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Imprinting in Birds

Research has borne out the concept of imprinting as a type of learning different from association learning.

Eckhard H. Hess

Thirty years ago Konrad Lorenz, the Austrian zoologist, formulated the concept of imprinting as a result of his observations of the primary socialization process in newly hatched birds (1). At the time, studying species such as greylag geese and partridges, where the young are able to locomote on their own soon after hatching, he thought the process to be peculiar to birds. Basically, Lorenz found imprinting to be an emotional bond of the young to the parent, formed very rapidly soon after hatching. This specific attachment to the parent was dependent on the parent's being the first moving object experienced by the young; when Lorenz himself took these young animals while they were still a few hours old and had them follow him before seeing their own mother, they would thereafter regard him as their parent, ignoring their biological mother.

Although little experimental work on imprinting has been done by the Lorenz group since these initial observations, there has been a steady increase in imprinting research in laboratories in Europe, and even more in the United States. The first paper by Ramsey and myself (2), published in 1954, was the beginning of mounting series of studies by numerous investigators; the bulk of this work is covered by an excellent review article by Moltz (3). Rather than duplicate his efforts, I discuss here the work which has been going on in our University of Chicago and Maryland laboratories

since publication of my last article of this type, which appeared 5 years ago (4). Since that time, a great deal of observation and laboratory research on imprinting has been carried on with precocious bird species—that is, species in which the young are hatched at a relatively advanced developmental stage so that they are able to move about readily at an early age. While several experimenters in the area of imprinting seem to regard it as the same as simple association learning, our own research has led us to a different conclusion. Association learning is a widespread behavioral phenomenon and has come to dominate much psychological research. A great deal has been found out about association learning—for example, that practice makes perfect, old habits can be replaced by new ones, and so on. Thus, it is natural that some experimenters have approached the problem of imprinting with the assumption that it is a form of association learning. But all of our experiments have led us to discard this assumption, for the more we have studied imprinting, the more firmly we have become convinced that the imprinting phenomenon is considerably different from ordinary association learning.

Before considering our more recent research, I will review briefly some of the earlier experimental findings which led us to this conclusion. Knowledge of these findings is necessary to an understanding of the implications of our newer investigations.

Early Findings

One of the most important of these earlier findings is that there is a "critical period" in the life of the bird during which the imprinting experience is most effective in determining the character of its adult social behavior (2). The critical period for imprinting in chicks and ducklings lasts, at the most, from the time of hatching up to 32 or 36 hours of age, and the peak of sensitivity to the imprinting experience occurs at 13 to 16 hours of age in both species. We did not, of course, originate the idea of a critical period in imprinting, for Lorenz had already stated in 1935 that imprinting could occur only during a specific life period in the animal. Such limited "critical periods," during which the animal is extremely susceptible to the effects of certain kinds of experiences, have never been found in cases of association learning. This is apparently one reason why some researchers have resisted the idea of critical periods in imprinting. Nevertheless, my associates and I have found that the "critical period" is a basic characteristic of imprinting, for we have never failed to find its existence and importance. What is more, if experimentation on imprinting is carried out with animals who are beyond the critical age period, then only association learning, and not true imprinting, is possible. This fact has not been fully recognized by experimenters who believe that imprinting and association learning are the same processes.

Another basic difference which my associates and I have found between imprinting and association learning concerns the manner in which learning behavior is affected by drugs (5, 6). We found that administration of meprobamate or carisoprodol to chicks and ducklings learning a color discrimination problem involving food reward does not depress their ability to learn the problem. In fact, they may

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even learn it better. But when we attempt to imprint animals that are under the influence of these drugs they subsequently show little effect of the imprinting experience. We have found that these drugs interfere with the *process* of imprinting rather than with retention of imprinting effects, for animals imprinted normally but tested for strength of imprinting under the influence of either drug exhibit the usual effects of imprinting.

In association learning, spacing of effort or practice trials, rather than massing, promotes effective learning. The converse is true for imprinting. We have demonstrated that it is the amount of following done by the animal during the imprinting experience, not the amount of time spent in following, that determines the effectiveness of the experience in forming a bond between the young animal and the parent object (2). We determined this by having the young animal follow the parent object for fixed distances during varying periods, and by having it follow the object for varying distances in a fixed period; the actual distance followed was found to determine the strength of the animal's subsequent attachment to the object. Having an animal follow the mother object while climbing inclined planes, thus expending more effort than it would in traveling the same distance on a level surface, also resulted in stronger attachment to the mother object. This relationship between the amount of following, or of effort expended, during the imprinting experience and the strength of imprinting is described by the "law of effort," which states that the strength of imprinting is a logarithmic function of the amount of effort expended during the imprinting experience. We have now found that under certain conditions the law of effort must be further defined and qualified, for it operates in conjunction with certain specific conditions, particularly with respect to the critical period and to whether or not the animal has already become attached to a social object.

There is another striking difference between imprinting and association learning. In association learning, painful or aversive stimulation causes animals to avoid association with the object connected with the painful stimulation, but the opposite is the case in imprinting. If a young duckling is being imprinted to a human being who steps on its toes, the duckling does not

Table 1. Significance of differences between groups, according to the Mann-Whitney U-Test (see text). N/A, not applicable; N/S, not significant.

Group	16-Hour, control	24-Hour, control	36-Hour, control	48-Hour, control	16-Hour, socialized	24-Hour, socialized	36-Hour, socialized	48-Hour, socialized
16-Hour, control		.020	.010	.006	.007	N/A	N/A	N/A
24-Hour, control	.020		N/S	.008	N/A	.0003	N/A	N/A
36-Hour, control	.010	N/S		N/S	N/A	N/A	.0003	N/A
48-Hour, control	.006	.008	N/S		N/A	N/A	N/A	.0003
16-Hour, socialized	.007	N/A	N/A	N/A		N/S	.0003	N/S
24-Hour, socialized	N/A	.0003	N/A	N/A	N/S		.0003	N/S
36-Hour, socialized	N/A	N/A	.0003	N/A	.0003	.0003		.0008
48-Hour, socialized	N/A	N/A	N/A	.0003	N/S	N/S	.0008	

run away from the careless human being in fear; on the contrary, it stays even closer. This observation led us to conclude that the enhancing effect of such painful experience on the degree to which the animal imprints represents a basic difference between imprinting and association learning. Recent laboratory work has confirmed this conclusion drawn from naturalistic observation.

Finally, we have found another contrast between imprinting and association learning, one indicated by Lorenz's original work on imprinting, in which he found that hatchlings first exposed to him would not form an attachment to their own mother. In association learning, whatever has been *most recently* learned has greater influence on an animal's behavior, while in imprinting, the object to which the animal is exposed *first* is the one to which it is most strongly attached. This we have determined by exposing animals successively to two different imprinting objects during the critical age. The animals showed imprinting to the object to which they were exposed first more frequently than to the object to which they were exposed last. This greater difficulty in imprinting to a new object after having become attached to another object was the reason why Lorenz stated that imprinting, once set in motion, cannot be erased or reversed.

These five differences between imprinting and association learning which my co-workers and I have postulated have been amplified and confirmed by our recent laboratory investigations. In addition, we have discovered some of the factors which appear to be responsible for other experimenters' results which have led to conclusions divergent from our own.

For example, some experimenters have housed their animals communally,

in lighted pens, with or without food and water, prior to the first imprinting experience, while we have always maintained our subjects in visual isolation so as to preclude the effects of prior socialization. The observed effects of primacy versus recency have justified our adherence to this procedure, for if we are to properly study imprinting, we must make certain that no imprinting has occurred before the desired imprinting experience takes place.

Effect of Socialization on Following and Imprinting

In chicks. We decided to expose experimental animals to the company of their siblings at different times before the imprinting experience with a parent substitute in order to determine precisely the effect of such prior socialization on the animals' ability to imprint to this parent surrogate (see 7).

