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Effect of population density during development on adult social behavior of the rat

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Differential caging conditions (space/animal and animals/cage) during development resulted in altered adult open-field social behaviors even though adult animals had been individually housed for long periods before testing. Crowded cages during development resulted in a decrease of aggressive behavior and an increase in submissive behaviors when the adult animals were paired in the open-field. The observed changes in social behavior might be viewed as adaptations to the social environment in which the animal developed.

Open-field behaviors have become popular dependent variables in the attempt to understand the effects of limbic system lesions on social behaviors. Jonasen and Enloe (1971) have reported the reciprocal effects of amygdaloid and septal lesions in open-field contact time, number of contacts, and activity.

In our laboratory, we have been concerned primarily with the effects of septal lesions. We have replicated Jonasen and Enloe's results following complete septal lesions and have found that the similar increases in gregariousness are produced by only medial septal lesions. Lateral septal lesions have only a minor effect on open-field contact time (Poplawsky & Johnson, 1973).

The effects of complete septal lesions on open-field contact in our laboratory, while always in the same direction (increased contact time), have not always been of equal magnitude. The postoperative increase in gregariousness has ranged from 22% to 48% (Poplawsky & Johnson, 1973) across groups and studies. Moreover, within groups in a particular study there has been considerable range in postoperative effects on various pairs of animals. We, thus, became concerned over factors aside from the lesions which might account for these individual differences.

In one study (Poplawsky & Johnson, 1973) animals from the same strain and same supplier behaved somewhat differently after septal lesions (differences in degree of effect). The major difference between these groups of animals (so far as we could ascertain) was that one group had been housed during development in our colony room while the other group was housed under our colony conditions for only 2-4 weeks before being used in the experiment. Lesion placement was quite similar in both groups. We felt it quite possible that the conditions of housing during development might have influenced the animals. Latané, Cappell, and Joy (1970), and Latané, Nesbitt, Eckman, and Rodin (1972) have demonstrated clearly that short-term changes in number of animals per cage can alter gregariousness in the open-field. This study was an attempt to analyze the impact of housing conditions during development on adult social behaviors long after the developmental housing conditions had been discontinued. It occurred to us that we could use animals from a population density study (Diehl, Johnson, & Bellezza, 1972) already underway to determine if different rearing conditions during development might effect behavior.

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METHOD

Subjects

Animals used in this experiment were selected at random from groups used in a previous study (Diehl et al., 1972). In that study the development of social behaviors was observed as a function of crowding. At 21, 42, 63, and 100 days of age, all animals were handled, weighed, and observed in an open field. After the 100-day observations many of the animals in the Diehl et al. (1972) study were sacrificed and endocrine glands extracted. The remaining animals were used as subjects in the current study.

Sixty male Long-Evans hooded rats approximately 280 days of age at the time of observation were used in this experiment. The mean weight of all rats at the time of observation was 455 g.

Design

A completely crossed design was used to investigate the effects of two levels of number of animals/cage and two levels of space/animal during development on adult social behavior. In group low density–high space (LDHS, 6 pair) there were two animals/1814-cm^2 cage, in group high density–high space (HD-HS, 7 pair) there were 18 animals/16258-cm^2 cage, in group low density–low space (LD-LS, 8 pair) 18 animals/1814-cm^2 cage, and in group high density–low space (HD-LS, 9 pair) 2 animals/200-cm^2 cage. These housing conditions were maintained from 21-100 days of age at which time all animals were housed in 41 x 25 x 17 cm individual laboratory cages as are animals which are purchased at this age from commercial suppliers. After 6 months in individual cages, pairs of animals were placed together in an open field for observation.

Apparatus

Social behaviors were observed in a well-lighted Latané (1969) open field which was 1.22 m in diam with walls 46 cm high. The white field was divided into 49 equal-area sections by black lines.

