

FACTORS IN THE DEVELOPMENT OF FEEDING BEHAVIOR OF THE MUSCICAPA-HYPOLEUCA SQUEAKERS

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In Professor P. K. Anokhin's laboratory ecological factors have been shown to be significant in the development of feeding behavior in rook nestlings [1]. It was found that as soon as they were hatched the young birds responded by a complete reaction to three stimuli: intermittent movement of air blown upon them, vigorous shaking of the nest, and the sound "Kaar-r"; each of these stimuli presented alone also elicited a feeding reaction, which however was weaker and lasted for a shorter time than when all three were presented together. According to Y. A. Milyagin the feeding reaction in response to these stimuli is inborn. Because these factors have no special feeding significance the author proposed that the inborn response might be in the nature of a signal. The deciding factor in these early signalling reactions would then be the combination of ecological factors characteristic of the rook. The question arose as to how to test the view concerning the signalling nature of the inborn reactions in other species having a different ecology.

We have studied the influence of ecological conditions associated with the development of signal reactions in another bird species having a characteristic ecology. We chose the muscicapa-hypoleuca squeaker; these birds inhabit hollow trees where the feeding conditions are necessarily very different from those enjoyed by the rook.

EXPERIMENTAL METHOD

The experiments were carried out at the M. V. Lomonosov State University Biological Station in the Zvenigorodskaya territory natural for the bird species.

Observations were made on 55 muscicapa-hypoleuca squeakers 1-14 days old (from the time of hatching until the nestlings left the nest). This species is one which inhabits old hollow trees or which nests in boxes made for starlings or tits.

The nest was transferred from the ordinary starling box into one which was specially constructed and fitted with a transparent back wall. It was placed in a chamber insulated from light and sound and fitted with a photo-recording apparatus.

Altogether 42 experiments were carried out, each lasting 13-18 hours.

EXPERIMENTAL RESULTS

It is well known that the nestlings show little variation in their reactions. However we must note that in the first minutes after hatching there is a well developed complex feeding reaction which corresponds precisely to the ecology of the species. It may be regarded as a complete complex of very simple adaptive actions leading to the successful acquisition of food, and hence to survival of the species.

In response to the appropriate stimulus the fledgling rapidly raises the head, extends the neck vertically, and opens the beak wide. The stable position of the head and neck is maintained by the bird leaning the back part of the body on the base of the nest and its wings on the adjacent fledglings. This complex motor act is carried out to the accompaniment of loud cries, which cease when food has been received [1].

In the development of the feeding reaction the variety of natural stimuli eliciting this reaction is of special interest. The stimuli vary according to the age of the fledgling, but are always made up of a number of factors of which one is of principal importance in releasing the feeding reaction.

During the experiments it was found that the stimuli were as follows: 1) sound caused by movement of the wings of the adult in its flight to the box; 2) the scraping noise against the nesting box made by the claws of the adult bird bringing food; 3) the loud clucking noise made by either parent as they fly in with food. The complex reaction was observed every time the fledglings were fed. The feeding period lasted for 16-18 hours with intervals of $2\frac{1}{2}$ -3 minutes (the birds received food 400 times per day).

As our investigations showed, 1-5 minutes after hatching the feeding reaction occurs spontaneously and appears to induce in the parents behavior related to the acquisition of food. The adult bird flies onto the nesting box with food, sits on the edge of the nest, and makes a clucking noise. In conjunction with the other components of the signalling complex this sound in turn elicits the feeding reaction in the young (Fig. 1).

During the course of the experiments it was found that on the first day after hatching the bird produces a feeding reaction in response to any sound stimulus which is sufficiently strong (a whistle, sound of a bell, quiet speech, etc.), but later, on the second day, it begins to differentiate sounds and responds only to those produced by the parent as it flies in with food onto the nesting box (clucking noise). This marked differentiation is maintained for the whole of the first postnatal period (until the eyes are opened, i.e., until the 5-6th day). In this way in the first postnatal period the releasing signal for the feeding reaction of this species consists of strongly differentiate stimuli — the sounds given by the parent bringing the food.

Tactile and thermal stimuli (a stream of air) or tactile stimuli (rubbing the beak with a brush) induced not a feeding but a defensive reaction, consisting of retreat from the stimulus, behavior which appears to emphasize the strictly adequate central feeding connections and their relationship to one analyzer only.

The eyes open on the 5th or 6th day. Now the feeding reaction is elicited principally by visual stimulation. Flying up to the nesting box the adult bird carrying food closes the aperture to the box, so reducing the amount of light which enters. This change of illumination effectively elicits the feeding reaction although the other components of the signalling complex remain unchanged at this period (Fig. 2).

