Influences of social isolation during development on sexual behavior of the rat*

JOHN A. DUFFY[†] and SHELTON E. HENDRICKS

University of Nebraska, Omaha, Nebraska 68101

Male and female rats were weaned at 14 days of age and raised in social isolation or with three other animals. At maturity the male isolates displayed less male sexual behavior than the socially reared Ss. Female isolates, after ovariectomy and injection with androgen, exhibited much less male sexual behavior than control females similarly tested. After being brought into estrus by injections of estrogen and progesterone, the female sexual behavior of female social and isolate Ss did not differ. Data were interpreted as indicating that social isolation during development deprives rats of critical experiences necessary for development of appropriate responses to social stimuli eliciting male copulatory behavior in both sexes.

A frequently reported result of early social isolation is a disruption or inhibition of sexual behavior. This finding has been reported in numerous species. Harlow and Harlow (1966) and Mitchell, Raymond, Ruppenthal, and Harlow (1966) have all reported that social isolation severely disturbs or disrupts mating behavior in male and female rhesus monkeys. Turner, Davenport, and Rogers (1966) reported similar effects in chimpanzees. A decrement in male sexual behavior has also been noted in guinea pigs (Gerall, 1963) and dogs (Fox & Stelzner, 1966; Beach, 1968). However, Meier (1965) found no such effect in rhesus monkeys, and Harper (1968) failed to find that social isolation affected the male or female social behavior of guinea pigs. In rats the data are also contradictory. Some investigators have reported a complete lack of sexual behavior in isolated male rats (Gerall, Ward, & Gerall, 1967), while others (Folman & Drori, 1965; Gruendel & Arnold, 1969) have found a significant decrease, but not a lack, of male sexual behavior. On the other hand, Beach (Beach, 1942b; Beach, 1958; Kagan & Beach, 1953) has consistently failed to find a decrement in male sexual behavior. While most of the data seem to support the view that isolation during development affects male sexual behavior, some equivocation does exist. In rats in particular, there seems to be a need for clarification of the parameters involved in the effects of social isolation during development on male sexual behavior.

There are few studies available concerning the effects of social isolation on female sexual or maternal behavior in other than primate species. Signoret (1970) studied

sexual and maternal behavior in isolated female pigs, and Stern and Hoffman (1970) studied maternal behavior in isolated guinea pigs. Neither study reported any difference between isolated animals and controls. These findings are at variance with Harlow's findings in female monkeys. There are, to our knowledge, no published studies concerning the effects of social isolation on the sexual behavior of female rats.

The present experiments were designed to replicate previous studies dealing with the influences of social isolation on the sexual behavior of male rats. Further, the influence of isolation on the female sexual behavior of female rats was studied. Since male sexual behavior can be readily induced in ovariectomized female rats by injections of androgen (Ball, 1940; Koster, 1943; Beach & Rasquin, 1942), it should prove interesting to see the effects of isolation on this induced male behavior. It was expected that isolated females would show a deficit in the display of the heterotypic male behavior.

METHOD

Subjects

Seventy-eight Wistar albino rats, both male and female, born in the laboratory during a 14-day period, were used as Ss. At the start of the study, there were 31 isolate males, 15 isolate females, 16 control males, and 16 control females. All were maintained on ad lib food and water throughout the experiment.

Rearing Conditions

Ss were weaned at 14 days of age and randomly assigned by litter either to a control condition or to a social isolate rearing condition. After weaning, the pups were housed in dark enclosed boxes, approximately 28 x 15 x 15 cm, in a heated quiet room and bottle fed milk by hand every 4 h, the E using a damp gauze pad at each feeding to help each pup excrete. Each isolated S was housed alone, while each social S was with three other Ss of the same sex and age.