In this experiment 370 Vantress broiler chicks, all hatched in our laboratory darkroom, were studied. These chicks were isolated in individual boxes in the darkroom, without food or water, until they were used experimentally. The chicks that had been exposed to the company of their siblings before the imprinting experience were removed from their boxes and placed with siblings in a lighted section of a standard brooder for 2 hours. All the chicks were placed individually in the Hess imprinting apparatus (see 4) and observed during a 22-minute imprinting procedure. The imprinting model to which they were exposed was a blue ball (Ostwald pa 14), 16 centimeters in diameter, having a speaker inside it which gave a continuous and rhythmic call of "come, chick, chick, chick, chick." During the imprinting

procedure the ball was stationary for 10 minutes and then made four trips around the 10-foot runway, moving intermittently.

Two principal groups of subjects were established. The first, the control group, consisted of 220 chicks divided into four subgroups according to the age at which imprinting occurred. Each subgroup contained 50 to 70 animals. These chicks had all remained in the darkroom without visual or social experience of any kind until the time of imprinting.

The other principal group, the socialized group, was made up of 150 animals divided into four subgroups according to the age at which imprinting occurred; each subgroup contained 30 to 50 animals. All these chicks had been exposed, in the brooder, to the company of their siblings for 2 hours just prior to the imprinting experience.

Figure 1 shows the mean distance (in feet) that the model was followed by the animals of each of the eight subgroups. The control chicks (isolated prior to testing) showed the greatest tendency to follow the model if they were first exposed to it at the age of 16 hours. It is evident that the control animals show a steadily decreasing disposition to follow the model as a function of increasing age at time of exposure. As may be seen in Table 1, all the chicks that had had socialization prior to the imprinting experience followed the model significantly more than the isolated animals did; this was particularly true for chicks in the 36-hour age group. The effect of socialization is quite evident, particularly in animals exposed to the model at ages

when the imprinting response normally falls off sharply.

In a separate study (8) my associates and I were able to determine the effects of exposure to light alone on the "following" response and to assess whether increased amounts of following by the socialized animals results in a greater degree of imprinting. To test for the effects of light alone, 56 Vantress broiler chicks were divided into four groups of 12 to 16 animals each. The normal procedures for hatching and isolation, as outlined above, were followed. Two control groups of 14 chicks each were imprinted normally at 16 and 48 hours, and two experimental groups ($N = 12$, $N = 16$) were subjected for 2 hours to patterned light prior to exposure to the imprinting model. While exposure to the patterned light had little effect on the behavior of the animals exposed to the model at the age of 16 hours, it led to increased following in the group exposed to the model at the age of 48 hours, but the effect was much less than in the animals previously exposed to both light and socialization.

In the same study, 44 chicks, divided into isolated (control) and socialized groups, were first imprinted at 16 and 36 hours, then tested for strength of imprinting. Again, the procedures of hatching, isolation, socialization, and imprinting were those followed in the larger study, except that, after the imprinting experience, the animals were returned to their individual boxes and isolated in the darkroom for 24 hours, until the time of testing.

Testing for strength of imprinting

consisted of placing each animal in the imprinting apparatus between the model to which it had been exposed and a group of four chicks in a clear plastic enclosure. The scores were based on the degree to which the animal was attracted to the model. For 2 minutes the model was kept silent and stationary; for another 2 minutes the model emitted sound and was stationary; during the third 2-minute period the model was silent and moving; and during the fourth period the model emitted sound and moved. If the chick chose to be near the model during all four periods, it was scored 100 percent.

Table 2 shows the correlations between amount of following and test scores for each of the four groups. It is clear from these correlations that the only animals which gave evidence of imprinting to the model were animals in the 16-hour-old isolated group, although this group ranked third in regard to following of the model. In contrast, while the 36-hour socialized group showed the greatest amount of following and the 36-hour isolated group showed the least, there is no evidence of imprinting to the model in either group. Even though the socialized chicks in the 16-hour group followed the model well, it is clear that they were imprinted to their siblings and not to the model.

At each age, the socialized groups showed significantly more following behavior than the control groups did (for the 16-hour group, $p = .05$; for the 36-hour group, $p = .001$). While there was little difference between the means for the two socialized groups, there

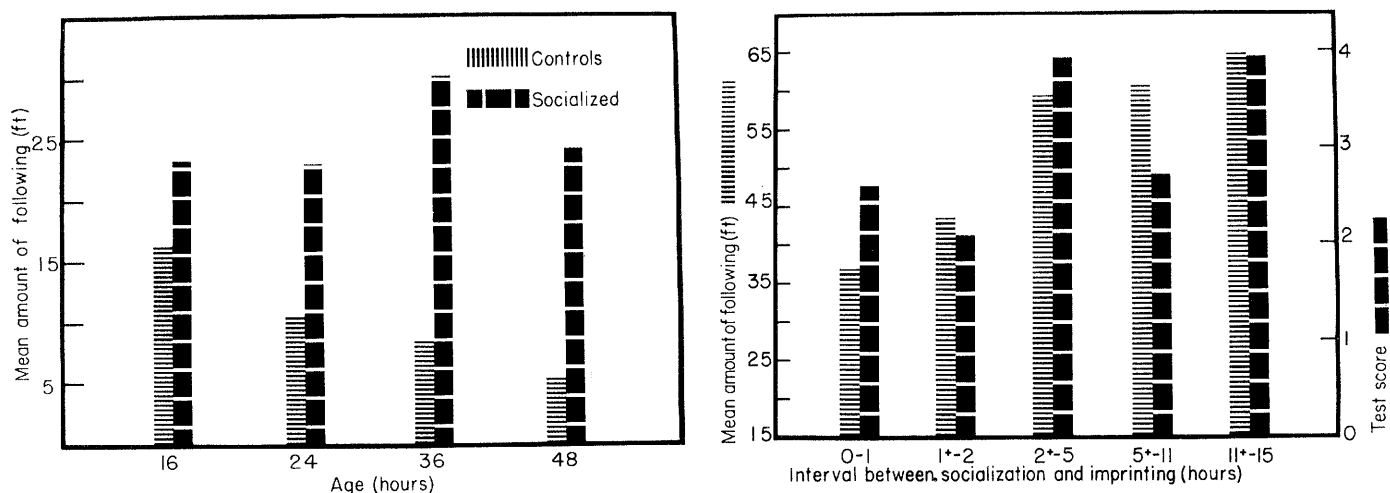


Fig. 1 (left). Mean distances (in feet) that the model was followed during imprinting by inexperienced controls and by chicks socialized prior to imprinting. Fig. 2 (right). The effect on following of the interval between socialization and exposure to the imprinting model in ducklings.

was a marked difference between the means for the two control groups; the results were significant at the 0.02 level, according to the Mann-Whitney U-Test.

It is evident from these results that the law of effort operates only if the chicks, at the time of exposure to the model, have not already been exposed to the company of their siblings and are not past the critical period for imprinting. The only group that met these criteria was the 16-hour isolated group, and here the amount of following is positively correlated with the strength of imprinting as determined in the tests made 24 hours later. Thus, the importance of the critical period and of primacy rather than recency are again apparent. If animals are past the critical period at the time of exposure to the model, or have had previous social experience, then it is questionable whether true imprinting can occur, and the amount of following by chicks under such conditions may indicate very little about imprinting.

In ducks. Ramsay and I (9) made another study of the effect of socialization, on the ability of ducklings to imprint to a model. We made the study on ducklings because we have found that the different bird species do not all imprint equally well; these differences are apparently related to some extent to the degree of domestication which has occurred.

Wild mallard ducklings ($N = 261$), hatched in our laboratory, were the subjects for the first phase of this study. Like the chicks, the ducklings were hatched in the dark and kept in

Table 2. Correlation, for four groups of chicks, between (i) amount of following and test scores and (ii) mean rank of following and test scores.

Group	Age at imprinting (hr)	Mean distance followed (m)	Rank	Mean test scores	Rank	Correlation*
Control	16	5.5	3	5.75	1	+0.76
Socialized	16	9.3	2	1.00	4	-0.78
Control	36	1.5	4	2.00	2	+0.02
Socialized	36	10.0	1	1.50	3	+0.08

* Spearman rank correlation coefficient.

individual isolation boxes. Ducklings in one group ($N = 144$) were exposed to the company of their siblings for 2 hours during the peak of the critical period for imprinting (13 to 16 hours after hatching) and then returned to their isolation boxes and kept in them for various lengths of time before exposure to the model. This group of ducklings was divided into five subgroups, according to the length of the period of isolation between socialization and imprinting. Another 33 ducklings were used as controls; these had no socialization or visual experience prior to imprinting at the age of 14 to 16 hours.