Here it is interesting to recall that in his experiments Ya. A. Milyagin obtained similar results; six seven-week-old birds did not react to the sound "Kaar-r". At this age the feeding reaction was elicited by visual stimuli. The sight of the parents flying in with food induced the feeding reaction.

During the work we attempted to find whether the feeding reaction to visual stimulation which develops on the 5-6th day is acquired or innate as is the reaction which appears initially to sound stimulation five minutes after hatching.

To decide this point, immediately after the birds had hatched we introduced an additional brighter light into the nesting box. Under these conditions the arrival of the parent bird did not change the illumination; thus when the eyes were opened there was no possibility of the formation of a conditioned reflex based on change of illumination and reinforcement by feeding. Before the eyes were opened the feeding reaction was induced by sound stimulation, but by the 5-6th day it was replaced by a visual stimulus. However, when the conditions were such as to prevent the necessary association of illumination and feeding reinforcement in fledglings aged 5-6 days the feeding reaction failed to appear, although the adult bird bringing the food did utter a clucking sound. We may suppose that by the time the eyes are opened the sound stimulus which has played a part in the feeding activity of the fledgling is inhibited. A few hours after the eyes were opened the additional illumination in the nesting box was removed, and under these conditions the very first arrival of the adult bird with food induced a marked feeding reaction mediated by the change of illumination.

In the light of P. K. Anokhin's conception of system development as a general law of the acquisition of function during the prenatal period, the results we have given suggest the presence of a marked heterochronism in the development of those structures which contribute to the feeding reaction of fledglings at each stage of postnatal development. At birth the auditory analyzer is completely functional and mediates feeding behavior during the first postnatal period; then when the eyes open the visual nervous structures become effective, and are involved in the feeding reaction, when they play a principal part.



Fig. 1. Feeding reaction in a two-day fledgling in response to sound stimulation. For a ten-day-old bird this stimulus is ineffectual.



Fig. 2. Feeding reaction in ten-day-old fledglings in response to visual stimulation.

In studying feeding activity of fledglings we were able to discover the astonishingly delicate adaptation of the organism to the conditions of the external medium. It was found that the birds in the nest rotate regularly in a circle in the same direction, counterclockwise.

By the time they are seven days old the cycle of rotation takes 80 minutes, and is reduced by the eleventh day to 30 minutes. We have provisionally named this reaction circular movement. It may be directly related to the feeding reaction, because under natural conditions feeding always takes place at the same place (the entrance to the nest), and the only fledgling to receive food when the parent arrives is the one in this position. Also, this place is the most brightly illuminated of the whole nesting box. We may suppose that the greater the excitation from hunger the more strongly will a bird strive to get into the illuminated zone. To test this hypothesis we kept two six-day old fledglings for ten-twelve hours without food and then placed them in the nesting box. On their arrival they immediately began to fight for the illuminated position continually pushing each other away from the entrance (source of light). As their hunger became sated they quieted down and left the illuminated spot, moving over into a darker region.

An analysis of our investigations shows that the fledgling hatch with an already developed acoustic system, which by the first day comes to play a principal part in the release of the feeding reaction. The reaction is elicited by a whole complex set of factors in which there is always present the principal stimulus, which plays a leading part in the release of the feeding reaction.

By the time the eyes open (second period of postnatal life) there is a marked change in the principal afferent stimuli releasing the feeding reaction. The acoustic system is almost completely eliminated and its place is taken by the visual system, i.e., the reaction is to the reduction in intensity of the light beam.

The feeding response to visual stimulation (change of illumination) is inborn and acquires chief importance at the time that the central and peripheral structures of the visual system reach maturity.

The reaction of circular movement is directly related to feeding activity and ensures an even distribution of food among the fledglings of one batch. The internal mechanism of this reaction remains unexplained. We have reason to suppose that the initial stimulus to circular movement of all the fledglings is set by the sated fledglings in whom a tendency develops to leave the illuminated zone when they have fed.

SUMMARY

This work deals with the effect produced by ecological conditions associated with the formation of food reactions in the squeakers of the *muscicapa-hypoleuca* in response to signals. Our investigations led us to conclude that in the early postnatal period the central structures responsible for adaptive activity of the species to feeding are brought about by different rates of maturation of the ecologically important bodily functions.

LITERATURE CITED

1. Ya. A. Milyagin, Determinative Influence of Ecological Factors on the Embryogenesis of Unconditioned Reactions. Dissertation for Doctorate, Moscow (1957).