Between 18 and 20 days of age, the isolated Ss were transferred to standard individual cages in the colony room, 24 x 18 x 18 cm high. Social rearing groups were maintained, and they were transferred at this age to cages measuring 24 x 36 x 18 cm high. For approximately 7 days, Ss were fed a

*This study is based upon a thesis submitted by the first author to the Graduate College, University of Nebraska at Omaha in partial fulfillment of the requirements for the MA degree in psychology. The research was supported in part by U.S. Public Health Service Grant 1R01 NS10027-01. Testosterone propionate was supplied by J. J. Chart of Ciba Pharmaceutical Company and the estradiol benzoate by Preston Perlman, Schering Corporation. The authors are indebted to Helen Peterson for her technical assistance.

[†]Present address: Department of Psychology, Tulane University, New Orleans, Louisiana 70118.

mixture of standard laboratory food and milk. After that time, the animals maintained themselves on dry food and water. A reverse light cycle, 12 h light and 12 h darkness, was maintained throughout the rest of the study. Only direct interaction with other animals was controlled; isolated Ss could presumably hear, smell, and, when cages were moved for cleaning, occasionally see other animals. When the animals were between 91 and 104 days of age, the control group was transferred to individual cages and the isolated group, to hold the amount of handling constant, was transferred to freshly cleaned individual cages. Also at this time, all female Ss were ovariectomized under ether anesthesia.

Male Sexual Behavior Tests

Testing for male behavior in both male and female Ss was begun when the animals were 96 to 109 days of age. Tests were conducted in a dimly lighted room, using semicircular observation cages 65 cm in diam and 24½ cm high. Ovariectomized female rats were used as lures for the male sexual behavior.

All lures were made estrous by intramuscular injection of 25 µg of estradiol benzoate (EB) 48 h before testing and 500 µg of progesterone 6 h before testing. Ss were tested in seven sessions, 5 days apart, each session lasting 15 min after a 10-min adaptation period. Testing was conducted with groups of six animals, one S and one lure per cage, at randomized times in the afternoon between 5 and 9 h after the beginning of the dark period. The animals were always tested in the same order in the same arena. Male sexual behavior was evaluated by recording the number of incomplete responses (mounting the estrous lure from the rear, palpating with the forepaws, and pelvic thrusting without a marked dismount), complete responses (mounting as described above, with a marked dismount), and ejaculations. Responses were recorded on a 20-channel Esterline-Angus event recorder. After the first test for male behavior, all female Ss began receiving injections of 250 µg of testosterone propionate (TP) intramuscularly every other day throughout the testing period. During the male behavior tests, the Ss were weighed weekly.

Female Sexual Behavior Tests

One week after the male behavior tests were completed, the females were tested for female sexual behavior. Each S received 25 µg of EB intramuscularly 48 h before testing was to begin and 500 µg of progesterone 4 h before. Testing was conducted in the same cages used for male sexual behavior tests. Proven sexually active males were used to elicit the sexual behavior. The female behavior, including degree of lordosis, holding of lordosis, and darting and soliciting behaviors, was rated according to a system presented by Gerall, Dunlap, and Hendricks (1973). Each S was mounted 10 times for each of four tests 1 week apart, and each mount was scored on all three scales by an experienced scorer using a single blind technique. The E doing the scoring did not know to which groups the Ss he was scoring belonged.

RESULTS

Of the 78 Ss initially included in the study, 61 survived to 90 days of age. Of the 17 that died, 14 were male isolates, while only 3 were in the social groups. None of the female isolates died. All but one of the deaths occurred during the immediate postweaning period (14-25 days of age). The survival rate for isolated males was found to be significantly poorer ($p < .01$) than any of the other groups, using a test for differences between proportions (Bruning & Kintz, 1968).

Analysis of the weekly weights of the Ss during the

male behavior tests, after randomly voiding Ss' data to obtain equal numbers of Ss per cell, revealed that there was no significant difference between the weights of the isolate and control Ss ($F = 2.01$, $p > .05$), nor was the interaction of Rearing Condition by Weekly Weighings significant ($F = .04$, $p > .05$). All Ss gained weight as the testing for male sexual behavior continued ($F = 4.36$, $p < .005$), and males weighed more than females ($F = 162.62$, $p < .005$).

