

IMPRINTING: THE INTERACTION OF LEARNED AND INNATE BEHAVIOR: II. THE CRITICAL PERIOD

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In the anatomical development of the embryo, there exist precise critical periods in which specific tissues are susceptible to environmental influences acting at that time but at no other, the fate and future of the tissue being fixed thereafter (9). It is now apparent that similar critical periods exist in behavioral development also—specific stages in ontogeny during which certain types of behavior normally are shaped with fate and molded for life, environmental influences losing effect after that time. Among insects, for example, inter-race compatibility (3), host preferences in parasites (10), even color and morphology (2, 5) have, in some instances, been found to originate exclusively under environmental control during certain periods of early life. Recently, the behavioral growth of dogs has been sectioned into critical periods in which certain types of adjustments, such as emotional behavior and social responses, are thought to be fixed for the rest of life (7). And in man, the notion of discrete stages in psychosexual development and of the lasting effects of fixation at one period or another, has been found helpful in interpreting some clinical syndromes.

The present study examines the critical period for filial responses in precocial birds, and the influence, on retention, of the age at which a neonate experience occurs. Previous experiments in this series (4) have revealed that domestic chicks will approach and follow an irregularly moving object shortly after exposure to it, and that this response, with no reward in the ordinary sense, increases in frequency upon further practice. Although the object to which the bird is trained can be accurately discriminated from others in a simultaneous presentation, considerable generalization occurs to strange objects during the neonatal period when such objects are presented alone.

The plan of the experiment reported here was to determine the critical period for imprinting by exposing birds at various ages to a moving object, measuring the incidence and

strength of filial responses at that time, and then to test for retention of this experience in the juvenile period.

METHOD

Subjects

Fifty-six New Hampshire Red chicks were used. They were incubated in a commercial hatchery and transported to the laboratory within an hour or two after hatching. They were housed collectively in several pens in a soundproof room, food and water being present at all times. The animals were maintained on a light-dark cycle of 12 hr. of light beginning with hatching, followed by 12 hr. of dark, the animals being tested for imprintability only during the light period. These procedures were directed by an effort to approach conditions occurring in nature. The alternative methods of keeping birds in darkness up until testing, or of testing at successive times regardless of light cycle, were rejected as introducing extraneous variables. Our reasoning here was that the food and water deprivation and possible nucleoprotein degeneration of the retina, which are consequences of keeping birds in prolonged darkness, or the abnormal effects of testing animals in their night, might result in an artificially short critical period, or one deviant in other respects.

Apparatus

The apparatus has been described in a previous report (4). It consisted of an alley 10 ft. long and $2\frac{1}{2}$ ft. wide over which was a pulley system, such that a stimulus object suspended from the pulley cord could be carried down one side of the alley and back on the other in clockwise direction. The motor mechanism driving the pulleys was adjusted so that the stimulus object traveled at a speed of 1 ft. per second and made three pauses per minute. The temporal pattern of progression for the object as it journeyed around the alley was: 4-sec. run, 8-sec. pause, 4-sec. run, 8-sec. pause, 6-sec. run, and a 30-sec. pause, and so on each minute throughout each session. The resulting journey was approximately five-sixths of a round trip in each minute's sequence. The stimulus object used in all parts of this study was a green 7-in. cardboard cube hung 2 in. above the floor of the alley. No sound was used. The motion imparted to the object as it traveled silently around the alley was a rapid progression with a slight swaying and twisting from side to side as it hung on threads from the pulley-cord.

Procedure

Standard procedure and measurement. Sessions of 30 min. in this apparatus were used throughout. The chick was taken from the soundproof room and placed in the

alley, beside the green cube, facing in the direction of motion. After a minute the motor was started and the object began its journey.

Measures of the S's tendency to approach and follow the object were made during the last 5 min. of each 30-min. session, preceded by a 2-min. rest in which the motor was turned off. The measure used was the number of seconds spent within 1 ft. of the object as it traveled and paused around the alley. As in previous experiments, if the object happened to begin its 30-sec. pause within 1 ft. of a stationary bird, a special switch was thrown which carried the object 2½ ft. away. This procedure eliminated high scores due to chance.

