ONTOGENY OF EMBRYONIC BEHAVIOR IN AVES: V. THE REFLEX CONCEPT IN THE LIGHT OF EMBRYONIC BEHAVIOR IN BIRDS

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INTRODUCTION

The concept prevailing in neuro-physiology and psychology, that instincts are innate combinations of reflexes while habits are postnatally acquired behavior patterns which are also integrated from simple reflexes, has been of late repudiated from several angles. In the first place, neuro-anatomy has failed to reveal that in the nervous system there are definite and more or less fixed anatomical patterns which are in definite correspondence with behavior patterns. Secondly, I have early pointed out (13, 14) that the so-called instinctive behavior is too variable to be operated by any definite and stable structural arrangement of the nervous system. Indeed, so common is the fact of variability in behavior that even the most ardent instinct psychologist, McDougall (19), cannot help abandoning the reflex arc concept in favor of a non-mechanistic or vitalistic view of instinct. Thirdly, Lashley (summarized in 18) and others have clearly demonstrated that the so-called ‘learning process’ does not involve the establishment of any definitely localizable reflex circuits in the central nervous systems corresponding to the ‘learnt’ act, as has been so commonly supposed by neurologists and psychologists. Fourthly, the reflex concept has been repeatedly
attacked by a certain school of psychology, namely, the so-called gestalttheorie, on the metaphysical ground of the supremacy of whole over parts. And, finally, and most important of all, is the fact revealed by recent studies of developmental behavior that the early behavior of most, if not all, vertebrate animals is characterized by massive movements, that is, movements which involve the body as a whole, rather than by separate or independent reflexes. In other words, separate reflexes of body parts are later differentiations from the early total and massive movements. Coghill's work on Amblystoma (3, 4, 5, 6, 7, 8, 9), has clearly demonstrated this point. The researches on the behavior of mammalian (1, 25) and human fetuses (Minkowski and others, for bibliography see Coghill's (6) footnote) seem to point to the same fact. Thus, the traditional view that complex behavior is a result of the chaining or coordination of separate reflexes breaks down entirely in the face of these facts. Coghill further points out that simple reflexes never occur in the life of the individual; since local reflexes can acquire only a certain degree of independence, the apparently independent reflexes are still more or less under the influence of the organism as a whole. In the following pages we shall present facts concerning the behavior of avian embryos which in general agree with Coghill's observations. However, while Coghill in his studies of the behavior of Amblystoma and others in their studies of the movements of mammalian and human fetuses have not been able to determine the conditions under which the independent movements of body parts are originated, we have worked out such conditions in our observations of the behavior of the avian embryo.

The facts concerning the origin of such independent movements will also be reported and discussed in this paper. Furthermore, in the following sections we shall give reasons to show that while we are in agreement with Coghill with regard to the fact that independent movements of body parts come about as a result of differentiation or individuation from massive movements, in consideration of the development of behavior we attach much less significance to the process of individuation of partial patterns from total patterns than Coghill has claimed, and we object to some of his neural interpretation of the dominance of the trunk movement over other parts of the body in Amblystoma, and, especially, his uncritical acceptance of the 'gestalttheorie.'

Massive Movements in the Bird Embryo

The chronological order of the appearance of the movements of various parts of the body in the chick embryo has been reported in the first article of this series (14). It has been found that the earliest movements in the embryonic chick are the lifting and bending of the head. The ventral bending and the lateral twisting of the trunk come next. These are then followed by the movements of the appendages and of the tail. Oral movements, eyelid reflexes and movements of the eye ball appear last. Now, during the first half of incubation the movements of these various body parts are synchronized with the movements of the head and the trunk. This is especially true during the period of violent swinging movements and amnion contractions (14). During this period, with the exception of the head, which may occasionally make some slight movements without being accompanied by perceptible movements of other parts of the body, the body almost always moves as a whole. The limbs and tail move when the trunk moves. So do the eyes and the beak. It is extremely rare to observe the tail, the bill or the limb move independently. Even in the later stage of incubation in response to sound, touch, pressure and electricity, the whole organism is involved. However, independent movements of body parts, i.e. local reflexes, may also be observed in the latter half of incubation. The conditions under which local reflexes are originated will be described in a later section.