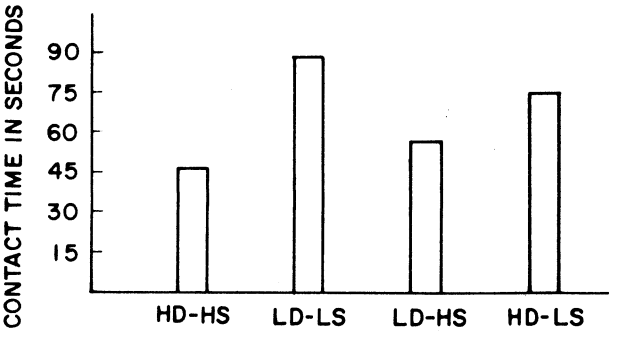

Figure 1.

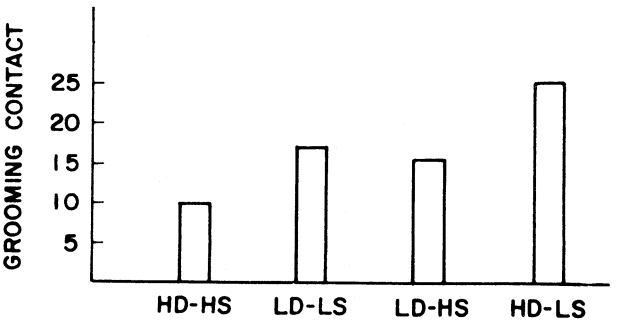

Figure 2.

Procedure

At 280 days of age, pairs of animals were selected at random to form each group. Pair members were marked (red dye on tail) for easy visual identification. Each pair of animals was placed in the open field for a 15-min adaptation session on 3 successive days to overcome some of the familiarity effects observed by Latané et al. (1970). No observations were made during adaptation. Contact time and types of social contacts were recorded during 5-min observation sessions on 8 successive days following adaptation. Two trained experimenters were required during observation. The group to which a pair belonged was unknown to the experimenters. Experimenter A recorded contact while Experimenter B recorded social interactions. On each successive day experimenters changed roles. Contact time was defined as the total number of seconds during which pair members were in physical contact with each other. In order to record qualitative aspects of social interactions, each interaction was observed from one pair member's point of view. The same pair member (red tail marking) was observed on all 8 days. Each contract was characterized qualitatively as aggressive (biting, threat posture, "boxing' position, chasing), sexual (sniff or lick genitalia, mounting behavior), submissive (evade, retreat, receive bites, expose under side), introductory-grooming (licking fur or feet of other, scratching, nibbling) or other. The frequency of each type of contact during each 5min open-field session was recorded. A comparison of even-odd day scores for each variable was made to determine interjudge reliability.

RESULTS

The number of seconds spent in physical contact (see Figure 1) differed as a function of rearing conditions ($F = 5.14$, $df = 1/26$, $p < .05$). Animals with little space/animal (Groups LD-LS and HD-LS) were most gregarious as defined by contact time while animals in Groups HD-HS and LD-HS spent the least time in physical contact. Space/animal during development accounted for the above differences while number of animals/cage independent of space/animal had little effect. Animals that were forced into close contact during development by low space cages continued to spend more time in physical contact in adulthood. The interjudge reliability for contact time was .95. Aggressive contacts were found only in Group HD-HS where about 30% of all contacts were aggressive in mature animals. Sexual approaches in male-male pairs were extremely infrequent in all groups. There were, however, differences between groups in grooming behavior ($F = 4.71$, $df = 1/26$, $p < .05$). Grooming behaviors comprised 60%-68% of all contacts in Groups LD-LS, LD-HS, and HD-LS. In Group HD-HS, however, grooming behavior comprised only 35% of all contacts (see Figure 2). Submissive behaviors were highest in Group HD-LS and lowest in Group HD-HS ($F = 3.71$, $df = 1/26$, $p < .10$; see Figure 3). Submissive behaviors comprised from 20%-30% of the animal encounters. Interjudge reliabilities for categorization of behaviors were as follows: aggressive, .93; sexual, .91; introductory, .78; submissive, .83.

