Effects of septal lesions on open-field gregariousness in rats reared prior to surgery in group versus individual cages

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Septal lesions were given to adult animals which had been reared in isolation or in group cages from 30-90 days of age. Septal lesions and isolated rearing produced additive increases in open-field contact time. These results were similar to those observed in a previous study in which septal lesions were produced in infancy and followed by differential housing. Emotionality and activity were also affected by lesion and housing condition; however, the pattern of results was interactive on these two variables.

Previous research has clearly demonstrated that open-field contact time in rats is markedly increased by septal lesions (Johnson, 1972; Jonason & Enloe, 1971; Poplawsky & Johnson, 1973). Animal behavior studies have also demonstrated that when animals are housed in isolation for several weeks prior to observation in the open field, contact times are increased (e.g., Latané, Nesbitt, Eckman, & Rodin, 1972). In a recent study (Johnson, Spiker, & Carlson, 1984), we investigated whether isolated versus group housing during development might interact with septal lesions produced in infancy. Results from this study indicated that both septal lesions and isolated housing produced increases in social contact time. Animals reared in isolation, however, displayed a more rapid increase in contact time across successive days of observation regardless of whether they were from normal or infant-septal-lesioned groups.

The current study was designed to determine if the impact of differential housing on normal and septal animals is similar to that described above when the lesions are produced in adulthood, rather than in infancy. In the prior study (Johnson et al., 1984), housing conditions and septal lesion were both developmental variables. The present study looks at contact time following septal lesions at 90 days of age in rats reared with either group or isolated housing histories since weaning.

METHOD

Subjects and Housing Conditions

All animals used in this study were Holtzman Sprague-Dawley albino rats. Five days after birth, the experimental litters were culled

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to 6-8 male pups. Culled litters were raised with the dam until 30 days after birth. At this point, animals were moved to the experimental housing conditions. Thirty-two animals were housed in standard (28 × 20 × 20 cm) stainless-steel rack cages, one animal per cage. Another 32 animals were housed 4 per cage in the same size cages. At 90 days of age, 12 of the 24 surviving animals from group housing conditions were given septal lesions and then were placed in individual cages for 21 days of postoperative recovery. The other half of the animals from group cages were not given lesions and were transferred to single rack cages for 21 days.

Twelve animals reared in isolation from 30-90 days of age were also given septal lesions at 90 days of age and were returned to single cages for a 21-day recovery period. Another 12 animals reared in isolation remained as normal controls in their isolation cages from 90 to 111 days of age. Normal controls were used instead of sham operates because prior studies indicated that sham and normal controls do not differ (Johnson, 1972; Jonason & Enloe, 1971), and because we intended to use the differentially housed normal animals in further experiments.

After all animals had completed the postoperative recovery period at 111 days of age, behavioral observations were begun. On Days 1 through 15 of observation, each animal was rated for emotionality (during handling) using the King (1958) emotionality scale. On Days 1 and 2 of observation, after being rated for emotionality, the animals were placed individually in the Latané open field (1979) for a 5-min adaptation period. On Days 3-17, animals were rated for emotionality and then placed by pairs in the open field and contact time was recorded for 5 min. Contact time was defined, as in previous studies (Jonason & Enloe, 1971; Poplawsky & Johnson, 1973), as cumulative number of seconds spent in any type of physical contact. Animals were paired in such a manner that pairs were not cagemates or siblings. The same pair of animals was observed interacting in the open field for 15 consecutive days. On Days 18-21 of observation, each animal was placed individually in the open field and activity was recorded by counting total number of squares crossed in 5 min.

Surgery-Histology

Bilateral septal lesions were produced by placing the anesthetized (.1 cc/kg sodium pentobarbital) rats in a Kopf stereotaxic device with the incisor bar elevated +5 mm from the interaural line. The lesions were produced at a depth of 5 mm below the dura at points 7.8 mm anterior to interaural zero and .5 mm bilaterally to the midline. During each electrode drop, 2 mA of dc was passed for 20 sec.

A stainless-steel monopolar electrode insulated except for .5 mm at the tip was used.

Upon completion of the behavioral observation, each animal was given a lethal injection of sodium pentobarbital and perfused intracardially with physiological saline followed by 10% Formalin. Brains were removed and 75- μ m frozen sections were taken through the extent of each lesion. Selected sections were stained with cresyl violet and reconstructions of the lesions were then produced.

RESULTS

Reconstructions of the largest and smallest septal lesions for group-housed and isolated groups are presented in Figure 1. The extent and location of the lesions were quite similar between groups. Lesions began just anterior to the genu of the corpus callosum and extended posteriorly into the fornix. There was no evidence of damage

Figure 1. Reconstructions of septal lesions for group-housed and isolated animals. Heavy black outline represents maximum extent of damage. Shaded area indicates minimum extent. Diagrams are adapted from deGroot (1959).

Figure 2. Mean postoperative emotionality scores for all groups by day of observation.

to the corpus callosum or the caudate nucleus. Lesions were complete and localized in the anterior half of the septum, and completely destroyed the anterior lateral and anterior medial septal nuclei in all animals. The lateral septum was also destroyed posteriorly in all animals. The greatest variability within groups was displayed in destruction of the posterior medial aspect of the septum. In both groups the largest lesions destroyed all of the posterior medial septum, but also extended through the dorsal bands of Broca and median preoptic area into the paraventricular nucleus of the anterior thalamus. In the smallest lesions the posterior medial septum and the dorsal bands of Broca were left intact. The larger lesion type was found in only two animals of each group. The smaller lesion was more typical of that found in the remaining animals of each group.