The Question of Neural Explanation of Massive Movements

In our study of the behavior of the bird embryo we have not attempted to find out whether there are any possible correlations between the growth of the nervous system and the
development of physiological reactions. Coghill, however, in his investigations of the behavior of Amblystoma has worked out such correlations in some detail. It may be well to review here his neural explanations of the massive movements in Amblystoma. Coghill reports that in the Amblystoma, the movements of the arms and gills are integrated with the trunk: The arms and the gills move only when the trunk moves. Based on his anatomical findings he explains the dominance of the trunk over the arm as a result of the fact that the motor nerve fibers which innervate the limb muscles are the branches of the same nerve fibers which innervate the muscle segments of the trunk. Such an explanation is highly plausible and one can hardly object to it on a priori grounds. But when we turn to Coghill's anatomical explanation of the dominance of the trunk over the gill, we feel that it is rather far-fetched. He says: "In a transverse section of the medulla oblongata of Amblystoma of the early swimming stage, the motor cells of the group which are to innervate the muscle of the gill are situated in the most dorsal part of the motor division of the nervous system. Large dendrites from these cells invade all sources of afferent impulses through the sensory system, the ascending trigeminal tract and the lateral line tract. They reach also into the zone of synapse between the commissural cells of the floor plate and the motor neurones that innervate the trunk muscles. The muscles of the external gills are therefore subjected to excitation not only by those afferent impulses which are on the way to the motor mechanism of the trunk, but also by those efferent impulses of the motor path which are on the way directly to the muscles of trunk. In general, therefore, by reason of these relations of the motor neurones that innervate the muscles of the gills, these muscles, after they have acquired sensitiveness to nervous excitation, would be expected to receive excitation from impulses that are on the way to the muscles of the trunk.

"Since the gills act with the trunk before they act independently in response to afferent impulses it must be that the motor neurones that control them establish functional synapses with the motor neurones that excite trunk movement before they establish such relations with the afferent neurones." (4, pp. 31-32.)

I wonder if such an explanation as quoted above has any significant and specific meaning at all. It tells us nothing more than the fact that the nervous system is integrated. Of course, every one knows that every neurone is connected in one way or another with all and every other neurone of the nervous system and that impulses from certain neurones may reach some other neurones at the furthest distance from them. But the question is: is it necessary to explain the synchronism of movements of body parts in terms of specific neural connections? I took chick embryos from eggs and put them in warm p.a.s. Weak electric stimulation was applied to the tail. The tail moved simultaneously with eye-lid reflexes and the opening of the beak. Of course, it is possible to demonstrate anatomically that the nerves of the tail are in some way connected (through the central nervous system at least) with those neurones which control the eyelids and the oral muscles. But here again such a demonstration tells us nothing specifically. The point I am driving at is this: as long as the reactions of the embryo are found to be neurogenic (regardless whether the motor nerves are activated by sensory stimulation or by some endogenous agencies (23, 9) and as long as the nerves controlling the reacting organs are integrated with the central nervous system, the synchronism of movements of different body parts is already explained. In other words, the mere fact that the nervous system as a whole is integrated is sufficient to account for the massive movements of the embryo; it is relatively unimportant to determine whether the synchronism of movements of two body parts is a result of direct synaptic connection, or a result of the fact that the two parts are innervated by the branches of the same nerve, or merely due to the fact that they are integrated through the central nervous system; for different body parts even without direct synaptic connections may move simultaneously. (The synchronous movement of the tail of the chick embryo, when stimulated by weak electric current, with the movements of the beak and eyelid is a case in point.)
I think that the most difficult and fundamental neurological problem is concerned not so much with anatomical explanations of synchronism of movements, since anatomically the nervous system is integrated from the start (to borrow Coghill's expression), as with the question why or how the so-called local reflexes are brought about in later stages of behavioral development in spite of the integrative nature of the nervous system from the beginning of behavior. This leads us to the question of the origin of local reflexes.

