Aggression and open field behavior in male mice¹

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Male mice from two inbred strains and their crossbred generations were tested for open-field behavior and noncompetitive intrasrain aggression. Both open-field activity and defecation were inherited as additive characters in this cross. The amount of aggression appeared to be a function of both genotype and genetic differences between opponents. The low-defecating, high-active genotype was low-aggressive, while the high-defecating, low-active genotype was high-aggressive. These results contradict findings reported elsewhere and suggest that there is not a necessary relationship between open-field behavior and aggressiveness in mice.

The existence of genetically influenced differences in open-field behavior and aggression in mice has been amply documented in the literature. However, no study reporting the results of systematic genetic crosses between different strains has appeared with regard to aggression, and few investigators have attempted crossbreeding studies of open-field behavior (DeFries & Hegmann, in press). One study of genetic selection for aggressiveness in mice has been reported (Lagerspetz, 1964). In that study, open-field defecation was found to be negatively related to aggressiveness in the third selected generation. From the association across selected generations, it is tempting to generalize concerning possible underlying physiological commonalities and obligatory relationships between open-field "emotionality" and aggressiveness (Lagerspetz, 1964, p. 115).

However, a correlated response to bidirectional selection, with only one selected line in each direction, provides a weak criterion of genetic commonality since chance factors operating in the selection environment could lead to the relationship. In closed laboratory populations, with small numbers of parents for each selected generation, and some inbreeding, random genetic drift could be an important factor in determining the values of characters not subject to direct selection.

The present study provides data on both open-field behavior and aggression from strains of mice that were not selected for either trait, so the relationship between the traits across strains may lend support to, or tend to refute, the suggested relationship.

In addition, systematic genetic crosses were made between the strains to provide information on the mode of inheritance of both open-field behavior and aggression in the same Ss.

METHOD

The Ss were from the mouse colony established by G. Lindzey at the University of Minnesota and consisted of males from the C57BL/1Bi and JK/Bi inbred strains and their F₁, F₂, and backcross generations. A total of 190 mice were tested for aggression and 130 were included in the open-field test. All Ss were individually housed at 60 days of age and began open-field testing at 125 ± 15 (range) days of age. The first day of aggression testing was 12 days later.

A 15 x 15 cm square arena, with 20-cm-high walls and a floor of heavy Kraft paper, was used for both open-field and aggression tests. Each S was tested in the open field for 5 min a day at the same time each day for 3 consecutive days. The walls of the apparatus were cleaned and the paper floor renewed between each S. A score of 1 was given for activity each time a S moved across the arena, placing all four feet across the midline of the apparatus. The defecation score was the number of boluses in the arena at the end of the 5-min test. Scores used in analyses were individual S's activity and defecation scores cumulated over the 3 days of testing. Testing for noncompetitive, intrasrain aggression was also conducted for 3 days. An even number of Ss of the same genotype ready to begin testing on the same day were divided into groups of four. Matches on the 3 days were arranged so that each S in a group met a different animal and started the trial from alternate sides of the apparatus on consecutive days. When two males were available, but not four, they met each other from alternate sides of the apparatus each day. For a trial, one S was placed in each side of the apparatus and a center partition then removed. A trial lasted for 5 min, or until a

definite fight started. If a fight started, the trial was immediately terminated, and Ss were removed to their home cages. A S received a score of 1 each time it engaged in a fight; thus, scores for individual Ss ranged from 0 to 3. Further details of the apparatus and testing are available elsewhere (Whitney, 1967).

RESULTS AND DISCUSSION

The open-field defecation and activity data were subjected to a biometrical genetic analysis following the classic method (Katzenmeyer et al, 1969). With defecation raw scores, a significant Genotype by Environment interaction was indicated from the scores of the nonsegregating genotypes (F_{max} = 3.41, p < .05). Transformation of the form $[X = \log(x + 1)]$ eliminated the interaction (F_{max} = 1.47). The A, B, and C scaling tests for the presence of epistasis, when applied to the transformed data, were also nonsignificant. Thus, with the logarithmic transformation, the defecation data fit the genetic model sufficiently well to proceed with analysis. The transformed scores for each genotype are given in Table 1.

The additive component of the mean (d = .709) was highly significant (F = 40.1, p < .0001), indicating a significant difference between parental genotypes. The JK strain defecated much more in the test than did the C57 (Table 1). The dominance component (h = .106) did not reach significance. Similarly, indications of directional dominance obtainable from analyses based on variances were all nonsignificant. Heritability, in the broad sense of the proportion of genetic variation to phenotypic variation, was estimated as 27%.