Data from emotionality ratings is presented in Figure 2. Emotionality ratings decreased rapidly across days in all groups [$F(14,190) = 76.0$, $p < .001$]. Septal animals were rated significantly higher in emotionality than were control animals [$F(1,35) = 10.21$, $p < .01$]. This effect was primarily due to the interaction of housing and lesion treatment [$F(1,35) = 5.9$, $p < .05$]. Group housing resulted in lower emotionality ratings for normal animals, but heightened emotionality ratings for septal animals. The isolated housing condition resulted in lower emotionality ratings for septal animals and elevated ratings for normal animals. There was no significant effect of housing conditions independent of the interactions. Emotionality ratings decreased across days similarly for all groups, as indicated by no significant days interactions.

Contact time data is presented in Figure 3. As can be seen, contact time was quite variable within groups during the first 5-7 days. Behavior then stabilized and remained relatively consistent from day to day within groups. This observation is consistent with our previous study involving contact time in albino rats (Johnson, Chang, Polenchar, & Patterson, 1985). If analyzed across all 15 days, the within-group variance in the first few days is so large that most between-group differences do not

Figure 3. Mean postoperative open-field contact time for all groups by day of observation. Break in graph represents post hoc split for subsequent analysis (see Results).

Figure 4. Open-field activity scores gathered subsequent to 15 days of contact-time measurement. Ordinate represents number of squares crossed in the Latané open field in a 5-min period.

quite reach significance. The effect of days is, of course, significant [$F(14,210)=5.5$, $p < .01$]. Septal groups also increased more rapidly across days than did control groups [$F(14,210) = 2.4$, $p < .01$]. We present the analysis of all 15 days' contact time to demonstrate that the data can be interpreted in spite of the extraordinary variability in the first few days. The following analysis considers only the contact-time data from Days 8-15; we regard the first 7 days as a period of stabilization, as proposed in our previous study (Johnson et al., 1985). Over the last 8 days of observation, animals with septal lesions displayed significantly higher contact times [$F(1,15)=9.6$, $p < .01$]. Animals reared in isolation also displayed increased contact times [$F(1,15)=4.8$, $p < .05$]. The effects appear to be additive, as indicated by the lack of a significant lesion $\times$ housing treatment interaction. The magnitudes of the effects of septal lesion versus housing condition in this study do not differ dramatically.

Activity scores collected on the last 4 days of observation did not differ significantly as a function of lesion or housing treatments; however, septal animals that were

reared in isolation were more active than all other groups [$F(3,96) = 2.75$, $p < .01$; see Figure 4].

DISCUSSION

In the present study, the results of septal lesions produced in Sprague-Dawley albino rats were found to be essentially the same as those reported in numerous previous studies using hooded rats (e.g., Jonason & Enloe, 1971; Jonason, Enloe, Contrucci, & Meyer, 1973; Poplawsky & Johnson, 1973). As previously reported, (Johnson et al., 1985; Jonason et al., 1973), the septal social cohesiveness effect apparently takes time to develop. In albino animals, the effect develops over the course of 5-7 days, somewhat more slowly than that reported for hooded animals (cf. Jonason et al., 1973). However, contact times reported here stabilized remarkably close to those reported by others. For example, Jonason and Enloe (1971) reported that contact time between septal animals (individually housed) stabilized at about 260 sec. This is within 10 sec of the average contact time we observed in septal isolates. Thus, the septal social cohesiveness effect appears to be an extremely reliable phenomenon.

The results of the present study indicate that housing conditions during development can have a pronounced impact on emotionality rating, open-field contact, and open-field activity. These effects of prior housing were manifest in spite of the 3 weeks of isolated housing that was maintained in all groups prior to observation. Most animals purchased from suppliers have developmental housing histories similar to that of animals in the present study reared in group cages. The present study indicates that this type of developmental history probably prejudices results in the direction of increased emotionality and decreased open-field contact and open-field activity ratings.

In a previous study (Johnson et al., 1984), we reported that open-field contact following septal lesions in infant hooded rats could be modified by the type of postweaning housing maintained until observation. The present study demonstrates essentially the same pattern of results in albino rats when septal lesions are produced in adult animals following a developmental history of differential housing. The effect of isolated housing on septal animals in the present study was not quite so pronounced as the effect on animals whose lesions were produced in infancy. In addition, we note that although housing conditions may affect social cohesiveness, the septal lesion effect appears regardless of whether the animals are group or individually housed. However, isolated housing appears to enhance the effect of lesion to some extent. Possibly this effect might have been more pronounced if animals had been maintained on differential housing schedules postoperatively.

Prior studies have also demonstrated that increased levels of activity tend to shorten the duration of individual contacts and diminish overall contact time (Jonason & Enloe, 1971). In the present experiment, septal isolates were found to be generally more active, yet these animals dis-

played the greatest amount of contact time. Jonason and Enloe (1971) reported that pairs of septal subjects tended to be hypomobile, but when paired with normal or amygdaloid animals, septal subjects displayed increases in mobility; septal subjects actively pursued amygdaloid animals (which tend to be hyperambulatory). They suggested that septal lesions might act to potentiate the animal's tendency to engage in social interactions. In the present experiment, activity levels were measured after the animals had been interacting with other animals in the open field over a number of days. Thus, the activity levels of septal isolates in the present experiment may reflect an increase in exploratory behavior in an attempt to make social contact with a now missing pairmate.

In summary, current and previous studies (e.g., Johnson et al., 1984) demonstrate that housing density during development can have a potent impact on the effects of open-field behaviors following septal lesions. This is observed in both hooded and albino rats, and is found whether surgery is performed in infancy or in adulthood. However, the increased social gregariousness produced by septal lesions is apparent regardless of housing condition.

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