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The Gaping Reaction and the Development of Fear in Young Zebra Finches (*Taeniopygia guttata castanotis*)

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With 6 figures

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Abstract and Summary

Responses of young zebra finches towards different stimuli were tested between hatching and 20 days of age. The stimuli applied were: tactile stimulation with a stick, acoustic stimulation from a loudspeaker playing begging calls of other nestlings, and stuffed dummies of zebra finches and Bengalese finches as visual stimuli. Tactile and acoustic stimuli resulted in gaping responses from the first day of life. Visual stimuli elicited gaping from about day 10 or 11, 4 days after the opening of the eyes. At day 13, gaping responses towards stimuli decreased and were replaced by fear responses from day 16. The implications of the results for sensory development and imprinting are discussed. The development of fear in the young zebra finches is compared with results from filial imprinting.

Introduction

The gaping reaction of young precocious birds has not received much attention. To our knowledge only a few papers dealt with this behavioral element since Tinbergen and Kuehnen (1939) published their experiments on young blackbirds.

Holzapfel (1939) analysed the development of gaping and pecking in the starling (*Sturnus vulgaris*). Tinbergen and Perdeck (1951) examined the role of the red patch on the herring gull's beak in the begging response of gull chicks, based on observations by Goethe (1937). Peters (1953) provided a critical analysis of the term "innate releasing mechanism" on the basis of experiments on young herring gulls. Prechtl (1953) discussed the role of

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innate releasing mechanisms in the gaping responses of different songbirds, and SCHUCHMANN (1983) provided observations on the development of gaping reactions in hummingbirds (Trochilidae).

These studies were mainly interested in an experimental evaluation of the concept of the innate releasing mechanism developed by LORENZ (1935). In contrast, our interest on the gaping reaction of young zebra finches came from a quite different question concerning sexual imprinting of the birds. IMMELMANN (1969, 1972) demonstrated that the object for courtship behaviour in the zebra finch is learned by the young bird in a period of early development, the so-called "sensitive phase" (IMMELMANN and SUOMI 1981) or, more frequently, "sensitive period" (BATESON 1981). Apparently, the birds learn the features of their parents during this sensitive phase and use them as a searching image for the right courtship object (IMMELMANN 1969). The information stored in early development cannot be forgotten, when the sensitive phase is over.

IMMELMANN's (1972, IMMELMANN and SUOMI 1981) cross-fostering experiments demonstrated that the "imprintability" of the young birds is best at an age of about 13—15 days. Sensitivity to external stimulation then decreases until day 40. However, at this time the imprintability of the birds is very low, but not zero. IMMELMANN could demonstrate that even when 70 days old, the birds can eventually learn new features very stably.

The experimental design used by IMMELMANN did not permit assumptions about the shape of the increase of the sensitivity curve or a precise definition of the onset of the sensitive period. Thus, we tried to find another experimental design to get information about the onset of imprintability. It is known (IMMELMANN 1959; BISCHOF 1977, 1980) that visual features play a major role in eliciting courtship in zebra finches. We therefore assumed that visual cues are also involved, to a major extent, in imprinting. Young birds have to learn visual features of their parents for both situations, in the process of specification of the releaser of the gaping response and that for sexual imprinting. There should be a connection between the two phenomena, as it is very unlikely that they learn these features independently and simultaneously. Therefore, it is likely that the development of the gaping response should also give information on the onset of sexual imprinting. However, the results of the experiments were not as clearcut as we had expected. Our birds were not as selective as the blackbirds used by TINBERGEN and KUEHNEN (1939) and were much more delicate to handle. Nevertheless the work seems to us to have been worthwhile, as some of the results were completely unforeseen and may contribute to the understanding of the learning process known as sexual imprinting.

Material and Methods

Zebra finch clutches of different sizes were incubated and reared by either zebra finch or Bengalese finch pairs, each in a 30 × 80 × 35 cm cage with a small breeding box of 10 × 10 × 10 cm hanging outside, giving free access to the parents. One side of the wooden nest box was replaced by a clear plexiglass cover for observation of the young birds. A paper tube with a slit for observation on the furthest end was attached to the breeding cage. This was covered by a piece of cloth between observations. An observer, looking at the young birds through the slit, was hidden from the sight of the adults by a cardboard blind. To prevent disturbances of the young by light and movements of the eyes behind the slit, this was covered by a black wrap which was attached to the paper tube. The cage was illuminated by an adjustable light in front of the cage wire. The reflection from the back of the cage illuminated the nestlings sufficiently for observation. A small loudspeaker was mounted at the top of the nest box which could be connected to a tape recorder to provide acoustic stimuli.