If over the 5-min. testing period an animal achieved a score of 60 sec. or more, the animal was judged imprinted. Such scores were always the result of the typical following and approaching behavior described previously (4), while scores below 60 were largely due to random unorientated movements about the alley.

Neonate imprinting sessions. Forty-two neonate birds were randomly selected in succession and distributed among seven groups. On hatching day, 6 chicks were given imprinting sessions when between 1 and 6 hr. of age, and 7 when between 6 and 12 hr. of age. Twelve hours of night then elapsed. On the second day, 5 neonates were run when between 24 and 30 hr. old, and 5 when between 30 and 36 hr. old. After 12 hr. of night, on the third day, 5 more were run when between 48 and 54 hr. of age, and 8 when between 54 and 60 hr. old. The rest of this group, 6 in number, were fully tested on the fourth day, and then not used further in this study.

Juvenile retention sessions. Retention sessions on animals exposed on the first three days of life were procedurally identical with the neonate sessions, and were run ten days after the first session. Thus, birds trained on the first, second, and third days of life were tested for retention of the experience on the eleventh, twelfth, and thirteenth days, respectively. In this manner, an equal time elapsed between the first neonate session and the juvenile retention session. Each bird was placed in the alley for 30 min., the last 5 of which were scored for proximity to the irregularly moving green cube as before. As a control for these retention tests, two further groups of seven birds each were first exposed to the moving object on the twelfth and thirteenth days of life in a similar manner.

RESULTS

Neonate Imprinting Sessions

Incidence of imprinting at various ages is shown in Figure 1. Of the youngest age group 83 per cent reached the criterion score. Incidence thereafter decreased. As older animals were tested, fewer and fewer followed the moving object. When exposure to the object was delayed for 54 hr. or more after hatching, no imprinting was observed. In contrast, in a previous study (4) birds exposed shortly after hatching vigorously followed throughout this age period.

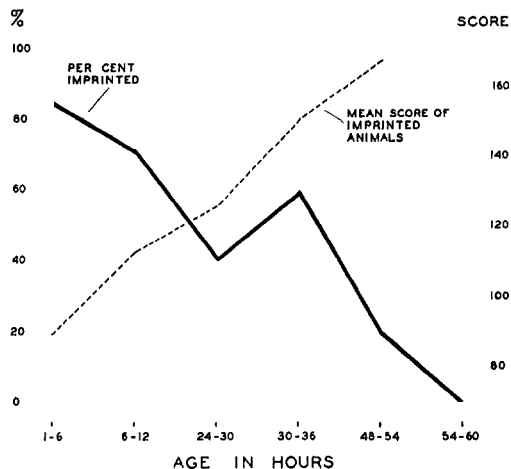


FIG. 1. The critical period for imprinting in neonates

Along with this drop in incidence with increasing age, Fig. 1 shows that there was a successive increase in the mean following score for those animals in which imprinting was successful. Statistical comparison of the scores of the youngest eight birds imprinted with the scores of the oldest eight birds imprinted showed that this increased vigor of responding with age was reliable ($p < .01$, Wilcoxon Test). It is apparent that imprinting occurs less and less frequently, but more and more strongly, the older the bird is when first exposed to the stimulus object.

Juvenile Retention Sessions

The results of similar tests ten days following the neonate session are shown in Figure 2. Whereas 83 per cent of the youngest group had reached the criterion score on the first day of life, ten days later only 33 per cent did so. A similar decrement was found in the next oldest group. But in all groups whose primary exposure to the object was at an older age, an increase in incidence was found. About half the Ss exposed on the second day of life displayed no evidence whatever of being imprinted at the time, but ten days later, surprisingly, all but one of these chased after the moving object vigorously. Similar increases in juvenile responding were found in the groups originally exposed on the third day, although scarcely any evidence of responsiveness to the object had been seen at that time.