The Origin of Local Reflexes

While it seems now to be established from Coghill's studies on Amblystoma and from those of others on mammalian and human fetuses that local reflexes appear as a result of differentiation from the total behavior pattern, the exact conditions under which the local reflexes are originated thus far have not been reported. In the bird embryo we have found that there are at least two fundamental factors—intensity of sensory stimulation and environmental interference—which are responsible for the origin of independent movements of body parts.

a. Local Reflexes as Produced by Environmental Interference.—As has been stated, excepting the head, which may occasionally make some slight independent movements, local reflexes of other parts of the body are rarely observed in the chick embryo in the first half of incubation. During this period the embryo either moves violently, involving the whole body, or rests motionless. Even in the slight jerking of the trunk, other body parts are also involved. In violent movements of the trunk, not only the head, neck, tail and limbs, but also the eyelid reflexes and oral movements are involved. But after the 11th or 12th day of incubation, several local reflexes begin to gradually appear one after another. In the second paper of this series we have reported that by about the 12th day the yolk sac begins to come over the ventral side of the embryo, covering its ventral wall, the legs, the beak, the forehead and both eyes. In most cases a part of the right side of the body and of the right wing is also covered by the yolk sac after about the 13th day (15). In this position, the dorsal side of the body and of the neck is in direct contact with the egg shell with the allantois and egg membranes between them. It must be emphasized that even in the later stage of incubation the yolk sac which contains the yolk is still heavy; shortly before hatching, it weighs several grammes. These conditions greatly interfere with the movements of the embryo (16), the bending of the trunk and the lifting movement of the head are reduced to a minimum, the frequency and extent of the turning of the head and of the opening and closing of the beak are also diminished. During this period, jerking and wriggling movements are frequently observed. Such movements involve the body as a whole. But when the embryo is at rest, the clapping and opening and closing of the bill and movements of the eyeball and the eyelids may be seen to occur independently, that is, without the participation of the head or the trunk or the legs. Such independent movements of the bill and of the eye are observed more frequently when the beak and the right eye are not covered by the yolk sac. After the embryo has turned so as to lie lengthwise of the long axis of the egg (15), even wriggling movements are not observed so often. The bird, at this time, is seen only to make occasional jerking. But clappings of the bill and the eyelid reflexes and eye ball movements occur more often than before. Independent movements of the toes (scratching movements) and slight wing movements may also take place without the participation of the trunk. In fact, from about the 15th day to the time just before hatching, the embryo is motionless most of the time so far as wriggling of the trunk and movements of the head and legs are concerned; (wriggling is seen to occur, however, at the time of the protrusion of the neck downward and forward into the air cell). Eye movements become most frequent after that portion of the yolk sac covering the head and bill has been drawn into the body cavity.

If we consider the position of the chick embryo in the egg during the last few days of incubation, we could easily see why independent bill clapping, and eyelid movements (and to some extent, the scratching of the toes and movements of the
right wing) occur frequently, while movements of the head, the trunk, and even the legs are reduced to a minimum both in extent and in frequency. The body is large and heavy at this time, its back is in contact with the shell and its ventral wall as well as the forehead and bill are covered by a rather heavy yolk sac. The neck is doubly bent. After the yolk sac has been withdrawn from the head the membranes in the large end are directly applied on the right face. Besides, the liquid content in the egg is very much reduced. In this position the bird is virtually ‘bound up’ in the egg; free and extensive movements of the head, neck, trunk and extremities are greatly impeded. The movements of the bill and of the right wing are also checked, at first by the yolk sac and later by the membranes. Hence the movements of the bill are reduced to clapping and slight and infrequent forward and upward thrusting (16). The right wing, which is held tightly against the body wall, can only be drawn up and down. The only part of the body that can move without much external interference is the eye. These are the conditions under which the independent movements of the eyes, bill clapping and, to some extent, toes scratching and wing movements are originated. In other words, environmental interference with the movements of the head and, especially, of the trunk give rise to these independent local reflexes.

It must be emphasized here that the acquisition of the above mentioned independent movements is brought about by a gradual reduction of the head and trunk participation in the movements. The process of the reduction is so gradual that even at the end of incubation one can often observe an independent eye movement or bill clapping to be accompanied by some slight jerking of the trunk or of the head. In fact, the withdrawal of the head and especially the trunk participation in such independent movements is practically in every case incomplete even after hatching. Our observations agree with those of Coghill in Amblystoma in that local reflexes can acquire only a certain degree of independence; absolute independence does not occur in normal cases.