Figure 2 shows the mean amount of following and the mean scores obtained in the testing for imprinting strength 24 hours after imprinting. The test for imprinting strength was the same as that described by Ramsay and Hess (2). It is clear that, as the interval between socializing experience and imprinting increased, the amount of following also increased: the animals which had been isolated for 11½ to 15 hours after the socialization period followed the model to approximately the same extent that the control animals did [the average for the

controls was $\sim 19\frac{1}{2}$ meters (64.3 ft)]. On the other hand, whereas the control animals had test scores of 5.35, none of the animals in the experimental groups had test scores as high as this.

Thus it appears that when ducklings are exposed to the imprinting model soon after having been socialized, they essentially reject the model. However, the animals appear to have been "primed" by the socialization so that, long after socialization has taken place, they follow the model almost as much as 14- to 16-hour-old unsocialized ducklings do and more than unsocialized ducklings of their own age do. However, the test scores for the socialized ducklings are lower than those for the 14- to 16-hour-old unsocialized ducklings; thus it is clear that the processes occurring in these socialized animals are completely different from those occurring in 14- to 16-hour-old unsocialized ducklings, even though the amount of following is similar.

We can see the effect of the critical period more clearly if we rearrange the data according to the age of the animals at the time of the imprinting experience, as in Fig. 3. Here it seems that when both socialization and im-

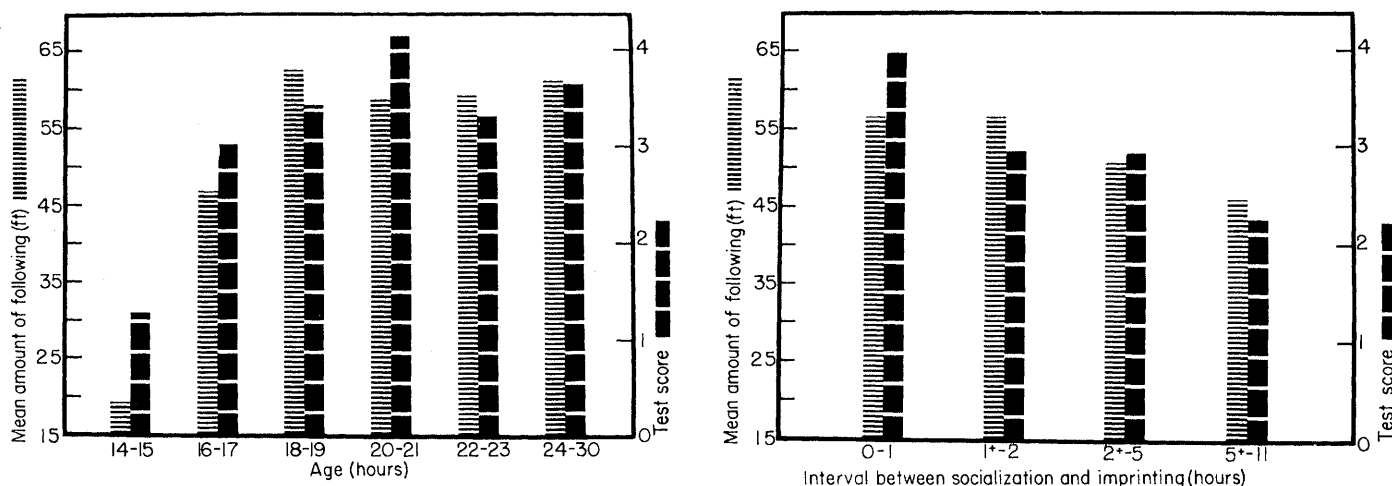


Fig. 3 (left). Mean distances (in feet) that the model was followed, and test scores, for groups of socialized animals imprinted at different ages. Fig. 4 (right). The effect on following of the interval between socialization and imprinting in ducklings imprinted during the critical period only.

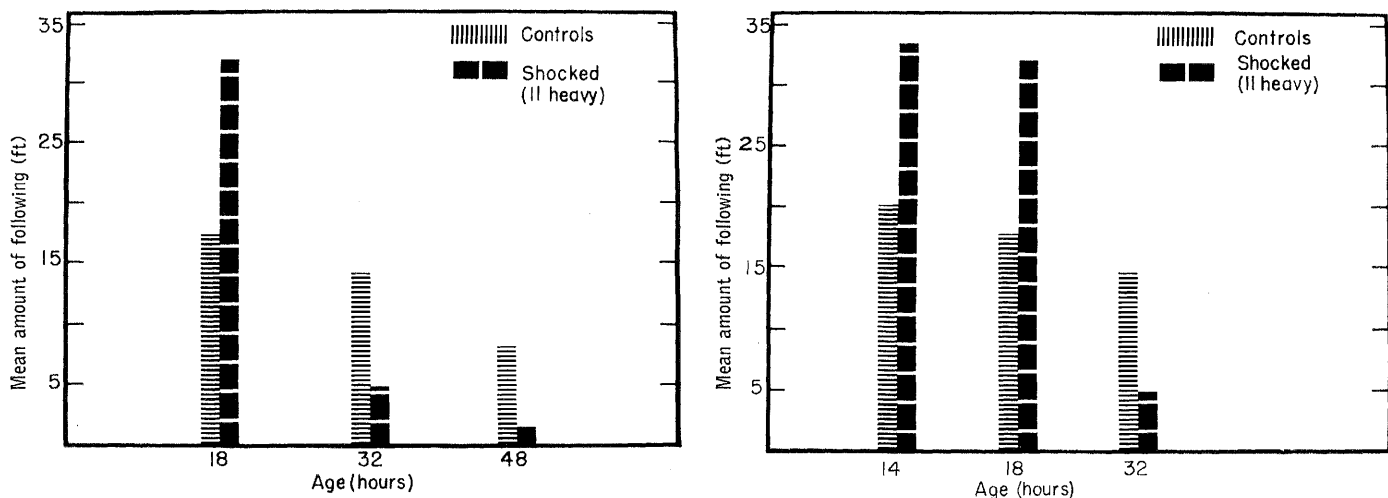


Fig. 5 (left). Mean distances (in feet) that the model was followed by three groups of chicks given 11 heavy electric shocks during imprinting at different ages, compared with distances for unshocked controls. Fig. 6 (right). Mean distances (in feet) that the model was followed by three groups of chicks given 11 heavy electric shocks during imprinting at different ages, compared with distances for unshocked controls.

printing occur early in the life of the animals, both the amount of following and the test scores are very low. As age increases, together with increase in the interval between socialization and imprinting, there is a rise both in test scores and in following. This trend is the opposite of that normally found with isolated ducklings, for which following and test scores decrease with age.

We used 84 mallard ducklings from the group of 261 for the second phase of this study. These animals were given 2 hours of socialization early in life and then were exposed to the model at the peak of the critical period for imprinting, 13 to 16 hours of age. As before, the intervals of visual deprivation and isolation in individual compartments between the socialization and imprinting were varied; these intervals ranged from 0 to 11 hours. The animals were divided into four groups, according to length of isolation time. Figure 4 shows the amount of following and the test scores for these groups at the time of testing, 24 hours after imprinting. For these 84 animals the effect of isolation on test scores was exactly the opposite of that for the animals in the group of 144. Evidently, then, when imprinting occurs during the peak of the critical period (13 to 16 hours), a relationship is obtained as follows: the longer the interval between time of socialization and imprinting (that is, the younger the animal at the time of socialization), the greater the inhibition of following and the lower the test scores.

