Male Rat Pups Are More Hesitant to Urinate in Response to Anogenital Stimulation Than Are Their Female Sibs

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Male rat pups required more anogenital stimulation before they began to urinate than did their sisters and males produced more urine than their female sibs during a fixed period of anogenital stimulation. These findings are interpreted as consistent with the view that neonatal mammals can manipulate the behavior of their dams.

Male rat pups are recipients of more anogenital stimulation by their dams than are their female sibs (Moore & Morelli, 1979). The additional anogenital stimulation that males receive as infants may contribute to development in adulthood of more effective masculine sexual behaviors (Moore, 1983).

In infancy, anogenital licking of pups facilitates both urine production and secretion (Capek & Jelinek, 1956). Consequently, anogenital licking of pups provides hypotonic sodium solution to dams (Friedman, Bruno, & Alberts, 1981; Gubernick & Alberts, 1983, 1985).

Alberts (1983) has suggested that anogenital licking of pups by dams may be influenced by the salt appetite of lactating females. Lactating females may be motivated to anogenital licking of their pups by the dilute saline rewards pups provide. From Alberts' perspective, the flow of milk from dams to pups and of sodium solution from pups to dams are parts of a symbiotic, mutually beneficial exchange of resources within a cooperative unit comprising mother and litter.

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Received for publication 8 May 1987
Revised for publication 7 September 1987
Accepted at Wiley 24 February 1988

Developmental Psychobiology 22(1):81–85 (1989)

CCC 0012-1630/89/010081-05$04.00

There is an alternative, more Machiavellian, view of the relationship between a rat dam and her litter. Galef (1981), following Trivers (1974), has argued that neonates manipulate the behavior of their dams to their own advantage. In the case of anogenital licking of rat pups by their dams, if, as Moore's (1983) data suggest, male pups stand to gain more from prolonged bouts of maternal anogenital licking than do their sisters, one might expect male pups to attempt to influence their mothers so as to divert the majority of anogenital licking to themselves. Such elicitation of maternal attention might be achieved in several ways: Relative to females, males could increase the magnitude of the reinforcement they provide to dams by delivering either more urine or more attractive urine to their dams than do their sisters. Moore (1981, 1982) has previously provided evidence consistent with the view that the odor of the urine of male rat pups is more effective in eliciting licking than is the odor of the urine of female rat pups. Males could also increase the amount or duration of anogenital stimulation they receive by increasing the amount of anogenital licking they require before delivering reinforcement to their dams.

Of course, if female reproductive performance in adulthood were impaired by excessive anogenital stimulation in infancy, one would predict that females might reduce the anogenital licking they receive by producing small quantities of unattractive urine in response to little stimulation. Our discussion will be oriented toward male pups because there is evidence (Moore, 1983) that they benefit from maternal anogenital stimulation in infancy and no evidence that females are harmed by it.

In the present experiment, we examined the possibility that male rat pups: (a) produce more urine during a fixed bout of anogenital stimulation than do their sisters and (b) require greater durations or amounts of anogenital stimulation before beginning to urinate than do their sisters.

Method

Subjects

Subjects were 10 litters of 4- to 5-day-old Long-Evans rat pups born in the McMaster colony to females descended from stock acquired from Charles River Canada (St. Constant, Quebec). Litters were culled to 10 pups/litter (4 to 6 males and 4 to 6 females) on the day of birth and both they and their dams were maintained in plastic shoe-box cages on ad lib Purina Laboratory Rodent Chow and water in a colony room on a 12 hr light/dark cycle.

Procedure

On the day of testing (4–5 days of age), a litter was removed from its dam and the pups placed, for 20 min, in individual containers floating in a constant-temperature bath maintained at 36.5°C. At the end of this 20-min period, each pup was removed from its container held ventral-side-up by the experimenter for 10 sec, and then stroked at a rate of 3 strokes/sec with a small piece of blotting paper until the pup started to urinate. Stroking was continued for 30 sec. This first period of stimulation was introduced both to void the bladder of each subject and to make

each subject familiar with the experimental procedure. Each pup was next toe-clipped for permanent identification and its sex recorded. Pups were then returned to their individual compartments in the constant-temperature bath for 1 hr.

At the end of this 1-hr period of isolation, each pup was again held ventral-side-up for 10 sec, stroked with a small (.7 g) piece of blotting paper (previously weighed to the nearest .001 g on an analytical balance) at a rate of 3 strokes/sec until 30 sec after it had begun to urinate, and then returned to its mother. The experimenter recorded both the time to initiation of urination and the weight of the piece of blotting paper at the end of the 30-sec period of subsequent stimulation.

Ten to twelve days after completion of the experiment, each pup was again examined to ensure that its sex at 4–5 days of age had been properly identified.

Data Analysis

To control for litter effects, we calculated both the mean latency to urinate of the male and female pups in each litter and the mean amount of urine produced by male and female pups in each litter. We then used the Wilcoxon Matched-Pairs Signed Ranks Test (Siegel, 1956) to establish the reliability across litters of differences in the mean scores of male and female pups within litters.