As mentioned above, two new groups of 7

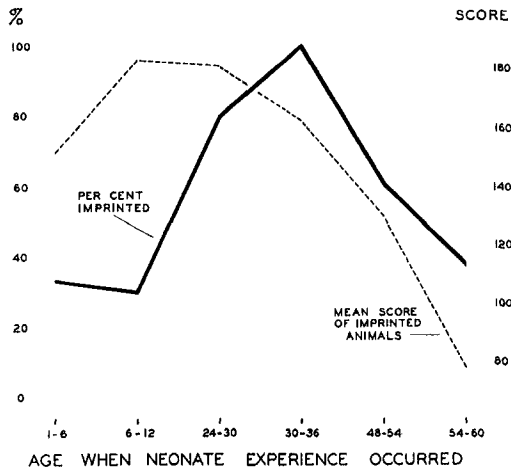


FIG. 2. Retention of neonate imprinting in juveniles

birds each were exposed to the moving object for the first time on the twelfth and thirteenth days of life as a control. None of these *Ss* was imprinted. The difference between this incidence (0 out of 14) and the incidence at the same age of imprinting in birds exposed but unresponsive on the second and third days of life (9 out of 17) is statistically reliable (chi square with Yates's Correction, $p < .01$). To this reminiscence phenomenon we give the name "latent imprinting," denoting effects of the neonate experience which do not manifest themselves in behavior until some later time.

Among birds which did follow the object as neonates, forgetting occurred only in those imprinted when very young. Less than half the animals imprinted in the first 12 hr. of life showed evidence of remembering the experience ten days later, while all birds imprinted when older remembered perfectly, a difference which approaches statistical reliability ($p = .06$, chi square with Yates's Correction). It will be recalled that the initial scores of *Ss* trained when under 12 hr. of age were significantly lower than scores of older birds; it is possible that the poorer retention of younger birds was due to their poorer performance initially. It is also possible that birds not following the object at this age were latently imprinted, as were older nonresponding neonates, but forgot it over the ten-day interval.

Flight Reactions

Figure 3 presents the appearance of fear reactions to the moving object during the

neonate sessions as a function of age. "Weak flight" means running from the approaching object at least once but not consistently. "Severe flight" signifies scores below 10, which in our apparatus are below chance level. Such scores could only be obtained by sustained flight from the moving object throughout the 5-min. testing period. The bar graph shows that no flight appeared until the birds were at least 30 hr. old. Thereafter, fear reactions increased with age. It is noteworthy that weak flight reactions occurred as often in birds which were imprinted during the session as in those which were not.

During the juvenile sessions, fear of the object was much diminished, even in those birds which had consistently fled as neonates. Two displayed weak flight, and none showed severe flight. Similarly, in the 14 birds exposed to the object for the first time at this age, only 3 showed any fear of the object, and in these cases it was transitory. The present data are insufficient to warrant a firm conclusion, but they do suggest that fear of strange moving objects in birds reared under our procedures

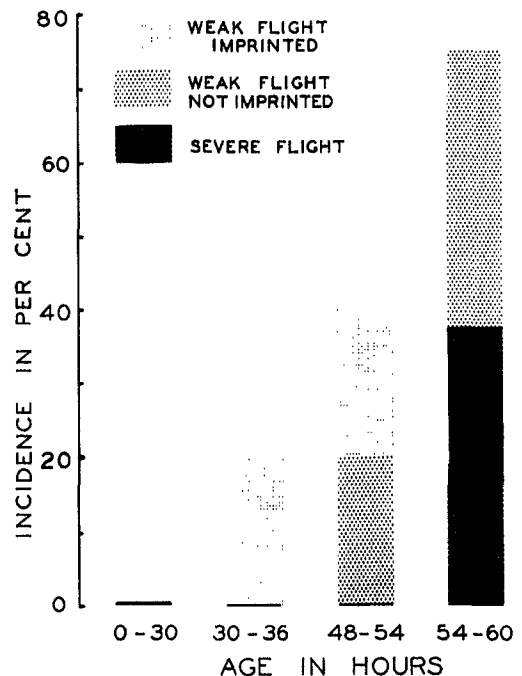


FIG. 3. Fear of the moving object in neonates as a function of age at which first exposure occurred. The four bars represent data on 18, 5, 5, and 8 animals, respectively.

may rise to a maximum in the first week of life and then decrease thereafter.

DISCUSSION

This study demonstrates that a critical period for the acquisition of filial behavior in this species does, in fact, exist; the age at which imprinting is most often obtained is not the potentially most effective age for it to occur when its influence later in life is considered. This is so because imprinting occasioned on the first day of life is more easily forgotten, and because a phenomenon called latent imprinting exists where effects of exposure to a moving object may not be manifest in behavior until later in life.