It must be pointed out also that in the bird embryo, even after the local reflexes have acquired the ability to move independently, in violent movements the body as a whole is involved.

Local Reflexes as Determined by Intensity of Sensory Stimulation.—In the chick embryo in response to strong stimulation of sound, pressure or electricity, practically every part of the body is involved. But in many cases if the intensity of electric or pressure stimulation is reduced, local responses may be elicited,—that is to say that with very weak stimulation only the stimulated parts are involved in the response. In our observation of many embryos delivered in warm physiological salt solution, we found that in response to electric stimulation, the stronger the stimulation, the more parts of the body are involved, and that there seems to be a gradation of the strength of the responses of different body parts, that is, the further away from the stimulated area is the part which is involved in the response the weaker will be its response. It clearly indicates, then, that the degree of intensity of sensory stimulation is an important factor in determining whether the organism will respond with a total pattern or with a partial pattern, or even in determining how many and what parts of the body will be involved in a given response. In this connection it must be stated that although a visual stimulus in general can only elicit eye reflexes in the chick embryo, bright light which is suddenly introduced into the incubator may sometimes set the whole organism in motion. This is true both shortly before and after hatching.

The Origin of Alternate Movements of the Legs

Graham Brown (2) and Windle & Griffin (25) have observed alternate movements of the legs in fetal kittens. But as they were unable to make continuous observation on the same fetus in the normal uterine environment, the conditions which give rise to such alternate movements were not known to them. Consequently, Brown was led to the conclusion that progression in animals (walking, etc.) is a hereditary pattern, since it appears before birth. But the following observations on the origin of alternate leg movements in the bird
embryo will clearly demonstrate that the concept of hereditary behavior is generally employed as a cloak to cover our ignorance of the causes of origin of behavior:

As has been stated, in the chick embryo in the first half of incubation, movements generally involve the body as a whole; not only do the legs almost always move together with the trunk, but also both legs are flexed or extended synchronously. But after about the 11th day alternate movements of the legs begin to appear. This is brought about by the changes in the positional relation between the yolk sac and the embryo. We have reported elsewhere (15) that before the 11th day the embryo lies with its back on the yolk sac, but after that day the yolk sac, in normal cases, is pushed over to cover the ventral wall and the legs. As a result, the legs are folded down on the breast. Under these conditions extensor thrust of the legs is interfered with by the amnion and especially by the yolk sac which are pressing against the legs. Now in order to permit movements, one of the legs has to push up the amnion and especially by the yolk sac which are pressing against the legs. In the beginning, the reciprocating movements of the two hind limbs are not well timed. Truly rhythmic legs movements are observed generally by about the 17th day of incubation.

The Question of Neural Correlation with Independent Movements of Body Parts

As has been pointed out in a previous section, it is relatively simple to explain in neural terms the integrative nature of embryonic behavior, but it is far more difficult to explain neurologically why the so-called discrete reflexes do finally appear in spite of the fact that behavior is integrated from the start. At any rate, laboratory findings for such an explanation are not forthcoming. Minkowski (20) has suggested that the myelination might be responsible for the genesis of the independent movements of body parts. But Angulo y Gonzalez (1) has found that discrete reflexes in the fetal rat appear before myelination, showing that the theory which proposes to make myelinogenesis a criterion of functional insulation of conducting path is not well grounded.

There can be no manner of doubt that there is some sort of change in the nervous system as a result of the appearance of the discrete reflexes. But precisely what such changes are remains to be worked out. Personally I will not venture to speculate on this question. But I will suggest just two points: (1) The neural explanation of discrete reflexes must be a physiological (central (?) or reciprocal inhibition or what not) rather than an anatomical one. Any attempt to find an anatomical basis of discrete reflexes is very likely to meet with failure. For anatomically, the whole nervous system is integrated from the beginning of behavior to the end of life. Furthermore it is a simple matter to explain the chaining of reflexes, as the concepts of the formation of new pathways and of the reduction of synaptic resistance through exercise will very well take care of the chaining process. But when we come to the question of the differentiation of partial pattern from the total pattern, the case is different. For, here, both of these two concepts break down entirely.

