2-day-old young were introduced, and the adults were observed for 15 min. The young were left in the cages overnight and the adults were again observed the next morning. Females were scored as maternal if they retrieved all the young within 15 min and thereafter were seen to crouch over

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them. Any animal that attacked and killed one or more young was considered a cannibal, whether or not the young were completely eaten.

Eight of the ten bulbectomized virgins killed and ate the young within 24 hr of the young being placed in the cage (Table 1, Group 1) while none of the control virgins attacked any young (Group 2). In marked contrast to the bulbectomized virgins, only one of the bulbectomized primiparous females showed cannibalistic behaviour, while four others displayed maternal behaviour toward young within 24 hr (Group 3). The difference in killing incidence between the two bulbectomy groups is significant at the 0.01 level, using the Fisher Exact Probability Test. One of the control primiparous rats killed all of her young, while three of the others in this group were seen to retrieve and huddle over young within 24 hr (Group 4). At autopsy, no olfactory bulb tissue was found on gross inspection in any of the experimental animals.

TABLE 1
BEHAVIOUR OF ANOSMIC AND CONTROL FEMALE RATS TOWARD YOUNG

Group	Reproductive state	Treatment	Effects	
			Cannibalism*	Retrieval*
1	Virgins	Bilateral olfactory bulbectomy	8/10	
2		Sham operation	0/10	
3	Primiparous	Bilateral olfactory bulbectomy	1/10	4/10 (within 24 hr)
4		Sham operation	1/10	3/10 (within 24 hr)
5	Virgins	Sensitized by exposure to young; bilateral olfactory bulbectomy	1/14†	14/14 (within 7 days)
6		Sensitized by exposure to young; sham operation	0/10	10/10 (within 7 days)

* Number of rats responding/number of rats used.

† The rat that initially killed some young began to retrieve the remainder by the 7th day.

The markedly different behaviour exhibited towards young by anosmic virgin and anosmic primiparous females implicated (a) the hormonal environment of pregnancy, and (b) the experiences of parturition and the presence of young. We therefore examined the influence of these factors before bulbectomy on subsequent maternal behaviour.

Twenty-nine virgin rats were screened for absence of retrieval or cannibalism at 90 to 100 days of age. They were then sensitized to young by being exposed continuously to three, aged 2 to 7 days, until all the young were retrieved within 15 min. The maximum period of contact permitted with young was 2 weeks; twenty-four animals were sensitized within this time. Fourteen were then bulbectomized and the remaining ten subjected to sham-operation. Twenty-four hours later, young were reintroduced and adults observed for the presence of maternal behaviour.

Only one of the fourteen sensitized bulbectomized virgin females attacked and cannibalized the young (Group 5 in Table 1). This difference is significant at the 0.01 level when compared with the bulbectomized virgins in Group 1. In group 5, seven females retrieved within 24 hr, and all fourteen animals were retrieving within 7 days. None of the control animals killed young, while nine retrieved spontaneously, and the tenth rat retrieved young about a week later (Group 6).

We then examined animals with a normal pregnancy but with no experience of parturition or of young before bulbectomy. Since Moltz, Robbins & Parks (1966) have shown that delivery by Caesarean section of primiparous rats near term does not interrupt normal maternal behaviour when young are presented up to 24 hr later, this procedure was used.

Sixteen virgin female rats were screened and the time of mating was noted. On the 22nd day of gestation, ten animals were bulbectomized, delivered by Caesarean section, and their young were discarded. The remaining six rats

TABLE 2
BEHAVIOUR OF ANOSMIC AND CONTROL PRIMIPAROUS RATS TO YOUNG
FOLLOWING CAESAREAN SECTION

Reproductive state	Treatment	Effects		
		Cannibalism*	Retrieval*	Litter reared*
Virgins	Bilateral olfactory bulbectomy and Caesarean section	0/9	9/9	7/9
Virgins	Sham bilateral olfactory bulbectomy, and Caesarean section	0/9	6/6	5/6

* Number of rats responding/number of rats used.

were subjected to sham bulbectomy and delivered by Caesarean section. Twenty-four hours later, each female was provided with four normally delivered 1- to 2-day-old young. Adults were then observed and the subsequent survival of the litter for the next few days was noted.

One animal was discarded from the experimental group because olfactory tissue was found at autopsy. Of the remaining nine, all retrieved their pups and seven of nine successfully reared litters (Table 2). In the control group, all animals retrieved immediately and five of the six reared litters successfully.

These results indicate that the display of lack of maternal behaviour and the display of cannibalism by the virgin rat following loss of olfaction is due (1) to the lack of previous experience of the animal since the sensitized rat does not attack young of its own species after bulbectomy, and (2) to the physiological changes involved in gestation since a pregnancy without exposure to young has the same effect. This raised the possibility that two factors are involved, a non-hormonal and a hormonal set of events. If cannibalism partially reflects lack of maternal behaviour, then the situation may be related to the

non-hormonal (Rosenblatt, 1967) as well as the hormonal (Moltz, Lubin, Leon & Numan, 1970; Zarrow, Gandelman & Denenberg, 1971) bases for maternal behaviour in the rat.

This study was aided in part by grant MH 19716 from the National Institute of Mental Health.

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