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CURRENT PROBLEMS IN RESEARCH

Imprinting

An effect of early experience, imprinting determines later social behavior in animals.

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Students of behavior generally agree that the early experiences of animals (including man) have a profound effect on their adult behavior. Some psychologists go so far as to state that the effect of early experience upon adult behavior is inversely correlated with age. This may be an oversimplification, but in general it appears to hold true. Thus, the problem of the investigator is not so much to find out *whether* early experience determines adult behavior as to discover *how* it determines adult behavior.

Three statements are usually made about the effects of early experience. The first is that early habits are very persistent and may prevent the formation of new ones. This, of course, refers not only to the experimental study of animals but also to the rearing of children. The second statement is that early perceptions deeply affect all future learning. This concept leads to the difficult question whether basic perceptions—the way we have of seeing the world about us—are inherited or acquired. The third statement is simply that early social contacts determine the character of adult social behavior. This is the phenomenon of imprinting.

At the turn of the century, Craig (*1*), experimenting with wild pigeons, found that in order to cross two different species it was first necessary to rear the young of one species under the adults of the other. Upon reaching maturity the birds so reared preferred mates of the same species as their foster parents. Other interspecies sexual fixations have been observed in birds and fishes.

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Heinroth (*2, 3*) and his wife successfully reared by hand the young of almost every species of European birds. They found that many of the social responses of these birds were transferred to their human caretaker. Lorenz (*4*) extended these experiments, dealing especially with greylag geese.

Lorenz was the first to call this phenomenon "imprinting," although earlier workers had observed this effect. He was also the first to point out that it appeared to occur at a critical period early in the life of an animal. He postulated that the first object to elicit a social response later released not only that response but also related responses such as sexual behavior. Imprinting, then, was related not only to the problem of behavior but also to the general biological problem of evolution and speciation.

Although imprinting has been studied mainly in birds, it also has been observed to occur in other animals. Instances of imprinting have been reported in insects (*5*), in fish (*6*), and in some mammals. Those mammals in which the phenomenon has been found —sheep (*7*), deer (*8*), and buffalo (*8a*) —are all animals in which the young are mobile almost immediately after birth. Controlled experimental work with mammals, however, has just begun.

The first systematic investigations of imprinting were published in 1951. Simultaneously in this country and in Europe, the work of Ramsay (*9*) and Fabricius (*10*) gave the first indication of some of the important variables of the process. Ramsay worked with several species of ducks and a variety of breeds of chickens. He noticed the importance of the auditory component in the imprinting experiment and the effect of changes in coloring on parental recognition as well as on recognition of the parents by the young. His findings also showed that color is an essential element in recognition, while size or form seemed to be of less importance. Most of Ramsay's experiments dealt with exchange of parents and young and did not involve the use of models or decoys as imprinting objects, although he also imprinted some waterfowl on such objects as a football or a green box.

Fabricius carried on experiments with several species of ducklings and was able to determine approximately the critical age at which imprinting was most successful in several species of ducks. In some laboratory experiments he found it impossible to do imprinting in ducklings with a silent decoy—something which my coworkers and I were easily able to do a few years later in our Maryland laboratory. After the appearance of this pioneer work by Ramsay and by Fabricius, no relevant papers appeared until 1954. At that time Ramsay and Hess (*11*) published a paper on a laboratory approach to the study of imprinting. The basic technique was modified slightly the following year and then was continued in the form described below. Papers in 1956 by Margaret Nice (*12*) and by Hinde, Thorpe, and Vince (*13*) include most of the pertinent materials published up to 1956 since Lorenz's classic statement of the problem.

Since 1956, however, there has been an increasing number of papers on imprinting in a variety of journals. However, most investigators report experiments which are primarily designed to look for ways in which imprinting can be likened to associative learning and are not primarily carried out to investigate the phenomenon itself. Later we shall return to a consideration of these experiments; for the present we shall concern ourselves mainly with the program carried out since 1951 at McDonogh and at Lake Farm Laboratory, Maryland, and at our laboratories at the University of Chicago (*14*).

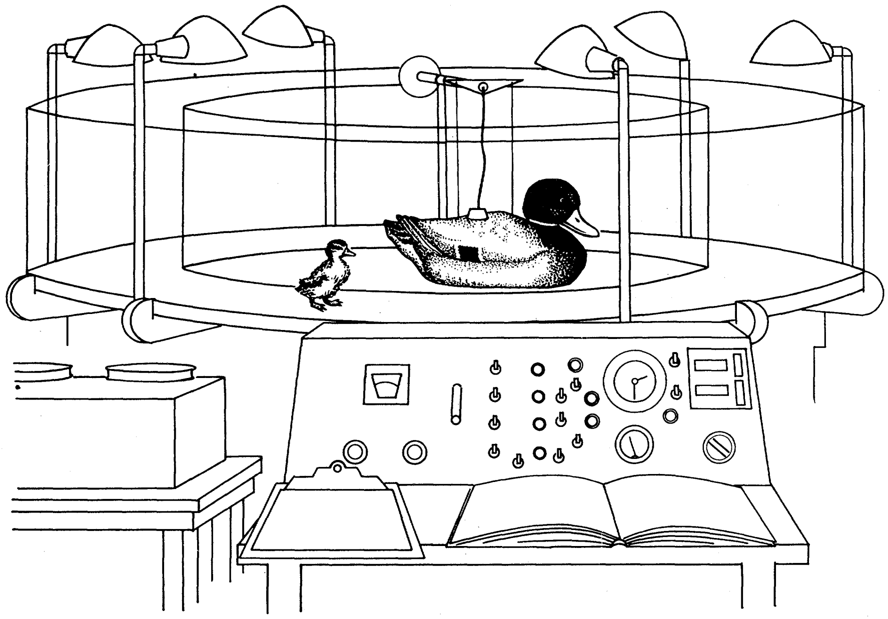


Fig. 1. The apparatus used in the study of imprinting consists primarily of a circular runway around which a decoy duck can be moved. In this drawing a duckling follows the decoy. The controls of the apparatus are in the foreground.