DISCUSSION

The tendency of animals in this study to remain close to each other and to engage in physical contact seems clearly related to housing conditions during development in spite of long periods of isolation before experimental observation. Animals with higher contact times were reared in cages with low available space/animal. Thus the tedency to remain close other animals continues even at 280 days of age and after 180 days of individual housing. Also, it would seen that alterations in social behavior occur during development under crowded conditions which decrease the probability of aggression in aggression-producing situations. Animals that had more space/animal during development displayed consistently lower levels of grooming and submissive behaviors than animals reared under crowded conditions. Conversely, grooming and submissive behaviors in adult animals in this study were more frequent in animals reared in crowded cages.

We were somewhat surprised to find that space/animal accounted for a greater proportion of the variance than number of animals/cage. This was particularly true for contact time. With regard to qualitative aspects of social behavior, both

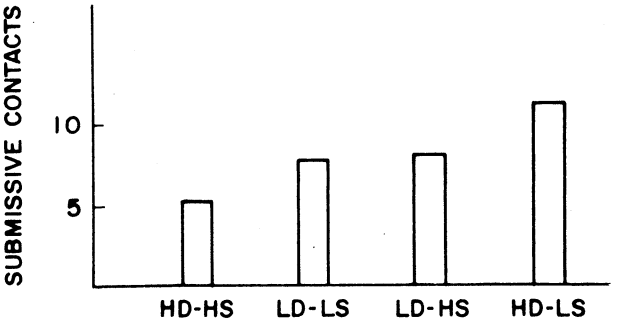

Figure 3.

space/animal and number of animals/cage during development seem to alter social behavior.

The reliability of qualitative ratings in this study were less than ideal, and the number of pairs observed was not large. Despite these limitations, differences were observed in social behavior resulting from different levels of crowding during development, even after a 6-month period of individual laboratory housing. The alterations which were observed seem to have been adaptations to population density that would tend to reduce aggressiveness in crowded living conditions.

Studies conducted by Latané and his students clearly indicate that housing conditions immediately prior to observation have an effect upon open-field social behaviors in the rat. They found little effect of number of animals/cage or density of cagemates on social behaviors. Perhaps the limited range of housing conditions accounts for the difference between our results and theirs. The present study shows that, under extreme conditions of space/animal or number of animals/cage, social effects are observed.

This study also emphasizes the importance of controlling developmental housing conditions, particularly if adult social behaviors are the object of study.

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Retrieval of categorized items increases without guessing

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Without any feedback to distinguish correct recall from intrusions, spontaneous retrieval (without further presentation after initial recall of each item) of a list of 20 animals increased rapidly during free recall verbal learning. Intrusions, elicited by requiring forced recall of 20 items on each trial, decreased as correct recall increased. List items were recalled with great consistency once they were spontaneously retrieved; total recall was limited more by the initial difficulty of retrieving an item from long-term storage for the first time. Since these results show that subjects know which items belong to the list, they indicated that spontaneous retrieval of items from the same category does show retention and retrieval, rather than guessing. Forced recall increases retrieval even more than extended recall does, not through guessing but by encouraging further search in long-term storage for recovery of more items, which are correctly discriminated when found.

Spontaneous retrieval from long-term storage during verbal learning has recently been shown by repeated retrieval without further presentation of each item after it has been recalled just once (Buschke, 1973, 1974). In free recall list learning of unrelated items, there is no question that such spontaneous retrieval without further presentation shows previous storage and subsequent retention. However, in spontaneous retrieval of related items from the *same category* (such as a list of animals), it is possible that at least some spontaneous recall might represent guessing rather than true retrieval from long-term storage. This could mean that some items in such lists were not really learned at the time of their initial recall and retained for later spontaneous retrieval, but were learned later when a lucky guess was confirmed as correct recall of a list item. This study shows that spontaneous recall of related items that might be guessed does represent true retrieval rather than guessing, by withholding any feedback during learning that might either confirm guesses or correct intrusions.

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METHOD

Each subject was tested individually, by reading aloud a list of 20 animals at a 2-sec rate for free recall in any order immediately after presentation. After an initial presentation of the entire list, only those items which had not yet been recalled at all were presented again, so that each item was presented only until it had been recalled just once. Since all items were recalled at least once by the third trial, there were no presentations at all on any of the last nine trials. However, the subjects tried to recall *all* of