The breeding cage could be separated into two parts by a piece of cardboard inserted through a slit in front of the cage. Before the tests started, the adult birds were separated from the nest site by inserting the cardboard while the birds were in the other half of the cage. The birds did not seem to be much disturbed by this procedure after the first experiments. Warning calls were only uttered accidentally. Feeding of the nestlings was resumed shortly after removal of the partition.

The test stimuli were applied to the nestlings in regular sequence:

1. Tactile stimulation from a small stick, touching them on the beak or other parts of the body.

2. Auditory stimuli from the small loudspeaker. Begging calls of other nestlings of 8 to 12 days of age were mainly used. In some cases, white noise was applied.

3. Visual stimulation was provided by two stuffed birds, a Bengalese finch and a female zebra finch dummy. In pilot tests we recognized that simpler stimuli rarely lead to gaping responses. Thus, we did not use these simple dummies for the main experiments, as we wanted to leave the birds as unaffected as possible and, therefore, reduced the number of different stimuli to its minimum. Sometimes, visual stimuli had to be preceded by tactile ones, as the birds had closed eyes when the observation started.

We also observed the reaction of the young to an unspecific stimulus, namely darkening of the cage, between stimulus 2 and 3. Gaping responses were recorded after separation from the parents without giving a stimulus to obtain levels of spontaneous or uncontrolled elicited gaping at the beginning of each experiment.

The strength of the reaction of the nestlings was estimated using a subjective classification. This extended from zero into a positive direction (gaping responses) and into a negative direction (fear responses), each with three steps. For each day, a preference score was estimated from the different observation frequencies of class zero to +3 for gaping and for 0 to —3 for fear responses. Class zero (no reaction) was accounted for in each of the two response types. The score was estimated by the following equation:

$$S(G) = \frac{\sum_{c=0}^{c=+3} Nc * c}{\sum_{c=-3}^{c=+3} Nc} \quad \text{or} \quad S(F) = \frac{\sum_{c=0}^{c=-3} Nc * c}{\sum_{c=-3}^{c=+3} Nc}$$

S (G) = gaping score
S (F) = fear score
Nc = number of observations within class c

This score simultaneously considers two parameters of our observations: the different strength of the reactions, and also, the percentage of each type of reaction (gaping, fear and zero responses) in the total number of responses. It allows to present these two factors simultaneously in one diagram.

More than 100 young birds were observed in this study. However, only data from 18 birds are provided here, as only these birds could be observed throughout their development. All the incomplete data sets on the other birds agree with those mentioned here and will be published elsewhere.

Results

As the development of the morphological features and the feeding behavior of zebra and Bengalese finch chicks are described in detail elsewhere (EISNER 1961; IMMELMANN 1962; SOSSINKA 1970), we do not provide those data here. Our results confirmed the findings of IMMELMANN (1971) that the eyes of the birds open at about 5 days. At this time, however, only a slit can be seen. The eyes are fully open around days 10 or 11. Most of our birds fledged on day 19; this is too early if compared with the data of IMMELMANN and may indicate some disturbance. However, this earlier fledging time is normal under lab conditions. All of the birds of this age survived, thus, the disturbance does not seem to be essential.

The results from the young zebra finches reared by conspecifics and those of the birds raised by Bengalese finches are presented together, as they are very similar. However, the results for both rearing conditions are presented separately in the diagrams, to demonstrate that the same results appeared in two independent subsets of the experiment.

1. Control Experiments (Fig. 1)

We learned in a pilot study that the young zebra finches and their parents are very sensitive to disturbances from outside. While the parents after some broods under experimental conditions got accustomed to the environmental disturbances, the young birds remained sensitive to each noise and vibration outside the nest during the observation period. Thus, we preceded each test with a control to prevent artifacts. In these controls, the gaping of the young was observed for 3 min before the experiment began. If the experimenter managed to reach his place without affecting the animals, very few gaping responses were observed. Gaping was otherwise the most frequent reaction of the birds to noise from outside, most obviously in the early stages of development. In later stages, gaping to a certain degree was replaced by fear reactions (freezing, moving away from the nest entrance). The young did not react in most controls (Fig. 1), but a certain number of fear reactions was detected from day 15 onwards.