Experimental Studies

Our laboratory in Maryland had access to a small duck pond in which we kept relatively wild mallards. The birds laid their eggs in nesting boxes, so the eggs could be collected regularly. After storage for a few days, the eggs were incubated in a dark, forced-air incubator. About two days before hatching, the eggs were transferred to a hatching incubator. Precautions were taken to place the newly hatched bird into a small cardboard box (5 by 4 by 4 inches) in such a way that it could see very little in the dim light used to carry out the procedure.

Each bird was given a number, which was recorded on the box itself as well as in our permanent records. The box containing the bird was then placed in a still-air incubator, used as a brooder, and kept there until the bird was to be imprinted. After the young bird had undergone the imprinting procedure, it was automatically returned to the box, and the box was then transferred to a fourth incubator, also used as a brooder, and kept there until the bird was to be tested. Only after testing was completed was the duckling placed in daylight and given food and water.

The apparatus we constructed to be used in the imprinting procedure consisted of a circular runway about 5 feet in diameter. This runway was 12 inches wide and 12½ feet in circumference at the center. Boundaries were formed by walls of Plexiglas 12 inches high. A mallard duck decoy, suspended from an elevated arm radiating from the center of the apparatus, was fitted internally with a loud-speaker and a heating element. It was held about 2 inches above the center of the runway. The arms suspending the decoy could be rotated by either of two variable-speed motors. The speed of rotating and intermittent movement could be regulated from the control panel located behind a one-way screen about 5 feet from the apparatus. The number of rotations of both the decoy and the animal were recorded automatically. Tape recorders with continuous tapes provided the sound that was played through the speaker inside the decoy. A trap door in the runway, operated from the control panel, returned the duckling to its box.

Imprinting procedure. The young mallard, at a certain number of hours after hatching, was taken in its box from the incubator and placed in the runway of the apparatus (Fig. 1). The decoy at this time was situated about 1 foot away. By means of a cord, pulley, and clip arrangement, the observer released the bird and removed the box. As the bird was released, the sound was turned on in the decoy model, and after a short interval the decoy began to move about the circular runway. The sound we used in the imprinting of the mallard ducklings was an arbitrarily chosen human rendition of "*gock,* gock, gock, gock, gock." The decoy emitted this call continually during the imprinting process. The duckling was allowed to remain in the apparatus for a specified amount of time while making a certain number of turns in the runway. At the end of the imprinting period, which was usually less than 1 hour, the duckling was automatically returned to its box and placed in an incubator until it was tested for imprinting strength at a later hour.

Testing for imprinting. Each duckling to be tested was mechanically released from its box halfway between two duck models placed 4 feet apart. One of these was the male mallard model upon which it had been imprinted; the other was a female model which differed from the male only in its coloration. One minute was allowed for the duckling to make a decisive response to the silent models. At the end of this time, regardless of the nature of the duckling's response, sound was turned on simultaneously for each of the models. The male model made the "gock" call upon which the duckling had been imprinted, while the female model gave the call of a real mallard female calling her young.

Four test conditions followed each other in immediate succession in the testing procedure. They were: (i) both models stationary and silent; (ii) both models stationary and calling; (iii) the male stationary and the female calling; (iv) the male stationary and silent and the female moving and calling. We estimated these four tests to be in order of increasing difficulty. The time of response and the character of the call note (pleasure tones or distress notes) were recorded. Scores in percentage of positive responses were then recorded for each animal. If the duckling gave a positive response to the imprinting object (the male decoy) in all four tests, imprinting was regarded as complete, or 100 percent.

Determination of the "Critical Period"

To determine the age at which an imprinting experience was most effective we imprinted our ducklings at various ages after hatching. In this series of experiments the imprinting experience was standard. It consisted in having the duckling follow the model 150 to 200 feet around the runway during a period of 10 minutes. Figure 2 shows the scores made by ducklings in the different age groups. It appears that some imprinting occurs immediately after hatching, but a maximum score is consistently made only by those ducklings imprinted in the 13- to 16-hour-old group. This result is indicated in Fig. 3, which shows the percentage of animals in each age group that made perfect imprinting scores.

Social facilitation in imprinting. In order to find whether imprinting would occur in those ducklings which were past the critical age for imprinting—that is, over 24 hours of age—we attempted to imprint these older ducklings in the presence of another duckling which had received an intensive imprinting experience. Ducklings ranging in age from 24 to 52 hours were given 100 feet of following experience during a period of 30 minutes. The average score for the ducklings was 50 percent; this shows that some imprinting can occur as a result of social facilitation. Two conclusions can be drawn. (i) Social facilitation will extend the critical age for imprinting. (ii) The strength of imprinting in these older ducklings is significantly less than that when the animal is imprinted alone at the critical age under the same time and distance conditions; under the latter circumstances the average score made is between 80 and 90 percent. A further indication of this dissipation of imprintability with increasing age is obtained when we average the scores for those animals which were between 24 and 32 hours old. The average score for these animals was 60 percent, while the score made by older animals ranging in age from 36 to 52 hours was 43 percent. One last item points to the difference; even when the time and distance were increased during imprinting of the older ducklings there were no perfect scores. With such a large amount of distance to travel during the imprinting period, approximately 40 percent of the animals would be expected to make perfect scores if they were imprinted during the critical period.

Field Tests of Imprinting

In this same exploratory vein we have also carried out some studies under more normal environmental conditions. To do this we took animals imprinted in our apparatus and placed them in the duck-pond area, where they could either stay near a model placed at the water's edge or follow the model as it was moved along the surface of the duck pond, or go to real mallards which had just hatched their ducklings. Imprinted ducklings did not follow the live mallard females who had young of an age similar to that of the experimental animals. In fact, they avoided her and moved even closer to the decoy. Naive mallards, about a day old, from our incubator, immediately joined such live females and paid no attention to the decoys. These records, which we captured on motion-picture film, offer proof that what we do in the laboratory is quite relevant to the normal behavior of the animals and is not a laboratory artifact.

