Fig. 1. Mean duration of aggressive responding during postreinforcement interval of the last seven blocks of discrimination (FR66 = red, FR2 = green) and the first seven blocks of reversed discrimination (FR66 = green, FR2 = red).

aggression in both birds came under the control of the green light.

Total durations of aggression in the reversed phase seemed to be somewhat smaller than total durations in the initial phase; also, there was a trend toward less aggression in the latter blocks of the reversed phase for S-2. Phasing out of aggression in the present study would not be unpredicted, since studies of the innate fighting response in *Betta splendens* (Baenninger, 1966) have shown that aggressive responses do wane with repeated trials.

The present findings suggest that Ss do respond much differently in a "frustrating" situation, depending on whether or not an attackable target bird is present. More precisely, birds seem to have a natural tendency to aggress target objects when a relatively difficult response requirement is in effect, or when an SD signals that such a schedule is in effect. Although making the aggressive response has no effect on the food-reinforcement contingency and serves only to delay food reinforcement, the aggressive act would seem to have certain reinforcing properties of its own. Investigations are presently being conducted in the Es' laboratory to determine more precisely the nature of these reinforcing properties.

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A quantitative genetic analysis of change in open-field behavior of mice¹

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Daily open-field activity and defecation scores were obtained on each of 2,641 mice, including members of two inbred parental strains (BALB/cJ and C57BL/6J) and their derived F1, backcross, F2, and F3 generations. Change in activity and change in defecation from Day 1 to Day 2 were calculated for each individual, and resulting scores were subjected to genetic analysis. Strain comparisons and estimates of heritability revealed proportionately less genetic variance for change in activity than for either daily or total activity. In contrast, change in defecation was found to be as heritable as the other defecation measures. These results suggest that change in activity in novel situations may be of evolutionary significance.

Although change in behavior as a function of experience is of considerable importance to the fields of psychology and evolution, little information is currently available regarding the inheritance of behavioral change (Broadhurst & Jinks, 1966). Evidence for the presence of genetic variance among strains of mice in pattern of exploration in a Y maze across successive

test days has been provided by Brookshire & Rieser (1967). In addition, some evidence for heritable differences in change in open-field defecation of rats across successive trials has been reported by Broadhurst & Jinks (1966).

Open-field behavior is a widely employed index of emotionality; thus, change in this behavior may indicate change in motivational state. The primary objective of the present study was to conduct a quantitative genetic analysis of change in open-field behavior in mice. Such an analysis may provide information not only about the genetic architecture of behavioral change, but also about its evolutionary significance (Roberts, 1967).

METHOD

Daily open-field behavioral scores were obtained from 2,641 Ss, including members of two inbred parental strains of mice (BALB/cJ and C57BL/6J) and their derived F1, backcross, F2, and F3 generations. Each S was tested for 3 min on 2 consecutive days at 40 ± 5 days of age in a brightly lighted open field (36 x 36 in.) constructed of white, painted Plexiglas. Two sets of five light sources on adjacent sides of the field were beamed through red filters and holes to photoconductive cells on the opposite sides. This divided the floor of the field into 36 squares (6 x 6 in. each) and activity was automatically recorded as individuals interrupted the beams. The number of fecal

Table 1
Mean Daily Open-field Activity and Defecation Scores, and Their Changes¹

Generation ²	Activity			Defecation			N
	Day 1	Day 2	Change $\pm$ S.E.	Day 1	Day 2	Change $\pm$ S.E.	
BALB/cJ	3.88	1.91	1.97 $\pm$.28	2.05	2.14	-.09 $\pm$.065	64
C57BL/6J	12.30	10.11	2.19 $\pm$.28	.79	1.01	-.22 $\pm$.043	112
F ₁	11.10	8.94	2.16 $\pm$.16	1.39	1.66	-.27 $\pm$.035	415
B ₁	7.16	5.21	1.95 $\pm$.16	1.64	1.82	-.18 $\pm$.051	257
B ₂	11.46	9.62	1.84 $\pm$.15	.98	1.09	-.11 $\pm$.033	315
F ₂	9.33	7.49	1.84 $\pm$.11	1.26	1.45	-.19 $\pm$.026	637
F ₃	9.05	7.27	1.78 $\pm$.11	1.37	1.55	-.18 $\pm$.024	841

¹ Mean daily activity and defecation scores were obtained from transformed (square root) data and were pooled across sex and mating type within generation. Pooled subclass variances were used in estimating S.E.