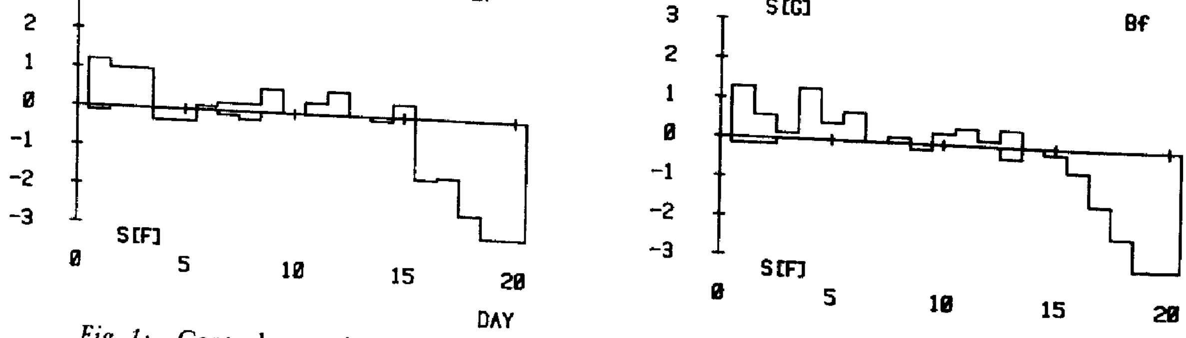

Fig. 1: Control experiment: Observation of the young birds without stimulation. S(G) = gaping score. S(F) = fear score. Zf = birds reared by their own species. Bf = birds reared by Bengalese finches. Further expl. see text

2. Tactile Stimulation (Fig. 2)

Zebra finches react to tactile stimulation very strongly from the first day of life (Fig. 2). Gaping could be elicited by touches with a little stick to each region of the body and the head. Stimulation of the beak region was most effective, as already described by other authors. From day 13, the gaping response decreased slightly until day 15. At day 16, the gaping response was at zero. Fear responses became more frequent from day 10 onwards and were the only reactions from day 16.

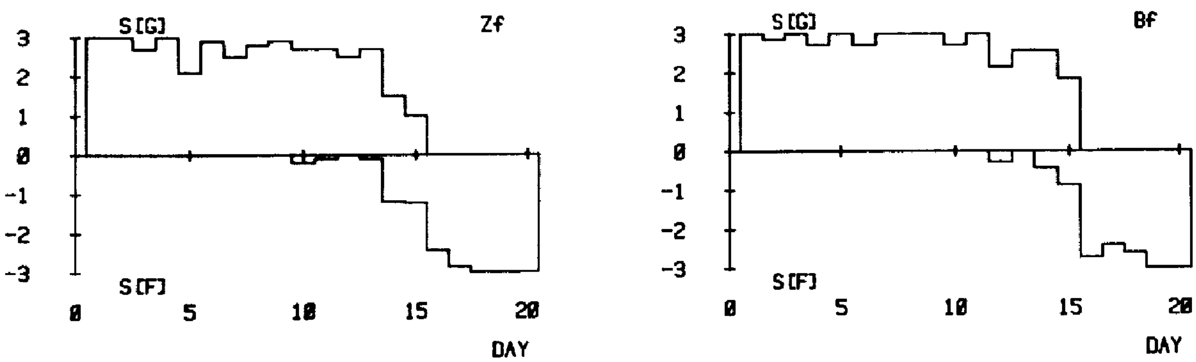

Fig. 2: Tactile stimulation. Abbrev. see Fig. 1

3. Acoustic Stimulation (Fig. 3)

The birds also reacted to acoustic stimuli from the first day of life. However, the response was not as strong as in the preceding experiment. In addition, the reaction seems to undergo a time shift. It was stronger in the first four days of life, decreased until day 8 and then became higher again until day 12. From this day on, it decreased again. This feature can more clearly be seen in the Bengalese finch reared chicks. From day 16 onwards to day 20 most of the reactions to acoustic stimuli were fear responses. However, some gaping reactions appeared in the foster reared birds after day 16.