And (2) such changes in the neuro-physiology which are correlated with the independent part movements must be the result, rather than the cause, of the origin of such movements. For we have found that independent local movements appear definitely as a direct result of environmental interference.
with total movements. Furthermore, as has been described, reduction in the intensity of stimulation can also produce independent movements of body parts. In this respect intensity of stimulation probably continues to play an important part throughout the life of the individual. For it is a common observation that even in adult life stimulation with high intensity generally throws the whole organism into activity, while weak stimulation effects only certain parts of the body.

**DISCUSSION**

From our observations on the behavior of the bird embryo and from various other studies cited in the introductory section of this paper three points regarding the reflex concept seem to have been established:

1. That there is no such a thing as a simple reflex.
2. That behavior begins as a total pattern, independent reflexes or partial patterns come about as a result of later differentiation from the total pattern.
3. That behavior is too complex and too variable to be explained by the concept of chain reflexes.

Let us take up these three points separately.

1. That the simple reflex concept is an abstraction was pointed out by Sherrington (21) many years before Coghill. It is true that in many of the textbooks on neurology, organ physiology and general psychology the fiction of simple reflex has been uncritically accepted and overemphasized. But for this Sherrington can not be held responsible. As a matter of fact during the past twenty years or so no leading student in neurology and behavior has ever taken the simple reflex concept seriously. Coghill's repeated assertion that he has failed to find in the Amblystoma any simple reflex does not seem to strike me as a new discovery. However, those who still hold fast to this fictitious concept of simple reflex must be reminded of the fact that even in such a simple movement as the Achilles reflex in the rat the whole nervous system is involved (24).

2. Credit must, however, be given to Coghill for his first observation that in the Amblystoma behavior is integrated from the start, while "partial patterns emerge within the total pattern." As far as I know, Coghill is the first person in point of time to announce and emphasize this fact. Judging from the studies in mammalian fetal movements and from our own observations on the behavior of the embryonic chick and other avian embryos, Coghill's principle seems applicable to all vertebrates. In the past we were wont to think that behavior appears first as separate reflexes and that only through later integrations are these reflexes linked together to form complex movements. But the facts of embryonic and fetal behavior in various vertebrate animals are now definitely at variance with such a belief.

Notwithstanding the fact that Coghill's observations in this respect are in agreement with mine, there are several points on which our views are widely different:

(a) As has been previously stated, I am inclined to think that to explain the total behavior pattern in terms of neural anatomy (that is, in terms of certain special connections between neurons) seems unnecessary or far-fetched, since all the neurons in the nervous system are interconnected in some way, and since body parts without direct neural connections may also move together, as in the case of the synchronous movement of the tail with the beak and eyes.

(b) Coghill has failed to study the environmental conditions which give rise to partial behavior patterns. This has led him to overemphasize the importance of the nervous system in the development of behavior at the expense of environmental and other physiological factors. On the other hand, while not denying the importance of the nervous system, we have demonstrated both in this and in the third reports of this series (16) that environmental conditions are a most essential factor in determining embryonic behavior in general and in the genesis of partial behavior patterns or discrete reflexes in particular. In this connection it is interesting to note that Coghill so far has not been able to report his morphological findings in the development of the nervous system in Amblystoma which he would regard as responsible for what he has called 'individuation of discrete reflexes.'
(c) I cannot agree with Coghll that his findings in any way tend to support the position of the gestalt view in psychology. The so-called gestalttheorie is a hybrid between the old fashioned mentalistic psychology and Bergsonian philosophy under the guise of science. It attempts to build a psychological (philosophical) system around a unifying principle by the empty and somewhat mystical name of gestalt or configuration. This is an old trick of philosophers. In the sciences, on the other hand, no one would care to postulate a theory and then apply it to the whole universe. But this is precisely what the gestalters have been trying to do.

