make comparisons between experiments when completely different phenomena are being studied.

This might help to explain some of the differences which have been reported in the literature on imprinting, and might help to avoid further misunderstandings among experimenters in this area.

JAMES M. POLT

ECKHARD H. HESS Department of Psychology, University of Chicago, Chicago, Illinois

References and Notes

- 1. A. O. Ramsay and E. H. Hess, Wilson Bull. 66, 602 (1954). 66, 602 (1954). 2. P. H. Gray, Science 132, 1834 (1960). 3. E. H. Hess, J. Comp. Physiol. Psychol. 52,
- (1959). 4. H. Moltz and L. Rosenblum, ibid. 51, 658
- (1958).

- H. James, Can. J. Psychol. 13, 59 (1959).
 J. Jaynes, J. Comp. Physiol. Psychol. 49, 201 (1956); E. A. Salzen and W. Sluckin, Animal Behavior 7, 172 (1959); B. A. Campbell and R. Pickleman, J. Comp. Physiol. Psychol. K. FICKERIAH, J. Comp. Physiol. Psychol. 54, 592 (1961).
 H. H. Schaefer and E. H. Hess, Z. Tier-psychol. 16, 161 (1959).
 S. Siagel M. C. Start, M. Start, M.
- S. Siegel, Nonparametric Statistics for the Behavioral Sciences (McGraw-Hill, New 8. York, 1956).

- York, 1956).
 D. M. Baer and P. H. Gray, Perceptual Motor Skills 10, 171 (1960).
 H. Moltz and L. J. Stettner, J. Comp. Physiol. Psychol. 54, 279 (1961).
 E. H. Hess, in Nebraska Symposium on Motivation, M. R. Jones, Ed. (Univ. of Nebraska Press, Lincoln, 1959).
 P. Guiton, Proc. Roy. Soc. Edinburgh, B 28, 9 (1958).
 G. Gottlieb and P. H. Klopfer, J. Comp. Physiol. Psychol. 55, 821 (1962).
 E. H. Hess, Experimental Analysis of Im-printing, Progress report, grant M-776, submitted to the U.S. Public Health Ser-vice, June 1962. vice, June 1962. This research was supported in part by U.S.
- 15. This Public Health Service, National Institute of Mental Health grant M-776.

26 November 1963

Early Arousal and Imprinting in Chicks

Abstract. Arousal outside the test situation and prior to response acquisition can affect strength of imprinting, if such treatment occurs early enough in life. Young chicks handled in darkness either at 5 or 9 hours of age and exposed to a moving surrogate a number of hours later were compared with nonhandled controls by means of following tests given at 30 and 54 hours of age. Handling at 5 hours resulted in a significant increment in the later following response. Handling at 9 hours produced no effect.

It has been suggested by several writers that the attachment formed between a young bird and its mother or some surrogate is dependent for its strength, duration, and time of occurrence on the emotionality of the young animal (1-3). Thus, the addition of emotion-arousing stimuli to the imprinting situation may increase the strength of following during (3)or after (2) the period critical for acquisition of this response. The results of Moltz et al. (2) and of Pitz and Ross (3) indicated that arousal is effective in producing strong imprinting only if it is elicited in close conjunction with the stimulus conditions in which the response is tested. Thus the subjects of Pitz and Ross, stimulated whenever they were not near the surrogate, and the subjects of Moltz et al., shocked outside the imprinting alley, followed poorly in comparison with animals aroused when near the surrogate or shocked inside the imprinting alley. Such data suggest that arousal may be important, not in general, but only as it is concerned with the formation of an associative bond between the stimulus

13 MARCH 1964

and the response. However, it is also possible that the generality or specificity of the contribution of arousal is age-dependent. Indeed, at the time of arousal, the subjects of Moltz et al. and of Pitz and Ross were 7 days old or more and 1 day old or more, respectively. In view of the large amount of work (3) showing the later effects on rodent behavior of early manipulations (for example, handling or shocking), it seems likely that nonspecific arousal outside the test situation, if applied early enough, might have considerable effects on imprinting in chicks. Concomitantly, the effects might be expected to decline as the stimulus is applied later in age. Such an interpretation is consistent with the results of Moltz et al. and of Pitz and Ross. Thus the experiment we report here was designed to offer a limited test of this hypothesis: that nonspecific arousal imposed on chicks outside the test situation and prior to acquisition of the imprinting response has greater effects on the latter when it is imposed at an early age than when it is imposed at a later age.