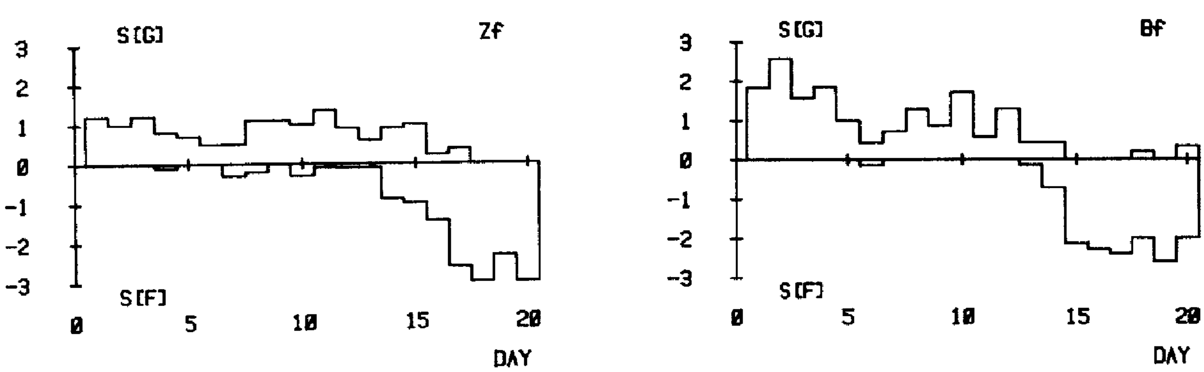

Fig. 3: Acoustic stimulation. Abbrev. see Fig. 1

4. Visual Stimulation

4.1. Darkening the Cage (Fig. 4)

Darkening of the cage only accidentally elicited gaping responses up to day 15. No apparent alterations of the strength of the response could be observed (Fig. 4). However, from day 16 darkening resulted in fear responses very often.

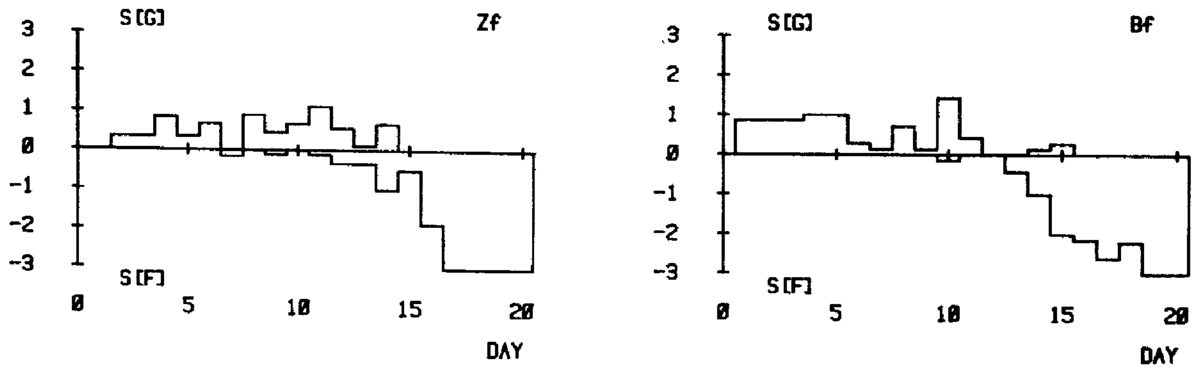

Fig. 4: Shadowing of the light. Abbrev. see Fig. 1

4.2. Stuffed Dummies as Visual Stimuli (Figs. 5 and 6)

Visual stimulation resulted in very different response diagrams compared to the preceding results. Responses to zebra finch or Bengalese dummies, respectively, appeared at about 10 or 11 days of age. Again, in 16 days old chicks, the gaping reaction dropped very quickly and was replaced by fear responses. No difference could be observed between reactions to the different types of dummies. Thus, the birds did not seem to differentiate between them at this age.