Results

The main results of the present experiment are presented in Figure 1 which shows: (left-hand panel) the mean latency of male and female subjects to begin to urinate in response to the second bout of anogenital stimulation and (right-hand panel) the mean amount of urine produced by male and female subjects in the 30

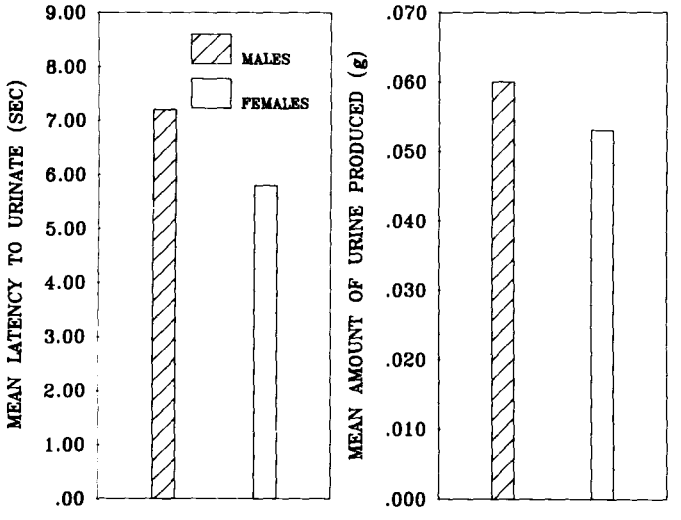

Fig. 1. Mean latency to urinate (left-hand panel) and mean amount of urine produced during 30 sec of anogenital stimulation (right-hand panel) by male and female rat pups 4 to 5 days of age. N = 10/group.

sec after each started to urinate during the second period of stimulation. In 9 of our 10 litters, the mean latency of males to begin to urinate was greater than that of their female sibs (Wilcoxon test, T, = 3, $p < .005$). We also observed that males excreted a reliably greater mean amount of urine in response to 30 sec of anogenital stimulation than did their female sibs ($T = 7$, $p < .025$).

Discussion

The results of the present experiment are in accord with predictions based on the hypothesis that male rat pups, relative to female rat pups, induce their dams to provide them with extra anogenital stimulation by manipulating the schedule of saline reward they provide to their dams. Preferred rewards (Moore, 1981), larger amounts of reward, and higher variable-ratio or variable-interval schedules of reward are provided to dams by male rat pups than by their sisters. Each might be expected to energize or direct the licking behavior of mothers.

Although the present results are consistent with predictions based on a view of the rat pup as a manipulator of its dam, they do not, of course, prove the validity of that view. It is, for example, possible, that the differences in male and female response to anogenital stimulation reported here have nothing to do with manipulation of dams by pups. Differences in the structures of the urinary tracts of male and female rat pups may suffice to explain the small but reliable differences we observed. Furthermore, we have not shown that small differences in the responses of rat pups to anogenital licking actually shape their dam's behavior. Neither have we shown that a dam's rate of licking her pups actually affects their adult reproductive success. Still, it is surely intriguing that differences in the responses of male and female rat pups to anogenital stimulation are consistent with predictions based on the assumptions that: (a) pups shape their dams' behavior and (b) maternal anogenital stimulation affects pups' reproductive success as adults. The present findings are thus indicative of the possible utility of viewing rat pups as active, somewhat Machiavellian manipulators of their dams' behavior.

Note

This research was supported by grants to B. G. G. Jr. from the Natural Sciences and Engineering Research Board of Canada and the McMaster University Research Board. We thank Elaine Whiskin for her technical assistance.

References

Alberts, J. R., and Gubernick, D. J. (1983). Reciprocity and resource exchange: A symbiotic model of parent-offspring relations. In L. Rosenblum and H. Moltz (eds.), *Symbiosis in Parent-Offspring Interactions*. New York: Plenum Press. Pp. 7–44.

Capek, K., and Jelinek, J. (1956). The development of the control of water metabolism. I. The excretion of urine by young rats. *Physiol. Bohemoslov., 5:* 91–96.

Friedman, M. J., Bruno, J. P., and Alberts, J. R. Physiological and behavioral consequences in rats of water recycling during lactation. *J. Comp. Physiol. Psychol., 95:* 26–35.

Galef, B. G., Jr. (1981). The ecology of weaning: Parasitism and the achievement of independence by altricial mammals. In D. J. Gubernick and P. H. Klopfer (eds.), *Parental Care in Mammals*. New York: Plenum Press. Pp. 211–241.

Gubernick, D. J., and Alberts, J. R. (1983). Maternal licking of young: Resource exchange and proximate controls. *Physiol. Behav., 31:* 393–601.

Gubernick, D. J., and Alberts, J. R. (1985). Maternal licking by virgin and lactating rats: Water transfer from pups. *Physiol. Behav., 34:* 501–506.

Moore, C. L. (1981). An olfactory basis for maternal discrimination of sex of offspring in rats (*Rattus norvegicus*). *Anim. Behav., 29:* 383–386.

Moore, C. L. (1982). Maternal behavior of rats is affected by hormonal condition of pups. *J. Comp. Physiol. Psychol., 96:* 123–129.

Moore, C. L. (1983). Maternal contributions to the development of masculine sexual behavior in laboratory rats. *Dev. Psychobiol., 17:* 347–356.

Moore, C. L., and Morelli, G. A. (1979). Mother rats interact differently with male and female offspring. *J. Comp. Physiol. Psychol., 93:* 677–684.

Siegel, S. (1956). *Non-parametric Statistics*. New York: McGraw-Hill

Trivers, R. L. (1974). Parent-offspring conflict. *Amer. Zool., 14:* 249–264.