Male Sexual Behavior

The variance of the Ss' male sexual behavior data proved to be too heterogeneous to permit one analysis of variance over all the Ss' data. Data from three Ss were randomly voided from the male isolate group to obtain an equal number of Ss per cell (14), and these data were analyzed by a Groups by Trials analysis of variance; data from the female Ss, which had an equal number of Ss per cell (15), were analyzed in a similar design. A measure of male sexual behavior was obtained by adding the total number of responses on each of the three response scales (incomplete responses, complete responses, and ejaculations) for each S for each test. Analysis of these data for the male Ss showed that the social Ss exhibited significantly more male sexual behavior ($F = 10.62$, $p < .005$) than the male isolate Ss. The increase in exhibited male sexual behavior over tests was also found to be significant ($F = 6.40$, $p < .005$). Each of these three component scales was also analyzed separately in two-way analyses of variance. The mean number of each response for isolated and social males over the seven behavior tests is presented in Fig. 1. On all three measures, the social males were found to have exhibited more sexual behavior than the isolates. The tests effect was significant for all measures (for all analyses, $p < .01$), and significant Groups by Tests interactions were noted for the incomplete and ejaculatory responses ($F = 2.19$, $p < .05$ and $F = 4.19$, $p < .005$, respectively).

Analysis of the total number of male copulatory responses exhibited by female Ss under the influence of exogenous androgen revealed that socially reared females exhibited significantly more sexual behavior than the isolate group ($F = 4.33$, $p < .05$). All Ss showed significant improvement over tests ($F = 3.24$, $p < .01$), but there was no significant Groups by Trials interaction. A separate analysis of the incomplete responses yielded the same results as the analysis of the total score. There were too few complete responses to be meaningfully analyzed. The mean number of complete and incomplete responses per group is presented in Fig. 2.

Since the nature of the male behavior data made the use of analysis of variance somewhat questionable, nonparametric procedures were also applied. Summing all responses over the seven tests and using the Mann-Whitney U test to evaluate the differences

between the social and isolate males and the social and isolate females revealed the same between-groups differences seen in the analyses of variance ($p \leq .01$).

Female Sexual Behavior

Analysis of the female Ss' female behavior total scores did not detect a difference between the two groups of females ($F = 1.93$, $p > .05$). All Ss showed a significant improvement over tests ($F = 3.49$, $p < .05$), but the Groups by Tests interaction was not significant. None of the component scales of the total score, lordosis, holding, or darting, showed a significant difference between the social and isolate animals. Again, application of a Mann-Whitney U test to the female behavior scores yielded the same result as analysis of variance: no difference between groups.

DISCUSSION

Data from the present study support the previously published finding that social isolation has a marked effect on the sexual behavior of male rats (Gerall et al, 1967; Gruendel & Arnold, 1969). While not totally suppressed, the male sexual behavior of the male isolate animals was much lower than that of the control

Fig. 2. Mean frequency of response on each of two components of male sexual behavior observed in females isolated at 14 days of age and control females under the influence of exogenous TP.

Fig. 1. Mean frequency of response for each of three components of male sexual behavior for 14 animals isolated at 14 days of age and 14 animals raised with 3 other animals from 14 days of age.

animals. The social males also scored significantly higher than the isolate males on each of the three component scales from which this total score was computed. The decline from Trial 4 through Trial 7 for the social Ss' complete and incomplete mean responses indicated that the social Ss began having fewer incomplete and complete mounts prior to an ejaculation. The isolate Ss showed no similar tendency over the range of male behavior tests employed here. This finding is in agreement with findings in rats (Gerall, Ward, & Gerall, 1967) and guinea pigs (Gerall & Dunning, 1958).