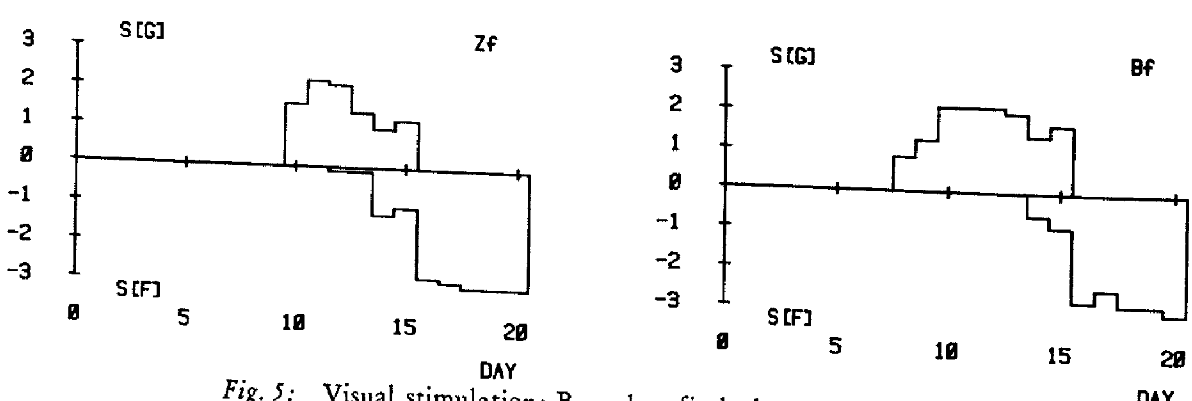

Fig. 5: Visual stimulation: Bengalese finch dummy. Abbrev. see Fig. 1

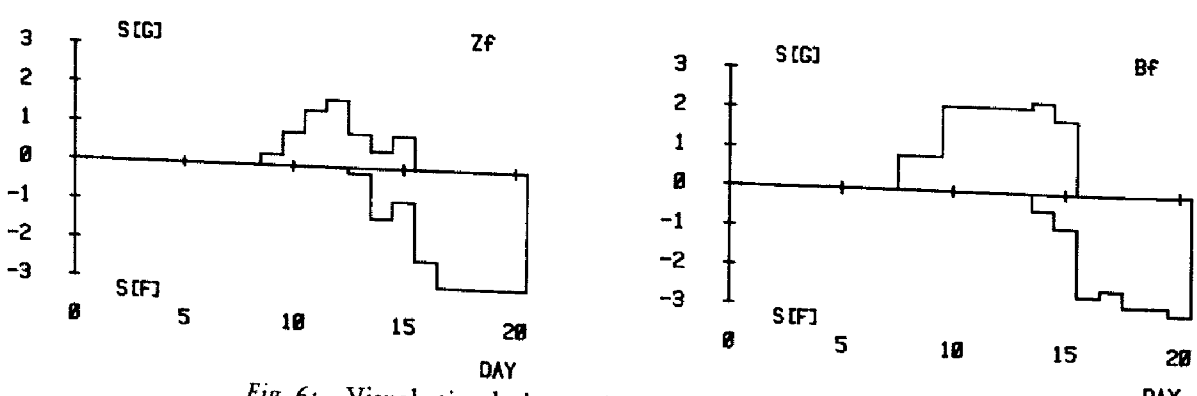

Fig. 6: Visual stimulation: zebra finch dummy. Abbrev. see Fig. 1

5. Combinations of Stimuli

We did not look at such combinations systematically. However, in some experiments the birds were asleep when the experiments should be performed; in these cases we had to wake them up before the visual experiment, using acoustic or tactile stimulation. Then, one could observe that a combination of visual and tactile stimuli elicited the gaping response much better than one single component. However, the time course of such combined stimulation was very similar to that obtained in the single stimulus studies. Especially the replacement of gaping by fear responses occurred at exactly the same time.

Discussion

1. Methodological Questions

In our control experiments a certain amount of gaping responses without apparent stimulation could be observed. We cannot decide whether these gapings were really spontaneous; however, no correlations between e.g. warning calls of parents and the gaping responses of young could be detected.

As can be seen from the controls, the situation changed somewhat after day 15. At that time, the birds obviously became much more sensitive to noises from the outside; most of the time they showed fear responses as a consequence of vocalizations of the parents or some undefined noises. This increased sensitivity to outside stimuli may be the reason for the early dates of fledging of our birds.