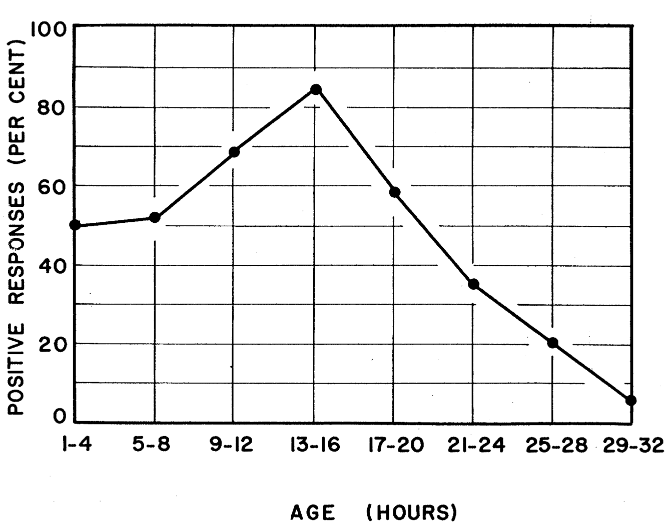
Color and Form Preferences in Imprinting Objects

An examination of the importance of the form and color of an imprinting object is relevant to any inquiry concerning factors contributing to the strength of imprinting (*15*).

Eight spheres approximately 7 inches in diameter in the colors red, orange, yellow, green, and blue, and in achromatic shades of near-black, near-white, and neutral grey were presented to 95 young Vantress broiler chicks as imprinting objects. The imprinting procedure was essentially the same as that described above in the duckling experiments. All the animals were exposed to one of the spheres during the critical period. Each imprinting experience lasted for a total of 17 minutes, during which time the imprinting object moved a distance of 40 feet.

Twenty-four hours after imprinting, each animal was tested in a situation where the object to which it had been imprinted was presented, together with the remaining four colored spheres if the animal had been imprinted to a colored sphere, or with the remaining two achromatic spheres, if the animal had been imprinted to one of the achromatic spheres.

It was found that the stimuli differed significantly in the degree to which they elicited the following-reaction. The stimuli, ranked in their effectiveness for eliciting following during imprinting, from the highest to the lowest, are: blue, red, green, orange, grey, black, yellow, white. These colors, in the same order, were increasingly less



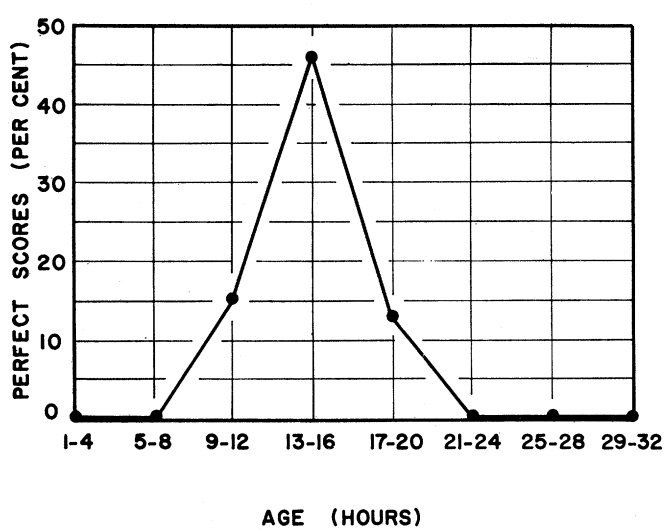


Fig. 2 (left). The critical age at which ducklings are most effectively imprinted is depicted by this curve, which shows the average test score of ducklings imprinted at each age group. Fig. 3 (right). Another way of showing the critical age is by plotting the percentage of animals in each age group that made scores of 100 percent in testing.

effective in terms of the scores made during the testing period. We concluded from this that the coloring of a stimulus is more important than its reflectance.

In order to determine also form preferences in imprinting objects, we took the same spheres we used in determining color preferences and added superstructures of the same coloring, so that the spheres had heads, wings, and tails (Figs. 4 and 5).

The addition of superstructures had a definite effect on the ease with which the following-reaction could be elicited: the plain ball was found to be the most efficient; the ball with wing and tail-like superstructures, less so; and the ball to which wings, tail, and head had been added, least efficient. We even presented a stuffed brown Leghorn rooster to the chicks, and it was found to be the least efficient model of all in eliciting the following response.

Auditory Imprinting in the Egg

Some investigators of imprinting have felt that vocalization of the incubating parent might cause imprinting to that vocalization even before the young fowl hatched. This seemed a likely hypothesis, so we carried out the following experiment. About 30 mallard eggs were incubated in an incubator with a built-in loud-speaker. For 48 hours before hatching these mallards were exposed to a constantly played taped recording of a female mallard calling her young. Eggs were removed just before hatching and placed in a different incubator. Later, when tested, these young made no significantly greater choice of this source of sound than of the "gock" call used in our normal imprinting procedure. [A preliminary experiment was reported earlier (*11*).] Auditory imprinting, while the mallard is still in the egg, is therefore considered to be unlikely.