The hypothesis that early social isolation would affect the mounting behavior of females receiving exogenous androgen was supported. There was a significant difference between the female isolates and female controls, and these differences were in the predicted direction. This finding suggests that the effects of social isolation are behavior specific, affecting a male sexual behavior system present in both sexes. There was no difference in the female sexual behavior of the isolated and control females. It is striking that within the same S the male sexual behavior was greatly affected by early social deprivation, while female sexual behavior remained essentially normal.

If body weight is taken as an index of the general condition of the Ss, the analysis of the body weights of the Ss over the male sexual behavior testing period suggests that isolation did not adversely affect the Ss' general health during adulthood. Furthermore, in

handling the animals the Fs could see no differences between the social and isolate Ss. The fact that so many male isolates died in the first week after weaning suggests that at that time this group was particularly affected by isolation, but this difference in death rates did not persist past the first week after separation from the litter. At the present time, we have no explanation for the sex difference in the loss rate resulting from isolation. It is interesting to note that it was isolation from litter peers rather than from the mother that produced survival problems. The early weaning seems inconsequential to survival as long as pups are kept together.

The conditions of social isolation employed in this study were much less severe than those employed by Gerall et al (1967), who found highly significant effects of social isolation on male sexual behavior, and were more similar to the conditions of the studies of Beach (1942) and Kagan and Beach (1953), who reported no effects of social isolation on male sexual behavior. Coupled with the findings of Gruendel (1971) that nonsocial environmental enrichments failed to ameliorate the effects of social isolation on the male rat's sexual behavior, the data of the present study strongly indicate that it is indeed social isolation that produces these effects and not other aspects of the isolation situation.

One possible explanation that could be advanced for the difference in the effects of social isolation on male and female behavior is that, in the rat, female sexual behavior is a simpler, almost reflexive behavior. Such evidence as the ability of the female, but not the male rat, to exhibit sexual behavior after decortication (Beach, 1944) is often presented as evidence for this view. It could be hypothesized that it is the different degree of complexity between the two behaviors that accounts for the differential effects of social isolation. An alternative explanation is to be found in one hypothesis presented by Gerall (1963) with respect to influences of social isolation on the male sexual behavior of the guinea pig. Using the terminology of ethological theory, Gerall suggests that social isolation prevents appropriate releasing stimuli involved in male sexual behavior from acquiring the capacity to activate the proper innate releasing mechanisms. Following this hypothesis, it would be presumed that the rat, socially isolated prior to the normal weaning time, misses experiences that are necessary to allow appropriate stimuli to acquire the capacity to evoke mounting behavior. Cues involved in the evocation of sexual behavior in the male rat have been shown to be multiple; that is, all sense modalities are involved (Beach, 1942b). The adequate stimulus might best be described as an estrous female rat. The behavior of the female rat is under a much different set of stimulus controls. Increased activity and soliciting behavior occur in the absence of other rats, seemingly requiring only a minimal supporting environment and certain internal

hormonal states for their emission. Lordosis is a specific response to palpation of the iliac crest and can be evoked in the estrous female by stimuli other than from the male rat (e.g., hand stimulation by E). It, thus, might be argued that the source of the differential effects of social isolation on male and female sexual behavior is that the former is, at least to some extent, a social response and seems to require exposure to the appropriate social stimuli during critical periods of development, while the latter responds more to internal states and specific somatosensory stimuli not dependent upon early social experience for their capacity to evoke the behavior later in life.