When the results for the two experimental groups are taken together, it seems that a 2-hour period of socialization with siblings has a negative effect on the imprintability of ducklings which are later exposed to the imprinting model, and that the earlier in the life of the duckling the socialization occurs, the stronger the negative effect is. This effect is especially notable when the ducklings are imprinted during the normal peak of sensitiveness. These findings seem to indicate that strong emotional attachments can be formed in ducklings before the critical age for imprinting, as determined in our laboratory.

It is apparent that, basically, socialization lowers imprinting strength in both species, ducks and chicks. It is also clear that these results support our earlier findings regarding the importance of primacy rather than recency in imprinting. The difference between the two species in specific effects of prior socialization also indicates the effects of domestication on the nature of the following response during the imprinting experience. Chicks normally do not imprint as well as ducklings do. In chicks, prior socialization with siblings enhances the amount of following, particularly in animals imprinted at the age of 36 hours, whereas, in ducklings, socialization decreases the amount of following. The two species are similar in that prior socialization with siblings prevents young animals from achieving imprinting test scores as high as those normally attained by 14- to 16-hour-old isolated and visually

inexperienced control animals. Therefore, it must be concluded that the fact that an animal can, under certain circumstances, follow quite well even though it was not exposed to the model until after the critical period does not mean that it is imprinting as well as previously unsocialized and visually inexperienced animals imprinted at the critical age. Thus, the importance of the critical period is again demonstrated, in the fact that the processes which occur during the critical period are different from those which occur afterward.

It may also be concluded, on the basis of these results, that animals imprint only to the first moving object introduced into their environment—that is, primacy, and not recency, is the more important principle. In fact, imprinting must function in this way to be of any value to an organism under normal circumstances, for in order that the young animals not stray away from parental protection when they are first able to move about on their own, imprinting must occur early in life, and to the first moving object seen, which, in the natural situation, is the parent. The high degree of following that can be obtained in already socialized animals which are past the critical age for imprinting must be considered to result from association learning processes or to be related to a completely different function, not to true imprinting, for it is apparent from our research that a different kind of social bond is being formed under such circumstances.

Effect of Electric Shock on Following and Imprinting

The importance of the critical period and the fundamental differences between imprinting and association learning have been demonstrated not only by the experiments on socialization but also by recent experiments on the effects of electric shock on the following tendency of birds during the imprinting experience (10). These experiments were begun in order to test our earlier informal observation that stepping on a duckling's toes apparently increased its disposition to follow a human being.

In the first such experiment the subjects were 60 Vantress broiler chicks hatched at our laboratory. These chicks were divided into three age groups (18, 32, and 48 hours at time of imprinting), and each age group was further subdivided into two treatment groups—a control group and an experimental group. All the animals were hatched in a darkroom and kept isolated in individual boxes until the time of exposure to the imprinting model. Again, the Hess imprinting apparatus was used, and the model to which the animals were exposed was a blue ball 16 centimeters in diameter. Inside the ball was a loudspeaker emitting the recorded sound "Come, chick, chick, chick, chick."

The experimental animals received 11 electric shocks, each of approximately 3-milliamper (ma) intensity and ½-second duration, during the imprinting procedure; the control animals received none. The shocks were delivered

through electrodes attached to the wings of the chick. The control animals also wore these electrodes but never received any shocks.

During the imprinting procedure the model was stationary for 10 minutes and was then moved intermittently around the runway until it had completed four turns. The animal was shocked once during the initial 10 minutes, once during the first turn, twice during the second turn, three times during the third turn, and four times during the fourth turn.

Figure 5 shows the total amount of following of the model for each of the three age groups. It may be seen from Fig. 5 that the administration of shock doubles the amount of following at the age of 18 hours, during the critical period, but halves it at the end of the critical period. For the 48-hour group, the amount of following in control animals is so low that there is little statistical difference between results for control and for experimental animals.

In order to clarify some of the factors involved in this enhancing effect of electric shock on following during the critical period and this inhibitory effect after the critical period has passed, a further experiment was carried out in which the intensity and number of shocks were varied for each age group.

A group of chicks ($N = 120$) was divided into three age groups (14, 18, and 32 hours at time of imprinting), and each age group was further subdivided into four different treatment groups. One of the four subgroups was

a control group; the second consisted of animals which received 11 shocks of 1-milliamper intensity, scheduled as before. The third subgroup received 27 shocks of 1-milliamper intensity during the imprinting experience, while the fourth consisted of animals which received 27 shocks of a higher intensity (3 ma) during imprinting. All shocks lasted ½ second. The 27 shocks for the third and fourth subgroups were scheduled as follows: three shocks during the initial 10-minute exposure to the stationary ball, six shocks during each of the four turns of the ball around the runway. In all other respects the imprinting procedure for animals in each of the groups was the same as for animals in the experiment just discussed.

Figures 6–8 show the total amount of following of the model for each of the three age groups and for various degrees of shock. In animals that received 11 shocks of 1-milliamper intensity, the 14-hour-old chicks followed approximately one-third more than the control animals did; as before, the shocked 18-hour-old animals followed almost twice as much as the control animals of the same age did. However, in the 32-hour group the amount of following by the shocked animals was only one-fourth that for the control animals.

When the animals were given 27 shocks of 1-milliamper intensity, the amount of following was one-third higher for shocked 14-hour-old chicks than for nonshocked control chicks of the same age. In the 18-hour group the

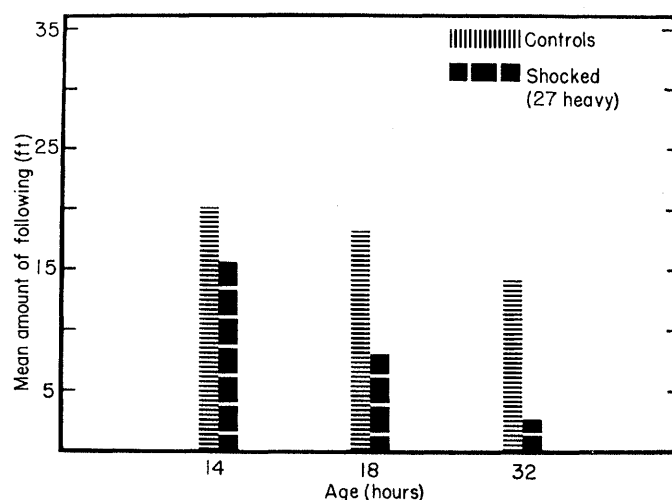
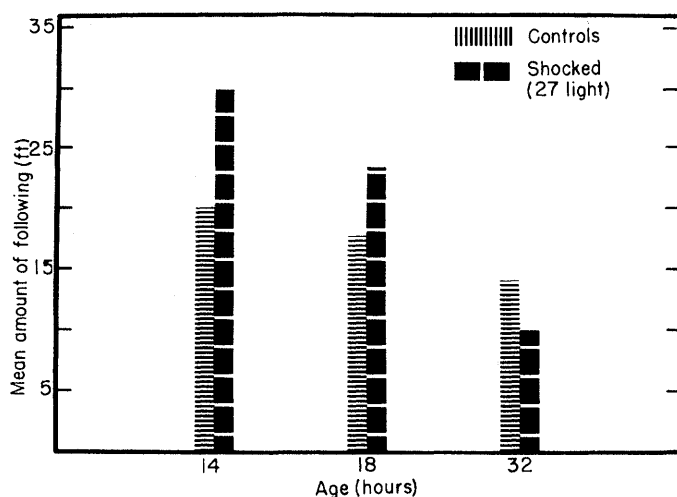


Fig. 7 (left). Mean distances (in feet) that the model was followed by three groups of chicks given 27 light electric shocks during imprinting at different ages, compared with distances for unshocked controls. Fig. 8 (right). Mean distances (in feet) that the model was followed by three groups of chicks given 27 heavy electric shocks during imprinting at different ages, compared with distances for unshocked controls.

amount of following was one-third higher for the shocked chicks than for the controls. In the 32-hour group the amount of following for the shocked chicks was about half as much as that of the controls.

In chicks that had been given 27 shocks of 3-milliamper intensity it was found that the amount of following was about one-fifth less in 14-hour-old shocked animals than in the controls. In the 18-hour-old chicks, shock definitely decreased the amount of following: the shocked chicks did only one-fourth as much following as the controls. The effect was just as drastic for the 32-hour-old chicks: the shocked animals did about one-fifth as much following as the controls.