The first determination of a critical period for filial imprinting in birds¹ was done by Fabricius on several wild species of duck (1). His incidence curve, obtained with himself as object in a natural setting, is similar in shape to that shown in Figure 1 of our study. The present results can thus be taken as confirming his findings, showing that the sooner after hatching that training is commenced, the greater the likelihood that imprinting will occur. More recently, Ramsay and Hess (6) obtained an incidence curve for filial imprinting in mallards which resembles Figure 2 of our study—the highest imprintability occurring in the middle of the critical period. They state that their results contradict the findings of Fabricius. In their procedures, however, measures were not obtained during the imprinting process itself; instead, its effect was measured at a later time. If their study is interpreted as one on retention, Figure 2 of the present study confirms their result, denoting the effect of neonatal imprinting at some later time as a function of the age at which the first exposure occurred. Thus, no contradiction exists between these two studies. We suggest that there are, in reality, two critical-period curves: one for the ease of eliciting the relevant responses,

and another for the effect of imprinting at a later stage of development.

It should be noted that the present investigation defines the time limits of the critical period only for particular imprinting procedures operating for a particular duration on a particular species reared in a particular way. It is probable that the duration of the critical period is a function of several important variables:

Species differences. The present writer has at some time imprinted geese, Bantams, several breeds of domestic chicks, mallards, pintails, Muscovy ducks, and Peking ducks, using various objects including himself. Considerable species differences in ease of imprinting at various ages were found.

Nature of the stimulus. Since, as found in our previous study (4), there are innate preferences for imprintable objects, it is likely that this factor influences the duration of the critical period. Fabricius (1), using himself, and Ramsay and Hess (6), using sound-producing facsimiles of adult mallards, found much shorter critical periods than the present work using a silent green cube. It is possible that the use of a less specific stimulus with fewer characteristics lengthens the period in which neonates respond.

Duration of imprinting session. In one of our later studies (unpublished), it was found that the longer the length of session, the greater the proportion of birds which were imprinted. With a longer session, the critical period could possibly be lengthened to a week or more. We have tried a few birds 5 and 6 days old in our apparatus for several hours instead of 30 min. and obtained a high level of following, although such birds had never experienced the object before.

Other factors, such as methods of rearing and incubation, probably influence the critical period also. The problem here is what determines the end of the period. One attractive hypothesis is that it is the appearance of flight responses incompatible with following. It is doubtful that this is the answer. Some of our Ss fled the object at times on the third day and yet were imprinted. Others showed no fear of the object and yet were not imprinted. Further, birds first exposed on the twelfth and thirteenth days of life rarely showed fear, yet did not

¹ Spalding (8), in the nineteenth century, using the technique of rearing birds in hoods from hatching, found good imprinting on the first three days of life, but violent flight reactions when birds were unhooded on the fourth day. These results are similar to those presented here. His procedures and data are not presented in enough detail, however, to warrant prolonged discussion.

follow the stimulus object. These things considered, and since so many variables probably affect the interval in which imprinting phenomena occur, determination of the physiological and/or behavioral basis for the length of the critical period may not be a simple matter.

SUMMARY

Fifty-six neonate chicks were given imprinting sessions at various hours after hatching. An imprinting session consisted of exposing the animal individually for a 30-min. period to a 7-in. green cube which moved irregularly about a 10-ft. alley. Ten days later, similar sessions were given to test for the effect of imprinting at a later time. The major conclusions were:

1. A critical period for acquiring filial responses exists in this species.
2. The older the animal at first exposure, the less likelihood that imprinting will occur.
3. The older the animal at first exposure, the more vigorous and consistent is its following performance when imprinting does occur.
4. Flight reactions on exposure to a strange moving object occur toward the end of the critical period, and thereafter increase in incidence and severity during neonate development. Towards the end of the second week of life, flight reactions diminish.
5. Retention over a ten-day period is poor when imprinting has occurred on the first day

of life, while retention over this period is high in animals imprinted when older.

6. Latent imprinting—imprinting which is not manifest in overt behavior while it is occurring in the neonate period—exists in this species.

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