For open-field activity, the A, B, and C tests for the presence of epistasis and the F ratio indicating the presence of Genotype by Environment interaction were nonsignificant when scores were transformed by $[X = \sqrt{x} + \sqrt{x + 1}]$. Hence, this transformation was used in analysis. Table 1 presents the transformed scores for each genotype. The additive component of the mean was again highly significant (d = 3.35, F = 116.4, p < .0001), while the dominance component of the mean (h = .46) was not

Table 1
Transformed Open Field Defecation and Activity Data for Each Genotype

Genotype	N	Defecation*		Activity**	
		Mean	Variance	Mean	Variance
C57BL	19	1.17	.5885	20.23	3.79
C57 x F ₁	22	1.47	1.0061	18.93	4.41
F ₁	22	1.77	.5593	17.34	4.01
F ₂	22	1.73	.7082	17.01	3.66
JK x F ₁	24	2.22	.8121	16.52	6.42
JK	21	2.59	.4013	13.53	3.92

* $X = \log (X + 1)$

** $X = \sqrt{x} + \sqrt{x + 1}$

significant. These results indicate either that genetic factors operating in a predominantly additive fashion were responsible for the observed strain difference or that balanced dominance was present. The C57 strain was more active than the JK (Table 1), thus replicating the often-observed negative relationship between activity and defecation in the open-field test. Since the variance of the isogenic generations was greater than that of the F_2 , analysis based on variances was precluded.

Figure 1 presents the results of the aggression test, with data grouped into dichotomous categories of Ss who never fought vs those who fought once or more. The C57 strain had 0% of fights, while 85% of the JK males fought at least once out of three opportunities. The .99 confidence interval for the JK covers the range from .625 to .960; a significant difference between the inbred strains is indicated since the C57 mean is far outside this range.

Partial genetic determination of aggressiveness is indicated from the significant difference between inbred strains. The mode of inheritance is probably not primarily dominance, since the means of the F_1 and both backcrosses are between the parental values. The high aggressiveness displayed by the segregating F_2 generation (Fig. 1) may have implications concerning the stimulus variables eliciting aggression. The F_2 can be expected to show the greatest average variation in segregating heritable characteristics. If increased difference or

strangeness between individuals paired in a match were positively related to the probability of a fight starting, then results similar to those found would be expected. The positive results of Bauer (1956), relating differences to likelihood of aggression, and of Ropartz (1968), implicating the olfactory system in the elicitation and control of aggression, lend support to this possibility.

In the present study, the JK inbred strain was clearly more aggressive, defecated more in the open field, and was less active, than the C57 strain. Therefore, with the present Ss and rearing regime, there is a strong positive relationship between open-field emotionality and aggressiveness. These results are sufficient to demonstrate that the negative relationship reported elsewhere (Lagerspetz, 1964) is not a necessary relationship and may have been due to accidental factors operating in the selection situation. Aggression and open-field emotionality are definitely not negatively related characters in all mice.

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NOTE

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Differences in home-cage-emergence in the rat in relation to infantile handling¹

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Adult rats, which had either been handled daily between birth and weaning or left undisturbed during this period, were tested on speed of emergence from the home cage. On opening the cage, handled animals reared sooner than did nonhandled ones, and females sooner than males; the additional time taken to raise the nose above the cage top showed sex differences only.

The time taken for an animal to leave a familiar environment is one index of exploration that has been termed, at various times, a measure of wildness/savageness (e.g., Stone, 1932), emotionality (e.g., Billingslea, 1942), shyness (e.g., Hess, 1953), and timidity (e.g., Bindra & Thompson, 1953). The most familiar environment to the animal is

probably the home cage, and measures have been taken simply of the time taken to emerge from it (e.g., Lester, 1967), or of the time taken to come onto a runway (e.g., Bindra & Thompson, 1953) or into an enclosed alley attached to the cage (e.g., Billingslea, 1942). This relatively simple technique has not produced entirely consistent results.

In an early study, Billingslea (1942) showed that emotional animals, as defined in terms of their behavior in Hall's open-field test, took a greater time to enter a tunnel attached to the cage than did less emotional ones. Later studies, however, with rats (Bindra & Thompson, 1953; Hunt & Otis, 1953) and mice (Willingham, 1956) failed to find any relationship between time taken to emerge onto a runway and behavior in the open field. Hunt & Otis (1963), however, went on to report that emergence from home cage was more sensitive in identifying differences between rats differentially stimulated in infancy

Fig. 1. Proportion of individuals in each genotype who fought in aggression test.