REFERENCES

- Ball, J. The effect of testosterone on the sex behavior of female rats. *Journal of Comparative Psychology*, 1940, 29, 151-165.
- Beach, F. A. Analysis of the stimuli adequate to elicit mating behavior in the sexually inexperienced male rat. *Journal of Comparative Psychology*, 1942a, 33, 163-207.
- Beach, F. A. Comparison of copulatory behavior of male rats raised in isolation, cohabitation and segregation. *Journal of Genetic Psychology*, 1942b, 60, 121-136.
- Beach, F. A. Relative effects of androgen upon mating behavior in male rats subjected to castration or forebrain injury. *Journal of Experimental Zoology*, 1944, 97, 249-285.
- Beach, F. A. Normal sexual behavior in male rats isolated at fourteen days of age. *Journal of Comparative & Physiological Psychology*, 1958, 51, 37-38.
- Beach, F. A. Coital behavior in dogs: III. Effects of early isolation on mating in males. *Behavior*, 1968, 16, 218-238.
- Beach, F. A., & Rasquin, P. Masculine copulatory behavior in intact and castrated female rats. *Endocrinology*, 1942, 31, 393-409.
- Bruning, J. L., & Kintz, B. L. *Computational handbook of statistics*. Glenview, Ill: Scott, Foresman, 1968.
- Folman, Y., & Drori, D. Normal and aberrant copulatory behaviour in male rats (*R. norvegicus*) reared in isolation. *Animal Behaviour*, 1965, 13, 427-429.
- Fox, M. W., & Stelzner, D. Behavioural effects of early experience in the dog. *Animal Behaviour*, 1966, 14, 273-281.
- Gerall, A. A. An exploratory study of the effect of social isolation variables on the sexual behaviour of male guinea pigs. *Animal Behaviour*, 1963, 11, 274-282.
- Gerall, A. A., & Dunning, H. W. Attempts to influence the sexual behavior of socially isolated male guinea pigs. *The Anatomical Record*, 1958, 131, 556.
- Gerall, A. A., Dunlap, J. L., & Hendricks, S. E. Effect of ovarian secretions on female behavior potentiality in the rat. *Journal of Comparative & Physiological Psychology*, 1973, 82, 449-465.
- Gerall, H. D., Ward, I. L., & Gerall, A. A. Disruption of the male rat's sexual behaviour induced by social isolation. *Animal Behaviour*, 1967, 15, 54-58.
- Gruendel, A. D. *The influence of experimental factors on the early development and sexual behavior of male rats*. (Doctoral dissertation. University of Nebraska) Ann Arbor, Mich: University Microfilms, 1972. No. 72-27,396.117.
- Gruendel, A. D., & Arnold, W. J. Effects of early social deprivation on reproductive behavior of male rats. *Journal of Comparative & Physiological Psychology*, 1969, 67, 123-127.
- Harlow, H. F., & Harlow, M. K. Effets de la privation précoce de contacts sociaux chez les primates. *Revue de Médecine Psychosomatique*, 1966, 8, 11-24.

- Harper, L. Effects of isolation from birth on the social behaviour of guinea pigs in adulthood. *Animal Behaviour*, 1968, 16, 58-64.
- Kagan, J., & Beach, F. A. Effects of early experience on mating behavior in male rats. *Journal of Comparative & Physiological Psychology*, 1953, 46, 204-208.
- Koster, R. Hormonal factors in male behavior of the female rat. *Endocrinology*, 1943, 33, 334-348.
- Meier, G. W. Other data on the effects of social isolation during rearing upon adult reproductive behaviour in the rhesus monkey (*Macaca mulatta*). *Animal Behaviour*, 1965, 13, 228-231.
- Mitchell, G. D., Raymond, E. J., Ruppenthal, G. C., & Harlow, H. F. Long-term effects of total SI upon behavior of rhesus monkeys. *Psychological Reports*, 1966, 18, 567-580.
- Signoret, J. P. Sexual behaviour patterns in female domestic pigs (*Sus scrofa l.*) reared in isolation from males. *Animal Behaviour*, 1970, 18, 165-168.
- Stern, J. J., & Hoffman, B. M. Effects of social isolation until adulthood on maternal behavior in guinea pigs. *Psychonomic Science*, 1970, 21, 15-16.
- Turner, C. H., Davenport, R. K., & Rogers, C. M. The effect of early deprivation on the social behavior of adolescent chimpanzees. *American Journal of Psychiatry*, 1969, 125, 1531-1536.

(Received for publication January 19, 1973;
resubmitted April 27, 1973;
accepted May 16, 1973.)