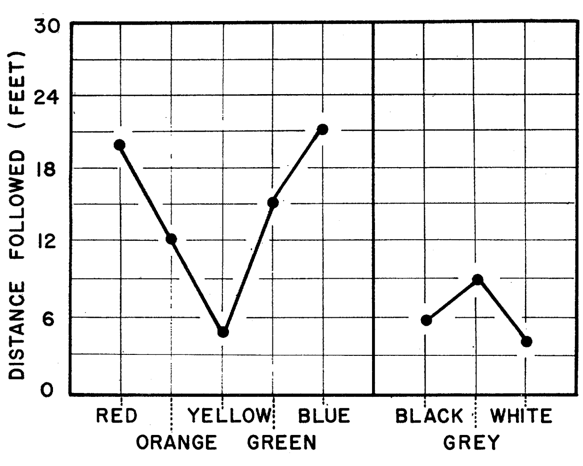
Law of Effort

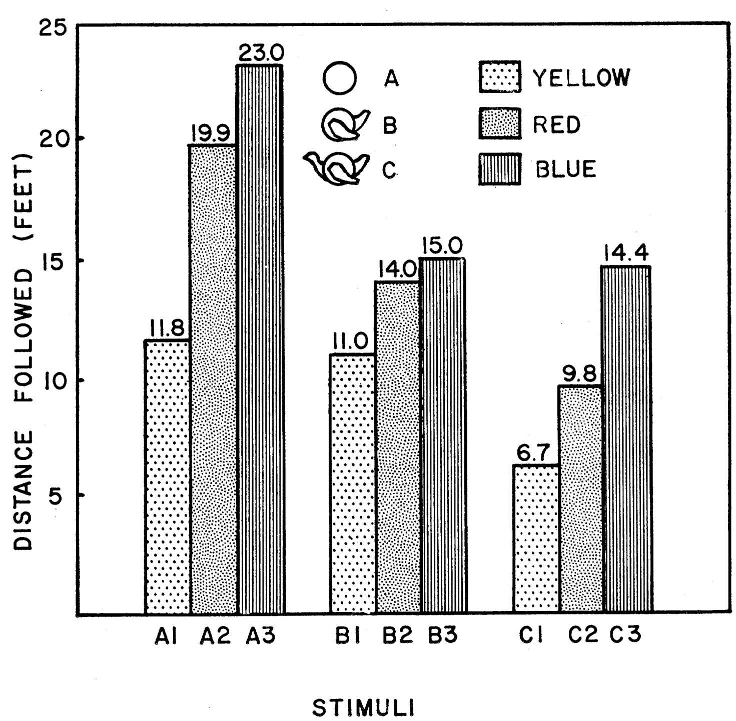
We decided to vary independently the factors of time of exposure and the actual distance traveled by the duckling during the imprinting period. Since previous results had indicated that a 10-minute exposure period was sufficient to produce testable results, we decided to run a series of animals, varying the distance traveled but keeping the time constant at 10 minutes. We therefore used one circumference of the runway (12½ feet) as a unit and ran groups of animals for zero, one, two, four, and eight turns. This resulted in imprinting experiences in which the ducklings moved about 1 foot, 12½ feet, 25 feet, 50 feet, and 100 feet, respectively. All ducklings were imprinted when they were between 12 and 17 hours of age, in order to keep the variable of critical period constant. The results showed that increasing the distance over which the duckling had to follow the imprinting object increased the strength of imprinting. A leveling-off of this effect appears to occur after a distance of about 50 feet. These results are shown in Fig. 6.

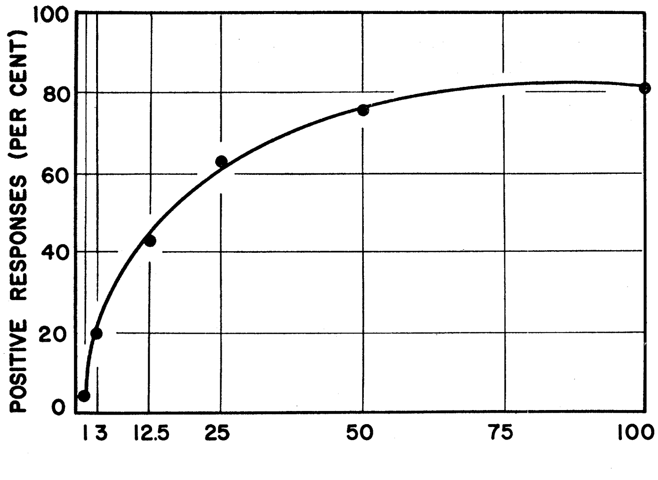
In order to determine the effect of length of exposure time on imprinting strength, we chose a distance that could be traversed by ducklings in periods of time as short as 2, 10, and 30 minutes. The scores made by animals imprinted for 2, 10, and 30 minutes, respectively, while traveling a distance of 12½ feet were essentially identical. Moreover, there is no significant difference between the findings for ducklings allowed to follow for a distance of 100 feet during a 10-minute period and those allowed 30 minutes to cover the same distance. These results are shown in Fig. 7.

The strength of imprinting appeared to be dependent not on the duration of the imprinting period but on the effort exerted by the duckling in following the imprinting object. To confirm this notion we tried two supplementary experiments (*16*). In the first, we placed 4-inch hurdles in the runway so that the ducklings not only had to follow the model but also had to clear the obstacles. As we suspected, the birds which had to climb the hurdles, and thus ex-

Fig. 4 (below). Mean distance, in feet, traveled in the course of following-response, by eight groups of animals, to eight different stimuli differing in color or reflectance. Fig. 5 (right). Effectiveness of models in eliciting the following-reaction, expressed as a function of stimulus complexity and color.