The finding that the effect of electric shock on the amount of following in the imprinting situation is highly dependent on the age of the animal is further evidence of the importance of the critical period in imprinting, and supports the postulation that the imprinting process is fundamentally different from the usual association learning with respect to the effect of aversive or painful stimulation. Administration of rather strong and frequent electric shock in the course of exposure to the model during the critical period interferes only slightly with the animal's tendency to follow, and animals shocked at lesser intensities actually fol-

low more than unshocked controls. But the administration of electric shock during exposure to the model after the critical period has passed decreases the tendency of the animals to imprint, and the effects are exactly the same as in association learning processes. This, of course, gives substantial support to the notion that the processes occurring after the critical period has passed are association learning processes.

Other Imprinting Situations

These experiments on the effects of prior socialization and the effects of electric shock on imprintability reflect the unique characteristics of the imprinting process during the primary socialization of young birds. By means of the imprinting process, in the natural situation the young bird learns very quickly the visual and auditory characteristics of its parents and also of the entire species to which they belong. However, we have recently discovered that imprinting processes do not occur only during the period of primary socialization but occur also in certain other important early learning situations in chicks and ducklings. Thorpe (11) has suggested the possibility that some animal species are imprinted to the habitat in which they

live, but this "environment imprinting" has not yet been demonstrated experimentally. We have found what appears to be an imprinting of young birds to the characteristics of food objects.

Several years ago Robert Fantz (12), using the Hess pecking preference apparatus (see Fig. 9), studied the innate pecking preferences of young chicks for small objects of different shapes. He studied these preferences by counting the number of times the chicks pecked the objects presented to them. He attempted to assess the effects of the opportunity to obtain food directly from objects of a certain shape upon the innate preferences and found that there were temporary changes in preference.

Since then my associates and I have carried out many experiments (13) in which, through food rewards, newly hatched chicks have been stimulated to peck at shapes they do not normally prefer to peck at and to neglect normally preferred shapes. We attached a hollow holder to the back of each stimulus object and filled the holder with fine grain. Figure 9 shows (dark area in stimulus object at upper right) how the chicks could peck through a small hole in the stimulus object and thus obtain food directly from the grain holder. It was found, when 3-day-old chicks were used, that if pecking at a stimulus usually not much pecked at is reinforced and pecking at a normally preferred stimulus is not reinforced, over a period of about 2 hours, the chicks will subsequently peck more at the normally less preferred stimulus, not only during the period of reinforcement but also during extinction, when the food reward is no longer given. The effect upon pecking preferences of such a short period of reward appears to be rather stable and can last over a 10-day period of extinction, in which the chicks are tested from 4 to 6 hours each day.

It is obvious that, in this situation, the chicks have learned what objects they must peck at in order to obtain food. This appears to be very much like ordinary discrimination learning, in which the animal learns which of two differently colored food boxes contains feed. Further work, however, has shown that the learning in the pecking studies differs a great deal from discrimination learning. We found the first indication of this difference in an experiment in which we varied the age at which the food reward was presented (14).

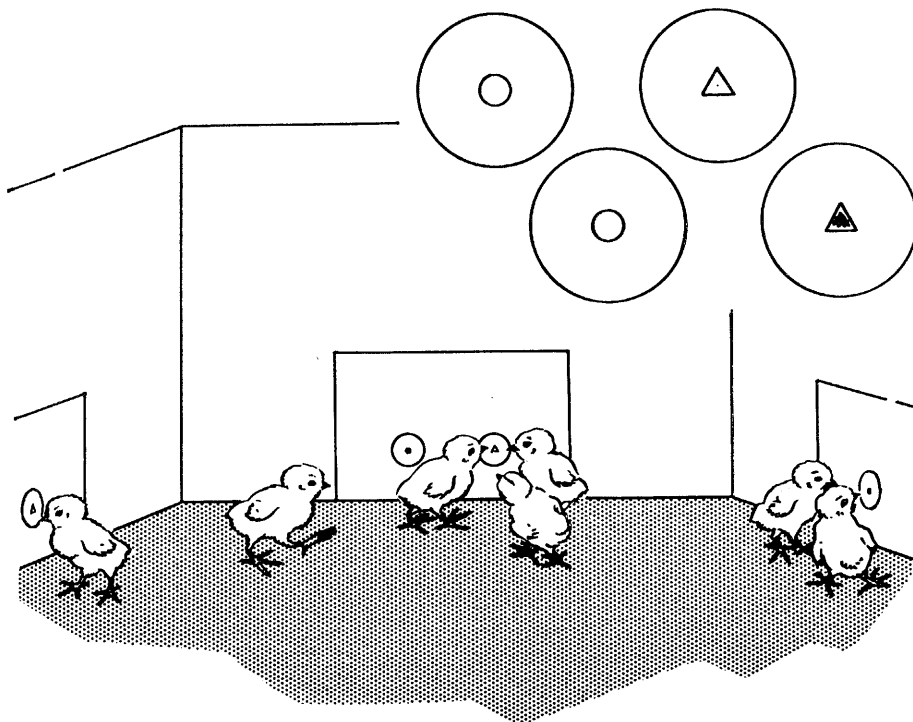


Fig. 9. Schematic diagram of the Hess pecking apparatus. Enlarged representations of the stimuli are shown at upper right.

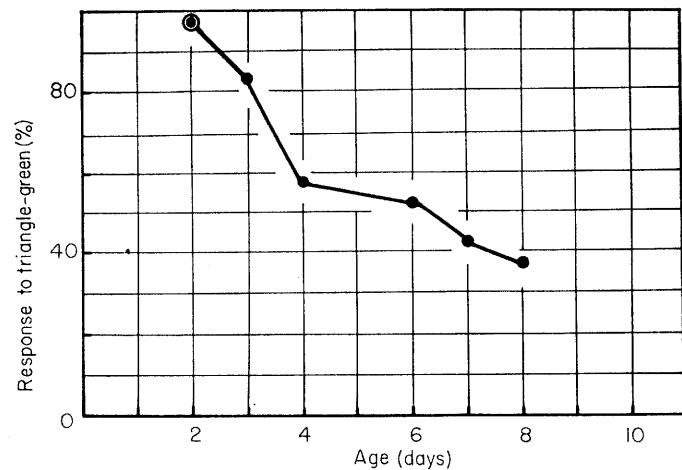
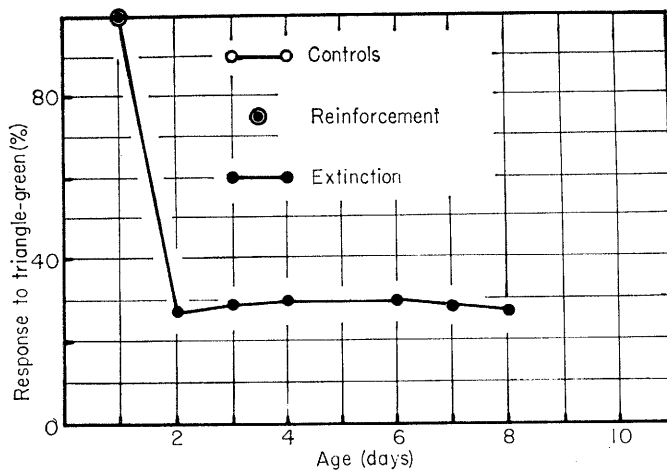


Fig. 10 (left). Responses of chicks given food rewards for pecking at the triangle-green stimulus at 1 day of age. Fig. 11 (right). Responses of chicks given food rewards for pecking at the triangle-green stimulus at 2 days of age.

In this experiment we used two stimuli: a small white triangle on a green background and a small white circle on a blue background.

Approximately 300 Leghorn chicks were divided into six groups. At the appropriate age, pecking at the less preferred stimulus, the triangle on green background, was rewarded with food for 2 hours. After this 2-hour period the chicks were tested without food reward for 2 hours each day. At no time was any food reward given for pecking at the circle on blue background, the stimulus which the chicks innately preferred.