Forty-eight commercially hatched

Vantress chicks were used. They were transferred to the laboratory in closed boxes within three hours of hatching and were individually housed in wooden cages (22 by 20.5 by 13 cm) with fine mesh nylon screening. Lighting was supplied by the 200-watt ceiling bulb. Cage temperatures were maintained at approximately 31°C.

The testing apparatus consisted of a runway measuring 3 by 0.3 by 0.6 m. Its floor was covered with white cardboard and its walls were painted white with heavy irregular black lines. Illumination was supplied by a single 200-watt bulb hung over the center of the runway. The imprinting object was suspended 5 cm above the floor from a rope belt run between two pulleys located one at each end of the runway, and geared to a variable speed motor. The imprinting object was a cellulose toy duck and the unfamiliar object (used in the "following" test) was a rubber toy man. A semicircular restraining unit of wire mesh, 30 cm high with a diameter of 23 cm, was placed against the middle of one wall of the runway.

The procedure was as follows. Chicks were assigned randomly to one of four groups: H5, handled 5 hours after hatching; C5, control for H5; H9, handled 9 hours after hatching; or C9, control for H9. Arousal was produced by tactile stimulation or handling for a single 10-minute session, either 5 or 9 hours after hatching; the chick was stroked from head to tail at the rate of approximately 15 to 20 strokes per minute. All such stimulation was done in complete darkness to avoid visual effects. Con-



Fig. 1. Median following scores at 30 and 54 hours of control chicks and chicks handled at 5 and 9 hours of age.

1187

trols simply remained in their cages until the training sessions. All chicks were given training sessions for imprinting at 12 and 16 hours of age. Each animal was transported to the apparatus in a container and then placed in the restraining unit for a 1-minute habituation period. The restraining unit was then removed, and the imprinting object was introduced and moved around the apparatus at a rate adapted to the following of each individual chick. At the end of 10 minutes, the chick was returned to its cage. A record was made of the strength of following, defined as the number of seconds during which the animal was in motion and within 30 cm of the object. Two 3-minute following tests were given to each chick at 30 hours and again at 54 hours of age. At each age, half the chicks were tested with the imprinting object first and the unfamiliar object second and the remaining half were tested in the reverse order. The surrogates were moved at a constant speed of approximately 30 cm per second. Each such test was preceded by a 1-minute habituation period. A record was again made of strength of following.

Our results indicate that arousal (handling) produced some increase in the amount of following during training, particularly in group H5. However, differences were not statistically significant. During the later test sessions, handling at 5 hours of age produced a clear increment in following, while handling at 9 hours produced no observable effect.

Median following scores in seconds for each of the four groups are shown in Fig. 1. Since we found no significant differences in the strength of following of the imprinting object as opposed to the nonimprinting object, we have combined these scores. In addition, since differences between groups were almost identical for the tests at 30 and at 54 hours of age, scores for these two sessions have also been combined. Statistical analysis of the resulting data in Fig. 1 showed that the animals in group H5 followed significantly more than those in group C5 (U = 34.5, p < .05). However, there was no difference between chicks handled at 9 hours (group H9) and the 9-hour controls (C9). Since this result applies equally to both objects, it indicates that the effects of arousal prior to training were apparently nonspecific.

The data reported here give defi-

nite, though limited, support to the hypothesis of early arousal. It is possible that the comparatively slight effects of arousal on following during training were due to our method of training, that is, adapting the speed of the surrogate to each chick. Alternatively, such differences as were evident during training may have been real in the sense that they were an initial reflection of the significant effects found in the later tests.