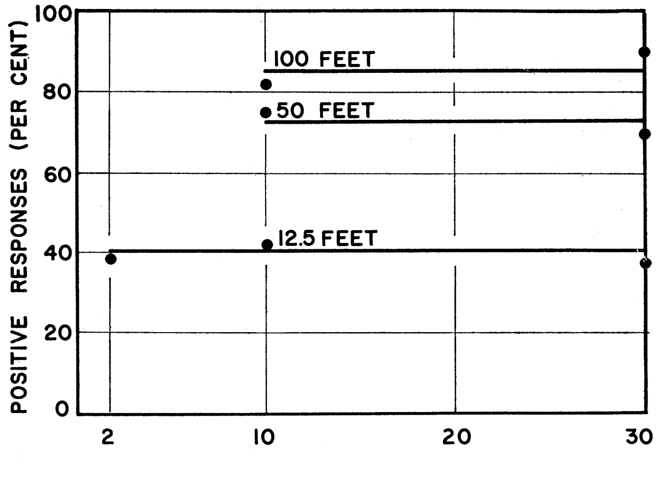


Fig. 6 (left). Strength of imprinting as a function of distance traveled by ducklings, with exposure time held constant. Fig. 7 (right). Strength of imprinting as a function of duration and exposure in minutes. Time had little effect on the test scores of the ducklings when the distance traveled was held constant.

pend more effort, made higher imprinting scores than those which traveled the same distance without obstacles. In the second experiment we allowed the duckling to follow the decoy up an inclined plane, with similar results. After further experiments we came to the conclusion that we could write a formula for imprinting: the strength of imprinting equals the logarithm of the effort expended by the animal to get to the imprinting object during the imprinting period, or $I_s = \log E$.

Previous accounts in the literature on imprinting have made the following of a moving object a necessary condition of imprinting. Our results, as formulated in the law of effort, indicate that the amount of walking done by the animal during the imprinting period is of primary significance. The following experiment was therefore carried out. Two identical decoys were spaced 3 feet apart. A light over each decoy could be turned on and off so that only the model giving the "gock" call was illuminated in the darkened experimental apparatus, and the illumination was made to coincide with the call. When the duckling reached the lighted and calling model, the light and sound were turned off in that model and turned on in the other, which was 3 feet away. In this manner we could shuttle the animal back and forth and have it cover a distance similar to that used in the normal imprinting situation, where it walks behind a moving object.

Animals were run at four shuttles and 16 shuttles. The results show scores similar to those obtained previously for the 12½-foot and 50-foot distances (see Fig. 6). They indicate, again, that imprinting strength is a function of the distance walked by the duckling, regardless of whether or not the more complex perception of *following* a moving object is involved.

Fear Behavior and Locomotory Ability

In the light of the "critical period" results, the question arises as to what developmental changes might be taking place that would account for the limits of the critical period.

During the very early hours of their lives, animals show no fear. We conducted an experiment with 137 White Rock chicks of different ages (*17*) and found that there is no fear up to 13 to 16 hours after hatching. Afterwards, the proportion of animals from age group to age group begins gradually to increase up to the age of 33 to 36 hours, when all animals show fear. Fear responses will prevent an animal from engaging in the kind of social behavior necessary for imprinting to take place, since a fearful animal will avoid rather than follow a potential imprinting object.

On the other hand, fear behavior cannot account for the limitation of imprinting before the peak of maximum effectiveness. Since the strength of imprinting is dependent on locomotor activity, we postulated that the ability to move about might thus be an important factor. The ability to move about is a growth function and would limit the onset of the critical period. Hence, we tested 60 Vantress broiler chicks of White Rock stock of different ages to determine the development of increasing locomotor ability.

The two curves we obtained from these two experimental studies—one for increasing locomotor ability and one for increasing incidence of fear behavior with increasing age—were found to be in substantial agreement with the limits of the critical period. In fact, in plotting these two curves together, we obtained a hypothetical "critical period" for imprinting which strongly resembled the empirical one obtained for that breed.

It seems likely that all animals showing the phenomenon of imprinting will have a critical period which ends with the onset of fear. Thus, we can predict in a series of animals, knowing only the time of onset of fear, the end of imprintability for that species. Even in the human being one could thus theoretically place the end of maximum imprinting at about 5½ months, since observers have placed the onset of fear at about that time (*18*).

Innate Behavior Patterns and Imprinting

Most commonly the following-reaction to a certain model has been taken as a means of observing the progress of imprinting during the first exposure to the imprinting object and also as an indicator of the effectiveness of this exposure.

Table 1. Percentage of positive responses made by ducklings under different conditions of testing and drug administration.

Conditions	Control H_2O	Mempro-bamate (25 mg/kg)	Nem-butal (5 mg/kg)	Chlor-proma-zine (15 mg/kg)
Drug at 12 hr, imprinting at 24 hr	14	54	31	57
Drug at 12 hr, imprinting at 14–16 hr	62	8	28	63
Imprinting without drug at 16 hr, test under drug	61	65	61	58
Drug at 24 hr, imprinting at 26 hr	19	17	16	59

However, the following-reaction is always accompanied by other innate behaviors which may also be observed and recorded. For the present purpose, the emission of "distress notes" or "contentment tones," maintenance of silence, and fixation of an object were checked for individual animals for a 2-minute period at the beginning of an imprinting session (*19*).

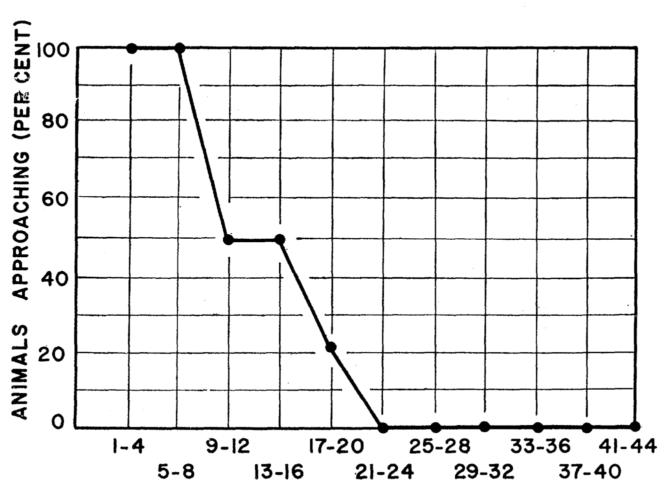
To differentiate between the "distress notes" and the "contentment tones" of chickens is comparatively easy, even for the layman who has never become familiar with them. "Distress notes" are a series of high-intensity, medium-pitch tones of approximately ¼-second duration in bursts of five to ten. Little pitch modulation occurs in this kind of call. "Contentment tones," on the other hand, are a series of high-pitch, low-intensity notes emitted in bursts of three to eight and with considerable pitch modulation during emission. The duration of the individual tones is much shorter, 1/12 of a second or less. During distress notes the animal usually holds its head high; during contentment tones it holds its head beak down. The designations *distress notes* and *contentment tones* are merely labels and should not necessarily be taken literally.