Chicks in the first of the six groups were 1 day old when they were given the food-reward experience. Only the triangle-green stimulus was presented, so as to increase the number of opportunities for rewarded pecking at this stimulus, as 1-day-old chicks normally do less pecking than older chicks. However, on subsequent testing days both the circle on blue background and the triangle on green background were presented. These chicks made 16,000 responses to the triangle-green stimulus, all of which were rewarded, yet for 6 days following the reinforcement experience the previous reinforcement had no apparent effect on the innate pecking behavior. More than 16,000 responses were made over the 6 testing days, with an average response to the triangle-green stimulus of 27 percent, which is within the control limits for triangle-green stimulus preference in comparison with circle-blue stimulus. The results for this group are shown in Fig. 10.

Chicks in the second group obtained food rewards at the age of 2 days

for pecking at the triangle-green stimulus but not for pecking at the circle-blue stimulus. They made over 27,000 pecks, 98 percent of them being responses to the triangle-green stimulus. In subsequent testing there was a short-term effect of previous reinforcement upon pecking behavior; on the first day of the extinction period 83.5 percent of the responses were to the triangle-green stimulus. However, preference for this stimulus rapidly dropped; after 5 days of extinction testing the total cumulative response to the triangle-green stimulus was 38 percent. For the last 2 days of testing the responses to the triangle-green stimulus were 16 and 24 percent, respectively. These percentages are no higher than percentages for the controls; thus, the effect of reward had been completely extinguished by the last 2 days of testing. The results obtained from this group are shown in Fig. 11.

On the other hand, chicks in the third group, given the food-reward experience at the age of 3 days, showed behavior quite different from that of the 1-day and 2-day groups: they made 45,000 reinforced responses, or 99 percent of all responses, to the triangle-green stimulus during the reinforcement period. During the 7 days of extinction testing the response to the triangle-green stimulus remained high, never dropping below 93 percent of the cumulative total of nearly 83,000 responses. Even on the last day of testing, responses to the triangle-green stimulus were 93 percent. Thus, the effect of reinforcement was quite strong and permanent for this group, as may be seen in Fig. 12.

The preferences of chicks in the

fourth group were tested for a 2-day period, when the chicks were 3 and 4 days old, prior to the food-reward experience. During this time the response was within usual limits for nonreinforced pecking, 23 percent of the pecks being made at the triangle-green stimulus. When the chicks were 5 days old, pecking at the triangle-green stimulus was reinforced. During this time, 98 percent of the responses, or 40,000 pecks, were made to the triangle-green stimulus. In the next 5 days, during the extinction period, there was definitely an effect of previous reinforcement upon pecking behavior, as shown in Fig. 13, but the effect was not as strong as it was for the 3-day-old group. The preference for the triangle-green stimulus gradually declined over the period of extinction to a total of 79 percent of cumulative responses. On the last day of testing, 69 percent of the responses were to the triangle-green stimulus.

Chicks in the fifth group, given food rewards at the age of 7 days for pecking at the triangle-green stimulus, showed no effect of reinforcement upon their innate preference, which had been tested when they were 4, 5, and 6 days old. During these days of pre-reinforcement testing, 35 percent of their responses were to the triangle-green stimulus. During the 3 days of extinction testing following reinforcement, the percentage was even lower than that for the pre-reinforcement period: at the end of the extinction testing, 14 percent of the total number of cumulative responses had been made to the triangle-green stimulus (see Fig. 14).

Chicks in the last group, given food

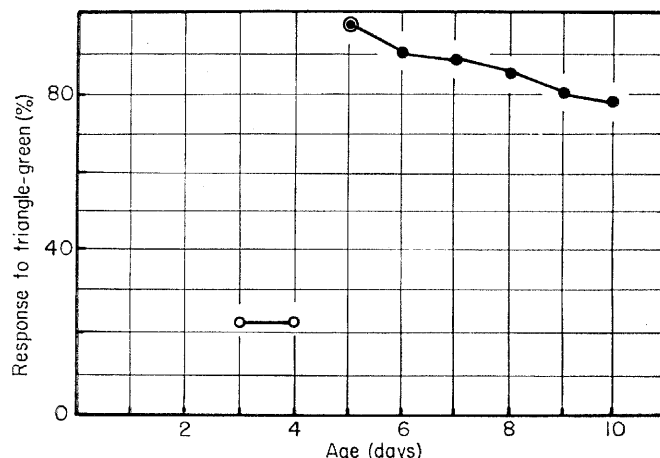
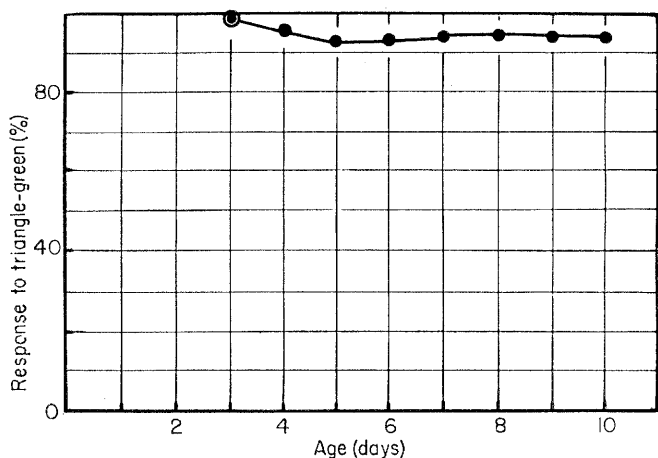


Fig. 12 (left). Responses of chicks given food rewards for pecking at the triangle-green stimulus at 3 days of age. Fig. 13 (right). Responses of chicks given food rewards for pecking at the triangle-green stimulus at 5 days of age.

rewards at the age of 9 days for pecking at the triangle-green stimulus, likewise showed no effect of reinforcement upon their innate pecking preference. Their response to the triangle-green stimulus during the 4 days of pre-reinforcement testing was 10 percent of all responses. After withdrawal of the reward, the response to the triangle-green stimulus was 20.5 percent (see Fig. 15).

In Fig. 16 are plotted, by age groups, the cumulative percentages of responses to the triangle-green stimulus during the extinction period. The resulting curve suggests very strongly that there is a period of maximum effectiveness for modification of innate pecking preferences by food reinforcement, and that the peak of this period is on the 3rd day of age. It may be that the peak is, in fact, at the 4th day of age and, in addition, that we would have an even smoother curve if we had data

for the effect of reinforcement at the ages of 4, 6, and 8 days. Nevertheless, the general conclusion is inescapable: there is a definite "critical period" during which food reinforcement is most effective in modifying innate preferences for pecking at certain objects. The more the animal's age differs from 3 days, the less effective food reinforcement is.

As in the case of imprinting, the existence of a critical period for this learning of objects associated with food distinguishes such learning from ordinary learning in which food is used as a reward and in which discrimination between two different visual stimuli is required. That there should be a critical period for the learning of food-associated objects seems reasonable, since after the age of 3 days a chick no longer has sufficient nutritional resources from the yolk sac to continue to survive without other nourishment;

unless it acquires food by pecking at appropriate objects it will die.

Further research on the modification of innate pecking preferences by means of direct food reward has indicated that the existence of a critical period is not the only difference between such learning and ordinary discrimination learning. As mentioned earlier, while the drugs meprobamate and carisoprodol have no effect on the retention of ordinary association learning after their effects have worn off, they prevent animals from retaining the effects of an imprinting experience. In view of this, we made another experiment to determine whether chicks given one or the other of these drugs would retain learning of food-associated objects (6).