If, in control observations without separation, the parents came into the nest, the behavior of the young was well synchronized. When the parent came into the nest, the young birds in most of the observations gaped synchronously; most reactions were apparently elicited by tactile stimulation. Visual stimuli were used from day 10 to stretch the head to the appropriate direction.

In our experiments, however, the chicks in a nest were often of different age and behaved according to their age rather than all showing a common, synchronized response to stimuli. This was especially noticeable when some birds were older than 15 days and others were younger. In this situation, the older birds reacted with fear, the younger with gaping. Thus, we presume that synchronization of responses in the natural situation is due to the combination of different stimuli, which in all birds elicits maximum response.

2. Development of the Gaping Response

The observation by TINBERGEN and KUEHNEN (1939) led us to expect that the stimuli which elicit the gaping response would become more and more specific in the course of development. For tactile stimuli, no such increase in specificity could be observed. Even when the birds had their eyes open and could see the stick we used for stimulation, they continued reacting to this stimulus with the same strength. However, on days 13 to 15, where the visual abilities of the birds became better, there was a decreased response to the tactile stimuli. This is comparable with data obtained by PRECHTL (1953), who stated that after the development of visual abilities the animals no longer react to tactile stimuli.

The responses switched from gaping to fear reactions from day 16. As this is common for all stimuli, it will be discussed at the end of the section.

Reactions to acoustic stimulation (begging calls of nestlings recorded on a tape), in contrast, were different during the first 15 days of life. The birds showed quite good reactions for the first days, then reacted to a lesser degree for some time. They improved again until day 15, when all stimuli resulted with fear rather than gaping responses. These shifts, we suggest, may be due to specification of the auditory system. Perhaps, for the first days of life the birds react very unselectively to each noise they hear, but afterwards the reaction becomes more specific and thus drops down. From days 6 to 7 most of the young zebra finches give begging calls if the parents arrive at the nest. Thus perhaps the birds may learn that, when the call of their siblings is heard, food is available. However, we did not confirm this by stimulating the birds with undefined noise instead of begging calls. According to the hypothesis, one should get only the first peak with such stimulation.

Reactions to darkening of the cage were quite low during the whole experiment. This is consistent with the results of TINBERGEN and KUEHNEN, who did not find a reaction to this type of stimuli in their experiments with blackbirds. However, this stimulus like the others elicited fear responses to a certain degree from about day 16.

We expected that there would be a decrease in the reaction to the stuffed dummies from the time of eye opening onwards, as with the development of the visual system by learning the releasing stimuli for the gaping response should become more and more specific.

What we found was that the gaping response was elicited by the dummies earliest at about day 10. As stated before, the eyes open partly from day 5 or 6 and are fully open by day 10 or 11. Thus, it appears that visual capabilities are used for detection of stimuli on day 10 at the earliest. Perhaps, it may be that the visual system is sufficiently developed to accomplish this task by that time. Even more puzzling was the finding that the young throughout the whole time of the experiment did not react differently to the different dummies. We suspected that at least after some time they would differentiate between the two and respond selectively to the parent-like stuffed bird. We cannot decide from our experiments whether the young birds really do not recognize the differences in the dummies. It may well be that differences in reactions can be found using more sophisticated methods or a larger amount of observations.

On days 13 and 14, the reactions to the stuffed dummies began to decrease. This may demonstrate a further progress in the perceptual abilities of the birds. As in the previous experiments, the birds consistently reacted with fear responses instead of gaping from day 16 onwards.

3. Development of Fear Responses

Reactions of the nestlings to the stimuli used in our experiments shift from gaping to fear responses around day 16. The same observation was made by PRECHTL (1953), who defined freezing and also crouching away from the stimulus as fear reactions. He stated that at this time an "Umstimmung" occurs, by which another reaction is coupled to the same stimulus.

One has to ask, whether this fear reaction is not developed before this time and coupled to the applied stimuli independently of progress in perceptual abilities, or whether these stimuli are no longer accepted by the birds as appropriate and are therefore answered with fear. Our observations indicate that the second possibility is more likely for two reasons. Firstly, the birds accidentally show fear responses much earlier than day 16. Indeed, a certain number of fear reactions to stimulation were recorded every day after day 13. Secondly, birds which react to dummies with fear, respond to the parents with gaping. We observed on several occasions that birds which reacted with fear during the experiment at day 16, immediately gaped at the parents on their re-introduction.