The subjects were 124 Vantress broiler chicks which had never experienced light until the time of the experiment. The experimental situation was much like the first 2 minutes of an imprinting experiment.

We found that the behavior of the animals changed markedly with age. The younger the animals were, the more pronounced was their striving to move under the cover of the nearby model. Figure 8 reflects the way in which this behavior diminished with age. Figure 9 shows that the proportion of animals fixating, or orienting toward, the model also diminished with increasing age. Although it was considerably more difficult for the younger animals to cover even the short distance between their original location and the model because of their poor locomotor ability, the time it took these younger animals to reach the model was much shorter than the time it took the older animals. However, the mode of locomotion for these younger animals was not walking but, rather, a kind of tumbling; they used both feet and wings as supports, and this left them exhausted after reaching the model a few inches away.

These results concerning behavior patterns during imprinting offer still further corroborating evidence for the location of the critical period as empirically determined. The emission of distress notes by animals older than 17 hours, even in the presence of an object that offers warmth and shelter, may be taken as an indication that a new phase of the animals' perception of their environment has set in. This behavior obstructs imprinting under the conditions of our laboratory arrangement. The high incidence of animals emitting contentment tones in the presence of the model is gradually replaced by an increasing number of animals emitting distress notes. No similar displacement occurs in animals remaining silent. The emission of contentment tones decreased as the animals became older, and the emission of distress notes increased at the same time.

The most important interpretation of these findings is that elicitation of following-behavior by various means after the critical period may not touch upon imprinting phenomena at all. Conventional training methods may be employed to overcome the fear response which the animals show after 17 hours, and it is not impossible to induce them, for example, to follow human beings. However, during the critical period, habituation or learning proper need not



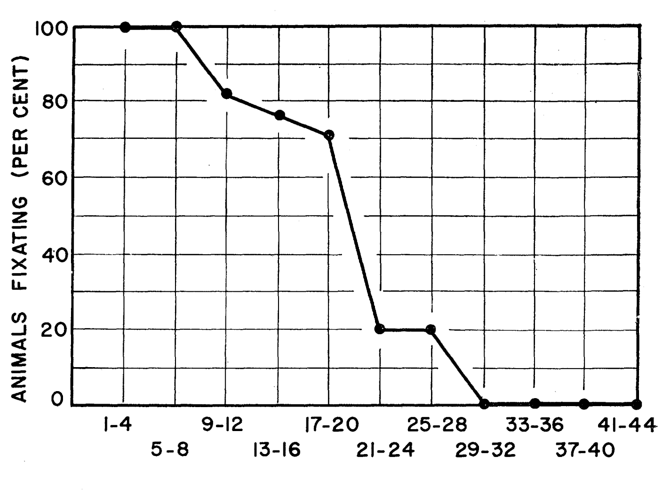


Fig. 8 (left). Percentage of 124 chicks that approached the stimulus objects at different ages. Fig. 9 (right). Percentage of 124 chicks that fixated the stimulus object at different ages.

be considered as far as lowering of fear behavior is concerned, since at that time there is little or no fear present in the animals.

Drug Studies

The rapid drop in imprinting, then, appears to be coupled with the developing emotional response of fear—a response that makes imprinting impossible. To examine this aspect of imprinting, reduction of the emotional response by means of a tranquilizing drug (*20*) seemed a logical step. Meprobamate was chosen because of evidence that it would reduce emotionality without markedly influencing motility or coordination. Preliminary experiments with dosages of meprobamate showed clearly that the emotionality of the ducklings was markedly reduced. In fact, the ducklings showed no fear of strange objects or persons, even though they were at an age where marked fear is normally a certainty.

To obtain the maximal information from this experiment, we then decided to test animals under the following four conditions: (i) drug at 12 hours of age, imprinting at 24 hours of age when the effect of the drug had worn off; (ii) drug at 12 hours of age, imprinting at 14 to 16 hours of age, test when the drug effect had worn off; (iii) imprinting at 16 hours, test under drug later; and (iv) drug at 24 hours, imprinting at 26 hours, test when the drug effect had worn off.

In general, the procedure for imprinting and testing was the same as that which has been described. Control animals were given distilled water, and chlorpromazine and Nembutal were used to obtain additional information. The results are shown in Table 1.

It is obvious that, while meprobamate reduces fear or emotional behavior, it also makes imprinting almost impossible. It does not, however, interfere with the effects of imprinting. This is clear from the results of test (iii). Chlorpromazine allows a high degree of imprinting under all conditions, whereas Nembutal reduces imprintability at all points except under the conditions of test (iii).

From the data, it appears that we might interpret the action of the drugs as follows. If we assume that meprobamate and chlorpromazine reduce metabolism, then we could expect the high imprinting scores found at 24 hours of age [test (i)], because metabolism had been slowed and we had thus stretched out the imprinting or sensitive period. This did not occur when we used Nembutal or distilled water. The second point deals with the reduction of emotionality. In test (iv) we had little evidence of emotionality in the meprobamate and the chlorpromazine groups. Emotionality did occur in the control and in the Nembutal group. Thus far, the only way we can interpret this former result is to consider the law of effort. Here we had found that the strength of imprinting was a function of effort or of distance traveled. It may be that, since meprobamate is a muscle relaxant, these effects of meprobamate cut into the muscular tension or other afferent consequences and thus nullify the effectiveness of the imprinting experience. Since, under the same circumstances, we attain perfectly good imprinting in all cases with chlorpromazine, this notion becomes even more tenable (*20a*).