Here we used 170 Leghorn chicks, divided into four treatment groups. One group consisted of animals given carisoprodol (16 mg) 1½ hours before

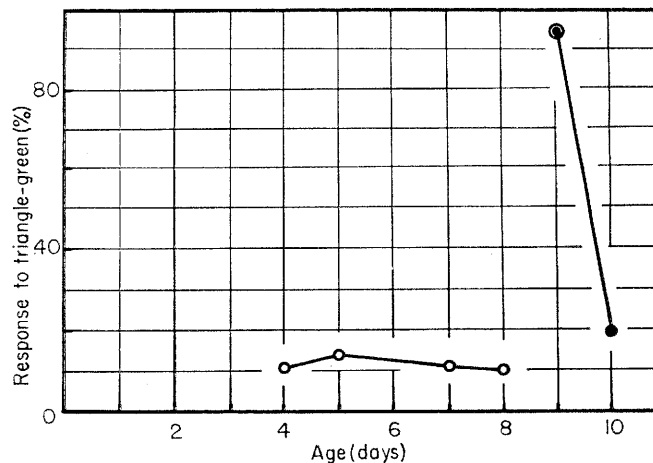
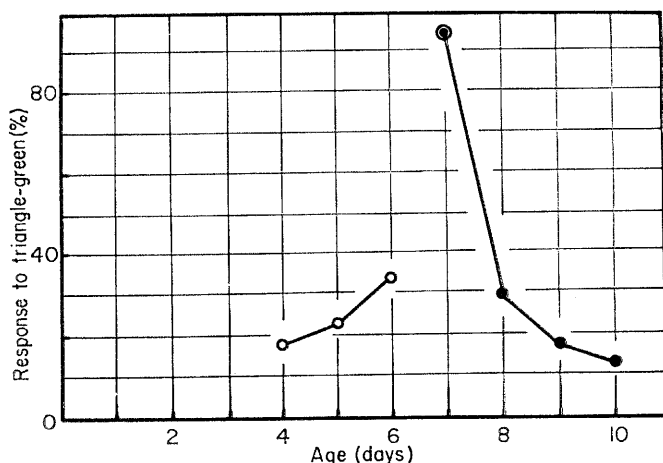


Fig. 14 (left). Responses of chicks given food rewards for pecking at the triangle-green stimulus at 7 days of age. Fig. 15 (right). Responses of chicks given food rewards for pecking at the triangle-green stimulus at 9 days of age.

the reinforcement experience; another group consisted of animals given meprobamate (16 mg) 1½ hours before reinforcement; animals in the third group were given water (0.2 cm³) 1½ hours before reinforcement; and animals in the fourth group served as controls, being given neither reinforcement nor a drug. For each of the three experimental groups, for a 2-hour period at the age of 3 days, pecking at the triangle-green stimulus was reinforced but pecking at the circle-blue stimulus was not.

On each of 6 days following the reinforcement experience, for each of the three experimental groups, there was a 2-hour period of extinction testing, in which pecking at one or other of the two stimuli was unrewarded. The animals in the control group were placed in the apparatus for 2 hours on each of these days, but pecking was not reinforced by food reward at any time.

Figure 17 shows the results, in terms of percentage of pecks at the triangle-green stimulus, obtained during the final 6 days of testing, in which there was no reinforcement or administration of drugs. Chicks in all three experimental groups had been pecking at the triangle-green stimulus during the reinforcement period at a level of precisely 99 percent. The value for the control group for the final 6 days of testing was between 7 and 21 percent, while for the group given water the value was between 55 and 58 percent, showing the effect of reinforcement. However, animals in the other two experimental groups (those given carisoprodol or meprobamate) showed a preference much closer to that of the con-

trol group than to that of the group given water before food reinforcement. The value for the animals given carisoprodol before food reinforcement was between 21 and 29 percent, while the value for the animals given meprobamate was between 10 and 12 percent. It may readily be seen that the animals given one or the other drug before the reinforcement experience behaved during the extinction period essentially as if they had never been given a food reward.

The adverse effect of carisoprodol and meprobamate on retention of the effect of food reinforcement on pecking preferences is, again, evidence of a difference between the processes involved in the modification of innate pecking preference—that is, the imprinting of food objects—and ordinary discrimination or association learning. Indeed, we now speak of “imprinting of food objects,” since all our experimental findings thus far have demonstrated that the processes involved in this early learning of food objects are more similar to the imprinting processes that we have seen in the primary socialization of certain bird species than to the usual discrimination learning processes.

A third, related area in which my associates and I are doing experimental work is environmental imprinting. As mentioned earlier, the existence of the phenomenon of environmental imprinting has been suggested (11), but no systematic study has been made. In an earlier paper (15), results were presented of studies in which chicks were exposed to a patterned environment at different times during the first several

days after hatching; it was found that a behavioral effect could be found only in animals exposed during the 2nd day of life. We have been impressed by recent observations, at our Lake Farm, Maryland, laboratory, of mallard ducks, maintained from hatching to adulthood in a natural environment, exhibiting long-range effects of early environmental experience. The free-environment area near the laboratory offers nesting birds the opportunity to choose nesting sites on the ground in surrounding marshes or in elevated nest boxes. Only animals hatched in the incubator have chosen the boxes; the nest-hatched birds nest on the ground.

These observations are the basis for a set of experiments currently in progress to determine whether exposure to the nest site is crucial during the 2nd day of life, as exposure to the patterned environment appears to be with chicks.

Implications for Analysis of Behavior

While we now consider food imprinting and social imprinting in birds to be highly similar, we do not expect to find them alike in all respects, for they are related to two very different vital functions—social cohesiveness, necessary for the survival of a social species, and ingestion of nutritious material, necessary for the survival of the individual. Further research will indicate which properties of these learning processes are basic to both and, therefore, characteristic of the imprinting mechanism in general. The critical period and the effects of drugs upon

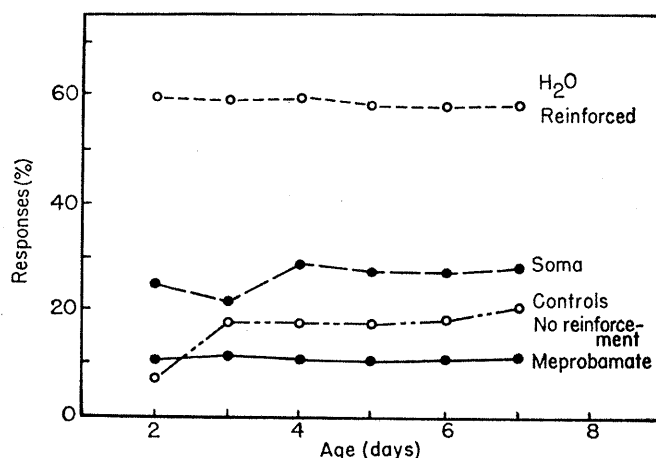
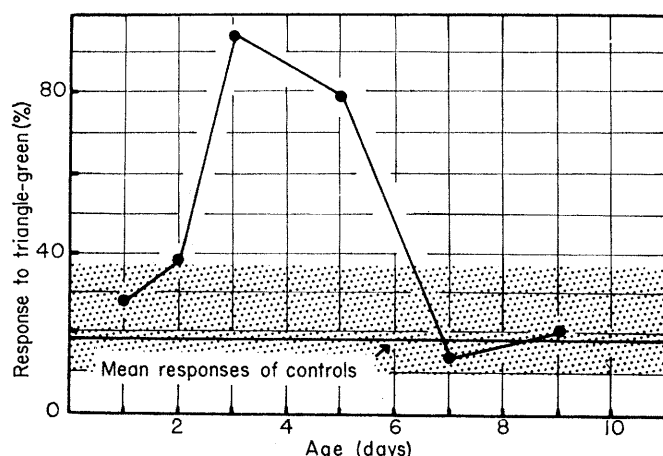


Fig. 16 (left). The mean rate of response to the triangle-green stimulus for animals rewarded with food at six different ages, as compared with the range for the unrewarded controls. Fig. 17 (right). Rates of response to the triangle-green stimulus on 6 days following food reinforcement in animals 3 days old which had previously been given water, carisoprodol, or meprobamate, as compared with rates for controls which had received no food rewards.

the retention of imprinting can already be considered primary characteristics of the imprinting mechanism, while the exact age or developmental period for the critical period and its peak, the class of objects which can be learned, and the specific responses involved (such as following and pecking) can be regarded as secondary characteristics of the specific imprinting situation. Food reward, for example, is completely irrelevant to social imprinting, while it is a *sine qua non* for food imprinting. Similarly, the presence of a social object is not at all essential to learning what objects are food objects, while it is absolutely essential to social imprinting.