² B₁ and B₂ are offspring resulting from matings of F₁ mice to members of the BALB/cJ and C57BL/6J parental strains, respectively.

boluses deposited by each S was counted at the conclusion of each test. Resulting daily activity and defecation scores were subjected to square root transformations. However, since defecation scores were low, 0.5 was added to each S's defecation score prior to transformation. Change in activity and change in defecation were then calculated for each S by subtracting the transformed Day 2 score from that of Day 1.

RESULTS AND DISCUSSION

The mean daily transformed open-field activity and defecation scores for members of the two parental strains and their derived generations are presented in Table 1. Corresponding mean changes in activity and defecation, and their standard errors, are also presented. With regard to mean daily open-field activity, a large strain difference is immediately obvious: BALB Ss are considerably less active than C57BL Ss on both Days 1 and 2. In addition, comparison of these means with those of the F₁ generation demonstrates directional dominance for high daily open-field activity.

In both parental strains and their five derived generations, Ss are less active during their second test exposure. This change in activity from Day 1 to Day 2 is not only statistically reliable, it is also quite consistent across generations. Thus, in contrast to the large strain difference in single-day activity scores, there is little evidence for a strain difference in change in open-field activity.

With regard to mean daily open-field defecation scores, a large strain difference is also apparent: BALB Ss have higher defecation scores than C57BL Ss on both Days 1 and 2. However, when these means are compared to those of the F₁ generation, no evidence for directional dominance in daily defecation scores is indicated.

Defecation scores on Day 2 are higher than those on Day 1 for both parental strains and their derived generations. However, this negative change for members of the C57BL strain is over twice that of the

BALB strain, demonstrating the presence of genetic variance for change in open-field defecation. Change in defecation for F₁ Ss is larger than that of either parental strain and, thus, provides some evidence of nonadditive genetic variance for this behavioral change.

Absence of a strain difference for change in open-field activity does not preclude the possibility of genetic variance for this character. In addition, although the presence of a strain difference in change in defecation provides evidence for genetic variance in that character, the relative magnitude of this variance is not evident. Thus, in order to more directly assess the relative magnitude of the genetic variance associated with change in open-field activity and defecation, the heritabilities of these characters were estimated. Heritabilities were estimated from the regression of scores of F₃ offspring on their F₂ midparental values. These regressions were calculated separately for male and female progeny and then pooled across sex of offspring. The validity of this method for estimating heritability has been discussed elsewhere (DeFries & Hegmann, in press). Resulting estimates of heritability for change in open-field activity and change in defecation were $0.03 \pm .08$ and $0.11 \pm .08$, respectively.

The heritabilities of daily open-field activity and defecation scores have been presented previously (Hegmann & DeFries, 1968). Heritability estimates for activity on Days 1 and 2 were 0.28 and 0.09, respectively, whereas those for defecation on Days 1 and 2 were 0.14 and 0.07. Thus, the heritability of change in open-field activity is extremely low, especially when compared to those of single-day activity scores or to that of total activity (about 0.25; DeFries & Hegmann, in press). In contrast, the heritability of change in defecation is intermediate to those of daily defecation scores and is not different from that of total defecation (0.11). It is interesting to note that these heritability estimates support the evidence obtained

from the strain comparisons in Table 1, i.e., little evidence for genetic variance associated with change in activity contrasted to that of the other activity measures, but some evidence for genetic variance in change in defecation.

The results of the present study appear to be in disagreement with those of Brookshire & Rieser (1967) who have reported that C57BR and LP mice were less active on the second of 2 test days, but that BALB/cJ Ss were more active on Day 2. However, the apparatus and test procedures which they employed were quite different from those of the present study. In addition, Weir & DeFries (1964) reported a strain difference for change in open-field activity across 5 successive test days. However, the strain difference which they observed was due to a differential change in activity across the last 3 test days, not to a differential change from Day 1 to Day 2.

The strain comparison and the heritability estimate obtained in the present study indicate the presence of little additive genetic variance for change in open-field activity. Roberts (1967) has recently suggested that the genetic architecture of a character as revealed by the methods of quantitative genetics provides some guide to its evolutionary history: In general, the fitness value of characters should be inversely proportional to their heritability. Thus, the results of the present study suggest that change in activity in a novel situation is more closely related to fitness than daily activity, total activity, daily defecation, total defecation, or change in defecation. However, the heritabilities of all defecation measures are also relatively low.

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