Cerebral Lesions

In addition to drug effects we also studied the results of cerebral lesions on the imprinting behavior of chicks. This was done partly because we had noticed a loss of the fear response in some chicks that had undergone operations—chicks which were old enough to have this response fully developed.

Chicks with a type 1 lesion showed good imprinting at the age of 3 days. This is considerably better than the finding for the control chicks, which only occasionally show this behavior so late in their first few days. Even with this lesion, chicks at 5 and at 7 days showed no imprinting.

Chicks with type 2 lesion showed no imprinting, although some that had been prepared earlier gave no evidence of fear responses to strange objects.

Completely decerebrate animals were run only at 2 days of age, and they followed well, but the tests were inconclusive insofar as imprinting strength was concerned. Diagrams of the various lesions are shown in Fig. 10.

Although the number of animals used in this study is still small, this seems to be a fruitful avenue of approach. Control animals that have had sham operations act essentially like normal chicks. Other experiments involving electrical stimulation are being undertaken, since such stimulation may reinforce imprinting behavior.

Genetic Studies

We have also considered the genetic side of imprinting. We kept ducklings which were highly imprintable and bred them separately from ducklings which showed very little imprinting response. We thus had two groups of offspring,

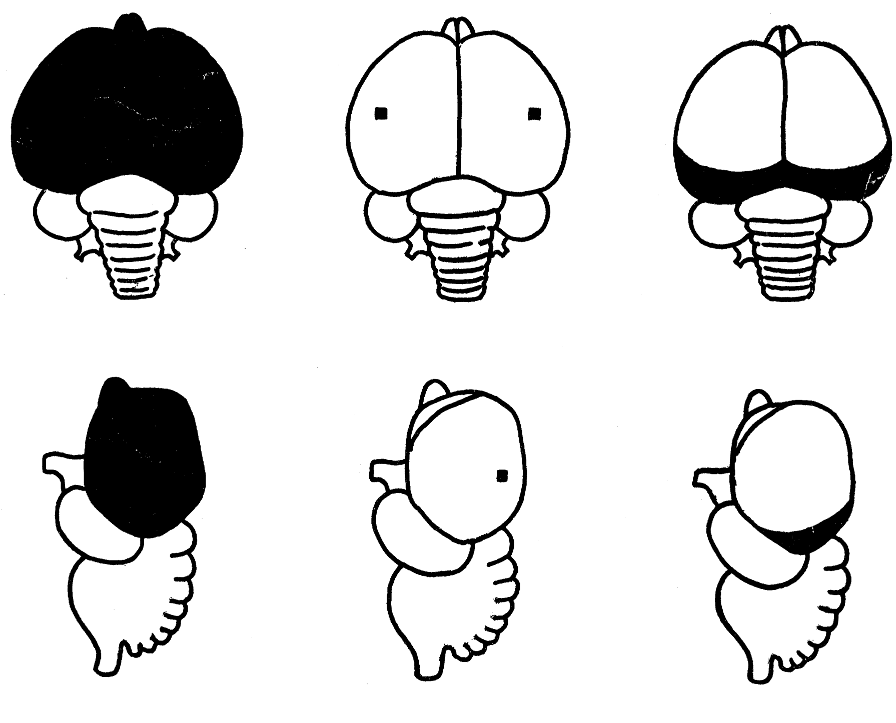


Fig. 10. Three types of lesions in the chick brain, used to study the effect of extirpation on imprintability.

those produced by "imprinters" and those produced by "non-imprinters." There was a clear and significant difference in the imprinting behavior of the two groups, even in the first generation. The offspring of imprintable parents were easily imprinted; those of less imprintable parents were difficult to imprint. The "imprinter" ducklings had imprinting test scores more than three times better than those of the "non-imprinter" ducklings. Similar results were also obtained in a study of bantam chicks. We are also following up those animals which have had experimental imprinting experiences to determine what influence, if any, these experiences have on their behavior as adults. So far the results are inconclusive, but they do suggest that experimental imprinting of mallards affects their behavior as adults, particularly with respect to courtship patterns.

Table 2. Number and imprintability of different experimental animals. Most of the animals were imprinted in runway and mallard decoy situations. Some of the Vantress broilers were imprinted on colored spheres, and the sheep were imprinted on human beings.

Animal	No.*	Imprintability†
	Ducks	
Wild mallard	3500	E+
Domesticated mallard	150	E
Peking	200	G
Rouen	100	F
Wood	50	P
Black	50	G
Total	4050	
	Geese	
Canada	30	E+
Pilgrim	50	G
Total	80	
	Chickens	
Jungle fowl	100	G
Cochin bantam	300	G
New Hampshire Red	100	G
Rhode Island Red	100	G
Barred Rock	200	G
Vantress broiler	500	G+
White Rock	100	F
Leghorn	200	P
Total	1600	
	Other Fowl	
Pheasant	100	P
Eastern bobwhite quail	50	G
California valley quail	20	E
Turkey	30	F
Total	200	
	Mammals	
Sheep	2	G
Guinea pig	12	G
Total	14	
Total	5944	

* Estimated for fowl, actual for mammals.
† E, excellent; G, good; F, fair; P, poor.

Birds of various species show differing degrees of imprintability. Domestic fowl do show imprinting responses, but the results are not as clear as for wild birds. We have had good success in imprinting some breeds of chicks, and the best imprinters among them are the Vantress broilers. Leghorns, on the other hand, appear to be too highly domesticated to give clear results. Other animals we have used in our experimentation are two kinds of geese, black ducks, wood ducks, turkeys, pheasants, quail, Peking ducks, and Rouens. The various breeds we have so far used in our work and the degree of imprintability found in each are shown in Table 2.