Nevertheless, while we fully expect dissimilarities in different imprinting situations, we predict that all imprinting processes will be found to be basically different from association learning processes. Even with our present limited knowledge regarding food imprinting, we have found this to be the case. During the past few years several experiments have been made in which it was attempted to treat this food imprinting just as if it were ordinary association learning. The results of these experiments have always been totally unlike those expected on the basis of the demonstrated laws of association learning.

Our experiments on nest site selection will, it is hoped, make it possible to plot a maturational sequence of three imprinting phenomena in the life of the bird, all of them occurring within the first days of life and molding adult behavior: filial imprinting on the 1st day; environmental imprinting on the 2nd day; and food imprinting on the 3rd day. Maturationally scheduled processes thus appear to be, to a large extent, responsible for imprinting's being a special kind of learning, different from conventional association learning.

While there is a point of similarity between imprinting and association learning in that a relationship or "connection" is established between an object and a response, there is a basic distinction in that in imprinting there is a critical period, developmentally timed, during which certain wide classes of stimuli act as releasers or unconditional stimuli for certain types of innate responses, whereas, in association learning, the object in question does not act as an unconditional stimulus for the response but is initially neutral in its effect on the animal's behavior. When imprinting has occurred during the crit-

ical period, the object to which the animal has been exposed continues to function as an unconditional stimulus for this response. Only this particular object, or objects very much like it, will act, from this time on, as unconditional stimuli, although the range of objects to which the animal might have responded before imprinting had taken place was initially quite broad.

Once the appropriate maturational period has passed without imprinting having occurred, for lack of exposure to a suitable object, it is possible to use any member of these classes of initially suitable stimuli as a potential conditioned stimulus to which the animal may be trained, through conventional means, to make conditioned responses. Moreover, after such training the animal can readily generalize to other objects, thus increasing the range of objects to which it can make conditioned responses. The learning processes which occur after the critical period has passed are therefore not imprinting but association learning.

Finally, even if imprinting has already occurred during the critical period, the animal still can be trained, through association learning, to make conditioned responses to objects to which it has not been imprinted. In such a case the response to the imprinted object may seem, superficially, to be just like the conditioned responses which the animal has been trained to make to the conditioned stimulus. But these two categories of responses are completely different in terms of the conditions of their origins and also in terms of their long-range effects on the character of the animal's behavior.

The distinction between imprinting and association learning thus becomes extremely important, because social imprinting, environmental imprinting, and food imprinting all have counterparts in association learning. In the case of social imprinting, taming is the association-learning counterpart; thus an animal may be tamed by human beings even though the primary socialization or imprinting to members of its own species has taken place. But the social bond created by taming is not the same as the bond formed by imprinting, for a tamed animal will court and attempt to mate with opposite-sex members of its own species but not with human beings. In the case of environmental imprinting, we find the association-learning counterpart in the fact that a wild-caught animal may be easily trained to sleep or otherwise spend long

periods in a particular place quite different from the habitat in which it was reared. In the case of food imprinting, we may find the association-learning counterpart in Skinnerian-type experiments in which birds are trained to peck at colored lights in order to obtain food or water. The bird's pecking response to a colored light can soon be extinguished by withdrawal of the food reward, whereas, in our food-imprinting experiments, the chicks which had been rewarded for pecking, on the 3rd day of age, at a stimulus which innately they preferred less were never observed to lose their new pecking preference, even after long periods without reinforcement.

In a laboratory situation one is often less concerned with the basic vital function, for the individual or the species, of the behavior being studied than with the immediate experimental situation. My associates and I have come to feel that where any behavior, and particularly innate behavior, is concerned, the experimenter must be constantly aware of its basic vital function. In the case of food imprinting, it is obvious that around the 3rd day of age the chick, in order to survive, must have a sensitivity to food objects which, in nature, are often called to its attention by the mother. The basic vital function of the imprinting experience is perhaps less obvious. In nature, imprinting insures continuation of a social species, a consideration which is often forgotten in a discussion of imprinting in the laboratory.

Laboratory work is ideal for determining at which periods the animal is most susceptible to imprinting, and what parameters of the imprinting object are of greatest importance to it, but laboratory work does not reveal the effect of the early experience on the adult behavior. Some of our studies, both in Chicago and in Maryland, are now concerned with the observation of animals over long periods, under more naturalistic conditions than those provided in a laboratory. Through studies of this type, we hope to come closer to determining the effects of experiences during critical periods, and of the imprinting processes, on the life of the animal.

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Politics and Higher Education

The relation between government and the universities is close and should be formally recognized.

Eric Hutchinson

In thinking about the mutual influence of politics and higher education, I have been interested by a number of remarks that British professors have made in recent times concerning the very rapid expansion of colleges and universities in Britain. Indeed, if one reads such magazines as the *Listener*, it almost seems that a person tuning into the B.B.C. programs today hears scarcely any other topic than that of how to deal with expanding educational facilities. And since the expansion of universities in Britain stems quite directly from explicit political decisions made in the late 1940's, it might be of interest to look briefly at the ways in which government and colleges interact, for in the next decade Britain should provide an unusual laboratory study of these processes.

I find it quite amusing that whereas, when I was an undergraduate in Britain, we had little but contempt for American universities and their (as we perceived them) low standards of learning, nowadays the stream of British academics coming here to find out how to deal with large-scale higher education has reached flood proportions. It would appear that, although there are still some British intellectuals who regard American education as barbarously crude, the British consumer and his supplier are showing as large an ap-

petite for our exported academic ideas as for such cultural exports as movies and rock and roll, to say nothing of the cult of youth.

The new universities, such as York, Lancaster, and Essex, are posing problems of a kind that the British have not had to deal with before, because higher education for a large fraction of the population has not until now been a component of their cultural or political pattern; and the general impression seems to be that, even if Americans do not have all the answers to these problems, we nevertheless have a good many. This, also, I find rather amusing since, unless my judgment in these matters has gone badly awry, we are ourselves in the middle of a fairly profound change concerning (i) the opinion of leading academics as to what the role of universities should be; (ii) the opinion of many government officials as to what the role of universities should be; and (iii) the opinion of the lay public as to what the role of universities should be. (Many of the questions raised by these groups are described in Kerr's book on the "multiversity," (1) but I do not find that there are many satisfactory answers.)

In considering this question in recent weeks, my thoughts have been influenced by an article "Education as a political exercise" by Brian Chapman (2); by Jacques Barzun's *Science, the Glorious Entertainment* (3); and by a series of articles by Christopher Rand

in the *New Yorker* (4). Fred Hechinger's article "Couch on Campus" (5) provides a useful glimpse of some of the personal problems which stem from practices in higher education.

The most comprehensive statement of educational policy in Britain has been the Robbins Report (6), and Chapman's analysis of the political and social implications of the Report is as clear as any that I have read in the British press. Although I do not agree with all of Chapman's conclusions, I think his article is useful reading for Americans, because our own problems are not essentially different from those of the British and, at least in California, are having to be answered by what are basically political decisions—for example, the Master Plan for Education in California.

Chapman sees the following pressures operating to bring about expansion of universities.

1) A purely social (and leveling) pressure that will, it is supposed, do away with what Anthony Sampson (7) calls the "old-boy network" which still dominates the Establishment. There is clearly a rich vein of political ore to be mined in this area, one that will become increasingly important in this country as civil rights programs and the war on poverty gather steam.

2) A purely utilitarian pressure that stems from the belief that an army of technologists and technicians is needed to prevent a nation from sinking in the quicksands of international competition in trade and political influence. When all else fails, this argument continues to command political support and can be used by almost any party with an axe to grind in the educational business. (There appear to be some serious doubts about the validity of this argument raised in Galbraith's *The Liberal Hour* (8), but Galbraith's questioning seems largely to go unnoticed.)

3) A more sophisticated pressure, which casts the argument in terms of intellectual wealth rather than technical utility. This pressure combines some of the features of utilitarianism with some taken from academic self-interest, to be discussed next. This argument

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