While the results of our experiments hold for mild tactile stimulation administered at specified ages, it remains to be seen whether arousal involving other modalities and of different intensity will have the same effects.

WILLIAM R. THOMPSON RICHARD A. DUBANOSKI* Psychological Laboratory, Wesleyan University, Middletown, Connecticut

References and Notes

- 1. E. H. Hess, in Nebraska Symposium on Motivation, M. Jones, Ed. (Univ. of Nebraska Press, Lincoln, 1959), pp. 44-77. Press,
- Halikas, J. N. 2. H. Moltz, L. Rosenblum. Comp. Physiol. Psychol. 52, 240 (1959). 3. G. F. Pitz and R. B. Ross, J. Comp. Physiol.
- Psychol. 54, 602 (1961). 4. E. H. Hess, Ann. N.Y. Acad. Sci. 67, 724
- (1957) V. De 5.
- V. Denenberg, in *The Behavior of Domestic* Animals, E. S. E. Hafez, Ed. (Williams and Wilkins, Baltimore, Md., 1962), pp. 109-138. 6. The research reported here was supported by
- The research reported here was supported by a grant from the National Science Founda-tion. The manuscript was prepared by the senior author while he was a fellow at the Center for Advanced Study in the Behavioral Sciences, Stanford, Calif. Present address: Department of Psychology, University of Minnesota.
- 6 January 1964

Inheritance of Avoidance **Conditioning in Mice: A Diallel Study**

Abstract. Significant genetic differences were demonstrated in the rate of avoidance conditioning among offspring from all 25 mating combinations of 5 highly inbred mouse strains. Hybrids of C3H parents learned fastest, while those of A/JAX parents learned slowest. Most hybrids learned better than either parent. Evidence that differential influences of the early maternal environment affected the rate of learning was not supported.

Although most genetic research has been concerned with the study of morphological and physiological characteristics, there is considerable current interest in the inheritance of behavior characteristics. Behavioral differences have been demonstrated among highly inbred strains of mice and their respective F1 crosses in areas of locomotor activity, exploration of novel environments, and other relatively simple classes of behavior (1). Whereas some recent evidence implicates the importance of hereditary differences in learning behavior (2), most previous studies considered only a few pure strains, or two pure strains and their crosses. Consequently, the findings may be applicable only to the strains chosen and may not be representative of genetic relationships in differing strains. The objective of this investigation was to study the range of genetic influence on learning in mice by using a diallel mating system in which all intercrosses among a set of inbred strains were tested for the acquisition of a learned avoidance habit.

Ten males and 10 females from each of the 25 mating combinations of the following 5 pure strains of mice were tested for acquisition of avoidance conditioning: A/JAX, BALB/c, C3H, C57BL/10, and DBA/1. A total of 500 mice were tested. At approximately 100 days of age, each subject was placed in a shuttle-box, measuring 26.5 by 5 by 4 cm, and received 200 consecutive avoidance-conditioning trials. The conditioning stimuli were a muffled buzzer and a 3000 cy/sec sine-wave tone which began 2.5 seconds after the onset of the buzzer. Electric shock was programmed to be delivered to the grid floors 5 seconds after the onset of the first cue. A jumping response across a continuously charged pit during the first 5 seconds of each trial activated a photosensitive control system which postponed shock for that trial and was considered an avoidance response. A pit-crossing after 5 seconds terminated the cues and shock and was considered an escape response. The interval between trials was fixed at 30 seconds. Four mice were trained simultaneously according to this schedule in separate automatic testing chambers. The score for each subject was the number of avoidances in 200 trials.

The data were arranged in a 5 by 5 square design, in which the rows represented the genotype of sires, and the columns, the genotype of dams. The 25 squares thus formed represented the 25 genotypic combinations from all matings of the 5 pure strains, and included 20 F1 crosses and the 5 pure strains. Two complementary statistical models were used to assess the data. Model 1 represented a factorial analysis of variance by which the genetic