Thus, it is most likely that the fear response is shown in our experiments as a consequence of the fact that the birds from day 16 can differentiate between dummies and their parents. If this is true, there are some implications of our findings to the imprinting process. These will be discussed in the next section.

4. Imprinting

It has been demonstrated that zebra finch males prefer visual features to select the appropriate object for courtship (IMMELMANN 1959, BISCHOF 1977, 1980). Thus, in this section we will only discuss the results concerning the reactions to visual stimuli.

Our data demonstrate that at about day 10 the young birds respond to the stuffed dummies and thus are capable of using visual stimuli as cues for gaping. Their response to dummies is high until day 13, then it decreases slowly. However, they make no obvious differentiation between the two types of dummies. Considered together, these findings may indicate that the birds between days 13 to 15 have learned to recognize some characteristics of their parents, but not enough to fully differentiate between dummies and parents. By day 16, the development of the nestling's perceptual abilities seems to be complete, as they can by then clearly distinguish between parents and dummies.

One then has to ask at which time the onset of the sensitive period for sexual imprinting occurs. It perhaps starts on day 10, when the birds begin to recognize visual stimuli, and is almost complete on day 16, when they apparently know what their parents look like. As a consequence, as argued by researchers of filial imprinting (BATESON 1964, 1966), the birds develop a reaction of fear. However, as IMMELMANN's data (1972, IMMELMANN and SUOMI 1981) demonstrate, the birds' preferences can still be altered when they are more than 15 days old. Thus, imprinting cannot be finished at that time.

Likewise, one could argue that imprinting starts at the age of 16 days, at the time when the birds can really recognize their parents. However, the birds can sometimes be stably imprinted as early as 13 days (IMMELMANN 1972; IMMELMANN and SUOMI 1981).

Thus, it is more likely that the observed process cannot really be divided into development of perceptual abilities and learning the distinct features of the parents. However, one has to differentiate between the two phenomena of learning the features of the parents and of really being imprinted on them, that is acquiring the features so definitely that they cannot be forgotten. Thus, the birds learn the features of their parents in parallel with the development of their perceptual performances from day 10, when they first react to visual stimuli, to day 16, when they can distinguish between dummies and parents. At this time, according to the results of IMMELMANN (1972), some birds are already imprinted. Thus, the process of irreversible storage of the parents' features has already begun. As a consequence of becoming familiar with the image of their parents, the nestlings develop a fear response to strange objects. As BATESON (1981) preferred to put it, the birds become unwilling to learn new features and concentrate on their parents' image. This mechanism guarantees that only the initially acquired features will be stored during the subsequent period of high susceptibility to external stimuli and the time when the birds acquire the learned features irreversibly.

This will result under natural conditions in a strong sexual preference later in life for birds which resemble the parents. However, under experimental conditions one can demonstrate that the imprintability of the bird has not definitely ended. If forced to attend to another object, the birds can learn its features and get imprinted to it. This can be demonstrated as well in filial as in sexual imprinting.

Zusammenfassung

Antworten junger Zebrafinken auf verschiedene Außenreize wurden täglich vom Schlupf bis zum Alter von 20 Tagen registriert. Die verwendeten Stimuli waren: taktile Reize, die mit Hilfe eines Stöckchens gesetzt wurden, akustische Reize (Bettelrufe anderer Junger, die über einen Lautsprecher eingespielt wurden), und optische Reize in Form von ausgestopften Zebrafinken bzw. Japanischen Mövchen.

Bei taktilen und akustischen Reizen antworteten die Jungen vom 1. Tag an mit Sperreaktionen; visuelle Reize wurden vom 10. bis 11. Tag an beantwortet, 5 Tage nach dem ersten Öffnen der Augen. Mit 13 Tagen nahm die Sperreaktion auf Reize ab und wurde vom 16. Tag an vollständig durch Furchtreaktionen ersetzt. Die Implikationen der Ergebnisse in bezug auf die sensorische Entwicklung der Tiere und auf sexuelle Prägung werden diskutiert.

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