Whether behavior starts with movements of the organism as a whole or complex behavior is built up as a result of chaining or linkage of simple reflexes, is a question of fact. If the former is true, we have to analyse in detail the exact causal factors which are responsible for the genesis of the so-called discrete reflexes, as we have done in the case of the bird embryo. Such vague statements as ‘whole dominates over parts,’ ‘partial patterns emerge within the total patterns,’ ‘qualities upon a ground’ or ‘configuration upon a ground’ and the like are meaningless as well as useless. To be sure, every one would accept the notion of the ‘organism as a whole.’ But as men of science we ought to learn much more than this empty and somewhat idle statement. In other words, we have to know exactly what parts are correlated, and how.

This can be studied only by analytical and quantitative methods and by control experiments and can be described only in strictly physical and mechanistic terms. But when one reads the gestalt literature, one cannot escape the impression that the analytical and quantitative methods of the exact sciences are superficial, that laboratory control is foolishness, and nothing but wholes.

(d) The problem of the development of behavior is not so simple as Coghll has thought. The question of ‘individuation versus integration,’ as Coghll expresses it, (8) is relatively unimportant in comparison with the question as to how the massive embryonic or fetal movements come to be reorganized in postnatal life into sequential order in accordance with environ-

mental conditions. The development of behavior is primarily a continuous process of reintegrating the bodily movements into serial responses. The individual acts, whether massive or discrete, are of no great significance unless they are hitched together into temporal order according to the demands of the environment. In other words, the development of behavior is fundamentally a continuous process of interaction between the organism and its environment, and as a result of such an interaction, the individual bodily acts are reorganized in various ways into serial order.

The point I am here stressing may be restated in this way: The individual is born with various sorts of embryonic movements which involve the organism as a whole. Now when this newly born organism comes into collision with a new environment, it is forced to rearrange these embryonic movements into various serial responses so as to meet the demands of the environment. In the rearrangement of such original, embryonic movements (that is, movements which originated in prenatal life) into temporal order both processes of ‘individuation and integration’ are involved. That is to say, in the process of reintegrating the massive embryonic movements into serial responses, certain of these movements have to be broken up (individuation) and then, are reorganized (integration) into new serial orders. The best illustration of this fact is to be found in the acquisition of speech. The new-born infant may utter certain vocal sounds together with total bodily movements. Now in acquiring speech the child has to analyse or individualize his original massive movements, selecting certain of the vocal acts, and then resynthesize them into word or sentence responses.

From this point of view the question as to whether the earliest embryonic movements involve the body as a whole or are merely discrete reflexes is not of great concern to the student of developmental behavior. For such embryonic movements are merely the material or basis upon which and out of which various response systems in serial order in postnatal life are organized. Given the embryonic movements as basic materials, the fundamental problem which the
student of developmental behavior has to solve concerns the manner and causal factors of integration or reintegration out of such basic materials, into temporal behavior. Of course, he is interested in knowing whether the basic embryonic reactions are massive movements or discrete reflexes. But this question is trivial as compared with the question of the manner and causal factors of temporal integration.

The question of 'individuation versus integration' in the development of behavior has been unduly emphasized by Coghill and by Herrick (10). Both of these authors appear to have entirely neglected the temporal aspect of integration, which is by far more fundamental than the question concerning the nature of the basic embryonic movements which are the building material of temporal integration. Neurologically it may be important to decide whether complex behavior is built up of simple reflexes, or discrete reflexes are differentiated from a total pattern. But behaviorally, our problem of development is much more fundamental and complicated than this. And, to repeat, the process of temporal organization of movements, which is the most fundamental aspect of behavior development, involves 'integration' as well as individuation.

(3) Some ten years ago (12, 13) I pointed out that behavior is so variable and so complex as not to permit any explanation in terms of definite or fixed anatomical arrangement of the nervous system or in terms of chain reflexes. Recently Tolman (22), Herrick (10) and Lashley (18) have also emphasized this fact. In this connection it may be well to bear in mind that while it may be possible to discover definite anatomical correlates of the nervous system with embryonic or fetal movements which are relatively simple and more or less uniform, any attempt to find such correlates in postnatal behavior is bound to fail in view of its complexity and variability.

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