Imprinting in Mammals

The guinea pig is similar to the chick and the duckling in that it is mobile and reasonably self-sufficient soon after birth. For this reason we used it in exploratory work. We first developed a method of obtaining the young from the mother with minimal parental contact. This was done by Caesarean section. However, further work showed that it was sufficient to obtain the young within an hour after they were born, and for the moment we are doing this. Guinea pigs imprint on human beings and follow them about as do the fowl with which we have been working. The maximum effectiveness of the imprinting experience seems to be over by the second day. So far, in using our imprinting apparatus with our usual duck decoy we have obtained best results sometime before the end of the first day of age. Work is being continued so that we can have a more standardized procedure before beginning a major program in this area.

Imprinting and Learning

The supposed irreversibility of imprinting has been particularly singled out by some investigators to show that imprinting is nothing but "simple learning" —whatever that is. We do have some isolated instances which point to a long-range effect, but systematic work is just now beginning in our laboratories. Canada goslings, imprinted on human beings for a period of a week or two, will from that time on respond to their former caretaker with the typical "greeting ceremony," as well as accept food out of his hand. This occurs in spite of the fact that they normally associate entirely with the Canada geese on our duck pond. A more striking case is that of a jungle fowl cock which was imprinted by me and kept away from his own species for the first month. This animal, even after 5 years—much of that time in association with his own species—courts human beings with typical behavior, but not females of his own species. This certainly is a far-reaching effect and is similar to the finding of Räber (*21*), who reported on a male turkey whose behavior toward human beings was similar. An increased amount of homosexual courtship in mallards has been observed with some of our laboratory imprinted animals, which, while not a statistically valuable finding, perhaps points also to long-range, irreversible effects.

Imprinting is currently receiving much attention, and papers on the subject are being published at an impressive rate. Unfortunately, most experimenters appear to be certain that imprinting is identical with simple association learning and design their experiments as studies in association learning. In many instances the animals are too old when used in the experiments to fall within the critical age for imprinting, with the result that only association learning can occur. Papers falling into this category are those of Jaynes (*22*), Moltz (*23*), and James (*24*).

Our own experiments on the relation between association learning with food as a reward and imprinting during the critical period show four distinct differences.

In the first place, learning a visual discrimination problem is quicker and more stable when practice trials are spaced by interspersing time periods between trials than when practice trials are massed by omitting such intervening time periods. With imprinting, however, massed practice is more effective than spaced practice, as shown by our law of effort. Secondly, *recency* in experience is maximally effective in learning a discrimination; in imprinting, *primacy* of experience is the maximally effective factor. The second difference is illustrated by the following experiment. Two groups of 11 ducklings each were imprinted on two different imprinting objects. Group 1 was first imprinted on a male mallard model and then on a female model. Group 2, on the other hand, was first imprinted on a female model and subsequently on a male model. Fourteen of the 22 ducklings, when tested with both models present, preferred the model to which they first had been imprinted, showing primacy. Only five preferred the model to which they had been imprinted last, showing recency, and three showed no preference at all.

In addition, it has been found that the administration of punishment or painful stimulation increases the effectiveness of the imprinting experience, whereas such aversive stimulation results in avoidance of the associated stimulus in the case of visual discrimination learning.

Finally, chicks and ducklings under the influence of meprobamate are able to learn a color discrimination problem just as well as, or better than, they normally do, whereas the administration of this drug reduces imprintability to almost zero.

Imprinting, then, is an obviously interesting phenomenon, and the proper way to approach it is to make no assumptions. To find out its characteristics, to explore its occurrence in different organisms, and to follow its effects would seem a worth-while program of study.

What can we say in conclusion about the general nature of imprinting? Our best guess to date is that it is a rigid form of learning, differing in several ways from the usual association learning which comes into play immediately after the peak of imprintability. In other words, imprinting in our experiments results in the animal learning the rough, generalized characteristics of the imprinting object. Its detailed appreciation of the *specific* object comes as a result of normal conditioning—a process which in the case of these animals takes a much longer time and is possible days after the critical period for imprinting has passed. It is an exciting new field and is certainly worthy of study.

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CURRENT PROBLEMS IN RESEARCH

Marine Sediments

Recent sediments give important clues about conditions under which sedimentary rocks may have been formed.

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Most sedimentary rocks are believed to have been deposited in the seas of the past. One of the primary purposes in geological investigations has been to interpret the conditions under which these ancient sediments were deposited. One of the obvious places to look for guidance in these interpretations is in the deposits of the present. It is, therefore, rather surprising to find how little attention geologists had paid to these recent marine sediments until very recent years. Up until World War II only a few individuals were interested in remedying the situation (*1*). Even the large-scale oceanographic investigations, which were initiated shortly before the war, had helped little in the interpretation of ancient sediments because they had been largely concerned with the deep-ocean floor, and most marine sedimentary rocks now on the continents were probably deposited in relatively shallow seas.

For many years some of the leaders in petroleum geological research had recognized the importance of carrying on investigations of the sediments of today, and finally, in 1950, they developed a project supported by the American Petroleum Institute which had as its aim the study of near-shore marine deposits as an aid in the interpretation of ancient sediments. To date, the field work of this project, which we have administered at the Scripps Institution of Oceanography, has been confined to the northwestern Gulf of Mexico (*2*), although plans are now under way to continue the studies in the Gulf of California. Meantime, a number of other projects, largely supported by petroleum companies, have been carried on elsewhere. Notable among these have been the studies of the Bataafsche Petroleum Maatschappii, of the Hague, around the Orinoco Delta, Trinidad, and the Gulf of Paria (*3*); of the U.S. Geological Survey among the coral reefs of the western Pacific Ocean (*4*); of the Hancock Foundation off the southern California coast (*5*); of the Soviet Union in the various seas that surround the U.S.S.R. (*6*); and of the Germans, especially in the Baltic (*7*).

As a result of these studies of recent sediments it is now easier to interpret

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